A Comparison of Growth Rates of Coarse Fish in Gravel-pit Lakes in South-East England and of Population Structure in Selected Lakes

by

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ABSTRACT

Age and growth rates of the coarse fish of 39 gravel-pit lakes in South-East England are compared. Species composition and growth rate are very variable, the commonest species being roach (*Rutilus rutilus* L.), bream (*Abramis brama* L.), tench (*Tinca tinca* L.), perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.). There was no apparent correlation between fish growth rate and age, size or any other measured parameter of a lake.

Two lakes dominated by pike and perch and four lakes dominated by roach, bream and tench were studied. Two annual estimates of fish population abundance were carried out in these six lakes using the following mark-recapture models: Lincoln Index (Bailey modification); Fisher and Ford (Triple Catch); Leslie (Method B grouping); and Jolly's Stochastic Model. An additional model involving a modification of the Triple Catch method to allow for mortality or change in catchability of marked fish is proposed. These models and methods of marking and tagging fish are critically appraised. A notable criticism is that marked fish cannot be regarded as behaving in the same way as unmarked individuals.

Population and community structure, growth rate, mortality and production of fish in each of the six lakes are compared. The growth and production of individual species and individual year-classes are not apparently related to density. Total fish production in each lake has the following relationship with biomass: $P = 2.4\bar{B}^{0.82}$, where P = production in gm/m^2/year and $\bar{B}$ = mean biomass in gm/m^2.

Seasonal growth of roach infected with plerocercoids of *Ligula intestinalis* L. was observed at monthly intervals and the time of check formation on the scales noted. The possible effects of parasitization by *Ligula* and predation by pike on the abundance of roach are discussed.

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CONTENTS

SECTION 1: INTRODUCTION

1.1 General Introduction

The increasing demand for sand and gravel during the past fifty years has created a number of artificial water bodies in the southern half of Britain. As a result of an accelerating demand by large urban populations the amenity value of such waters has become obvious, particularly for angling. Though gravel-pit sport fisheries are managed in the United States of America (Bennett, 1971) very little is known of the biology of such lakes in Britain.

Of some sixty gravel-pit lakes in this country, used as sport fisheries by Leisure Sport Ltd., forty-five have been surveyed by members of the Biology Department of the City of London Polytechnic for invertebrates, mainly molluscs (Powell and South, in preparation). This thesis is an account of an investigation of the growth rates of the fishes in thirty-nine of these forty-five lakes and further detailed studies on selected lakes. The ultimate aim of the work at the City of London Polytechnic is to establish an ecological basis for management. The value of estimating biomass and production has been emphasized by the activities directed by the International Biological Programme in recent years. Production assumes a particularly important role because of the labile nature of growth in fishes. This is true for both food and sport fish. As LeCren (1974) emphasizes, a knowledge of the processes governing production is essential for understanding both fish ecology and management of fisheries. As a matter of simple practicability, the present study was necessarily restricted to growth rates in thirty-nine lakes, and population studies in six lakes. In fish populations density, size and age structure are of basic importance (LeCren, 1949); appropriate estimates were therefore made for each chosen population, and the dynamic aspect was studied by censuses at the beginning and end of a growing season.

1.2 The Age Determination of Fishes

The age determination (ageing) of fish by examination of scales and bones is well documented. The periodic growth of fish in temperate conditions is reflected in scales and bone structure, giving an index of the growth history of the fish. The method was used for carp in the last century by Hoffbauer (1899). The general principles of such age-determination are described by Masterman (1913), Graham (1929) and Van Oosten (1929).

Following the nomenclature of Jones (1953), the roach scale can be described as consisting of a number of flat bony plates, the edges of these plates forming concentric rings. The number of ridges or rings and the distance between them vary. A discontinuity in the normally regular pattern of concentric rings is known as a check. This usually consists of two or three narrowly spaced, incomplete rings. The term 'circuli' and 'annuli' have been used extensively in the literature as synonyms for 'concentric rings' and 'checks' respectively.

Though the study of fish scales and bones has inevitably been concentrated on commercially important species including salmonids, the structure and use of scales for age determination of coarse fish is common. Masterman (1923), Pentelow (1937), Hartley (1947) and Jones (1953) describe the scales of roach. Wallin (1957) gives a very detailed account of the finer structure of these scales. More recently the histochemistry and cytology of fish scales (including those of goldfish) have been described by Mackawa and Yamada (1970 , 1972). The use of scales of coarse fish other than roach for ageing and growth is also well documented. Backiel and Zawisza (1968) list a large number of workers who have used the method successfully for bream. Cragg-Hine and Jones (1969) describe the scales of dace and chub, Kennedy and Fitzmaurice (1972) those of the gudgeon; whilst Williams (1967) points out the scarcity of information regarding those of bleak. However, Williams describes bleak scales as having 'clearly-defined bands of widely and narrowly spaced rings', and concludes that they may be used for ageing. He was also able to show that there was one period of check formation each year occurring chiefly during April-May. In this present work the scales of rudd and crucian carp were found to be generally similar to those of the other cyprinids described and were therefore used in the same way.

The scales of perch and pike are notoriously difficult to interpret. LeCren (1947) describes the use of the opercular bone for age and growth determination in perch, whilst Frost and Kipling (1959) discuss the use of opercula in pike. Although Weatherley (1959) successfully used the scales of tench, I have found considerable difficulty in their interpretation. Consequently, opercula have been used in the present work.

The occurrence of structures described as checks is normally annual; however, there are a number of instances reported where this is not so. Mathews and Williams (1972) describe the scales of Thames dace in which the first check did not appear until the beginning of their third year of life. Buchholz and Carlander (1963) noted the failure of yellow bass, *Roccus mississipiensis* (Jordan and Eigenmann), to form annuli in certain years.

The precise nature of check formation is not yet understood, although Bilton and Robins (1971) found a correlation between the number of checks and the number of weeks fish were offered an *ad libitum* diet. There was no correlation with the number of weeks they were starved. Bhatia (1932) showed that food influenced the secretion of growth hormone and was the greatest factor affecting scale growth. Beckman (1943) found a good correlation between temperature and the time of annulus formation in Michigan game fishes. Simkiss (1974) asks 'is the reading of scales therefore really just a bioassay of fluctuating levels of growth hormone which itself simply reflects environmental variables?'.

Many attempts have been made to overcome the possible objections to the use of scales for age determination. Sych (1971) prepared a theoretical procedural guide which is, however, difficult to put into practice. LeCren (1947) listed five main kinds of evidence which should be sought to substantiate the interpretation of scale and bone rings. It is not usually possible to fulfil all of these criteria because of practical difficulties and time restrictions, but satisfying some of them will aid in confirming the reliability of the interpretation. During this investigation the time of check formation in roach was studied in monthly samples taken in Yateley 4 (see p. 50).

The problem of ageing fish has recently been discussed at an international symposium (Bagenal, 1974). Hofstede (1974) and Steinmetz (1974) gave strong evidence for the validity of ageing and back-calculating methods for roach, dace, bream and rudd in Dutch waters.

The assumption of Lea (1910) that the size of the scale is proportional to the size of the fish initiated the practice of using scales to calculate the growth history of the fish (back-calculation), but its validity has been vigorously disputed. Creaser (1926) gave a detailed account of the structure and growth of the scales of the sunfish, *Eupomotis gibbosus* (L.), though the corrections he included in his expression for large fish were particularly cumbersome. It was not until Segerstrale's (1933) paper that the inter-population variability of this relationship was fully accepted. Subsequent workers have appreciated the need to derive the empirical relationship between these two parameters. The types of empirical relationship between scale size and body length have been discussed in great detail by many workers. Schuck (1949) and Hile (1970) give comprehensive reviews of the problem of back-calculation, including summaries of the main types of relationship. The straight-line relationship with zero intercept is often used in fishery biology today even though it is rarely strictly valid. The apparent change in growth rate during the first year when calculated from scales of older fishes is an anomaly described originally by Lee (1920). The straight-line relationship with intercept other than zero is commonly found. The biological significance of a positive intercept on the body length axis has prompted a great deal of speculation. Lee (1920), Meriman (1941) and Carlander and Smith (1944), interpreted the intercept as corresponding to the length of the fish when scales were first formed. However, this is difficult to prove and unnecessary for the purposes of back-calculating annual growth. Frank (1970) examined scales of young roach, and found that scales were first formed when the standard length was 16 mm. It is also known that scales appear on some parts of the body before others; for example, Balon (1956) describes the first scales of roach developing on the tail. Though Frank found the scale/body-length relationship in roach to be 'from the beginning of life typically parabolic', for the purposes of back-calculation this is irrelevant. It is the relationship from the time of formation of the first annulus that is important. Sometimes the relationship is curvilinear: Mann (1973) found that a second-degree parabola gave the line of best fit for a plot of fork length v. anterior scale radius in roach.

Once the most suitable empirical relationship had been found back-calculation was carried out by many workers with the aid of nomograms. Some, for example Hile (1948) and Schuck (1949) were elaborate and awkward to use. Today the whole process of calculating the scale/ body-length relationship, performing the back-calculations and summarizing the results is efficiently performed by computer.

Only occasionally has back-calculation been used to determine the growth of British coarse fish. The method is well illustrated in the work of Mann (1973). Banks (1970) used back-calculations from roach opercula to check the growth for mean length-at-age data, but only discussed back-calculated lengths for the first three years' growth, because length-at-age data were not available. The practice of compounding a growth rate for a species from mean lengths of aged fish sampled over a short period of time is common. This approach is bound to obscure differences in growth pattern between year-classes and can lead to the formulation of growth rates which would be inaccurate over the life history of any individual. Accurate growth curves from such data require considerably larger samples of fish of all year-classes than do curves from back-calculated data. Provided that some of the criteria listed by LeCren (1947) for testing the validity of these ageing methods are met, and provided that an accurate, constant, predictive relationship exists between the size of the scale or bone and that of the fish, there should be no impediment to using back-calculation. However, there is an inherent error associated with firstly, the degree to which the observed data fit the scale/body-length relationship, and secondly, any change there may be in the structure of the scale with age. The scale/body-length relationship will be different for every scale of any one individual. It follows therefore that some error will be inevitable through the use of scales from different sites on the fish. The precise relationship might also be different for different individuals of the same population.

1.3 Capture-Recapture Methods for Estimating the Abundance of Fish Populations

Most gravel-pit lakes are too large to satisfy the conditions of methods of abundance estimation that depend on catch depletion (de Lury, 1947; Zippin, 1956); and the efficiency of seine-netting in these lakes is too variable for catch-effort analysis. It was therefore necessary to use capture-recapture methods. There are many capture-recapture models currently available, though most fishery investigations still employ the older, simpler methods. The choice of a model for this work was difficult so several were used and the results compared in the light of the requirements of the models and the probable behaviour of the experimental populations. (See Section 3.3.3).

Since Petersen (1896) used marked individuals to study fish populations, the science of capture-recapture had developed extensively in application and mathematical sophistication. The method is now widely used for mobile populations of many species, including fish. As Cormack (1968) points out in his review of the subject, there are two distinct types of information which can be obtained by introducing into a population individuals that will be identifiable in subsequent sampling. Firstly, the recovery of marked individuals can provide estimates of such population parameters as death rate (or emigration) and birth rate (or immigration). Secondly, a comparison of marked and unmarked individuals can provide estimates of population size. All models make assumptions about the behaviour of marked and unmarked individuals in relation to the type of sampling device used; the suitability of any of these models naturally depends on how realistic these assumptions are. The following is intended as a brief summary of the various types of models that can be used, particularly in the field of fisheries research. Only those used in this investigation are discussed in detail although others are mentioned in order to clarify the differences and similarities between them.

(a) Simple Recapture

This method can be applied to the type of situation originally met by Peterson (1896) in fish, and by Lincoln (1930) in waterfowl. Although first described by Peterson, it is commonly referred to as the 'Lincoln Index'.

Into a closed population of unknown size N, are introduced M individuals in some way, usually by marking : in a subsequent sample of size n, m are found to be marked. Assuming identical behaviour of marked and unmarked individuals

$$\frac{m}{n} = \frac{M}{N}$$

$$N = \frac{Mn}{m}$$

giving an estimate of the original population.

Like other simple formulations, this one involves simplistic assumptions:

(a) that the population is closed, i.e. free from any mortality or recruitment;

(b) that release by the experimenter, and subsequent dispersal, of the marked animals occurs in such a way that the probability of recapturing a marked animal is equal to the frequency of marked animals in the population; which implies

(c) that marked and unmarked individuals are equally vulnerable to the sampling gear;

(d) that there is no loss of marks nor failure by the experimenter to recognise them; and

(e) that marking does not itself affect the animal's chances of survival.

Vulnerability is the probability of being caught by the fishing gear. Catchability is the proportion of fish caught.

Moreover, the fact that recapture is only carried out once means that none of these assumptions can be tested. The basic assumptions imply that m has a hypogeometric distribution, however, when N is large, reasonable approximations are obtained using a binomial, Poisson or normal distribution, for which tables are available to find the required confidence limits.

Junge (1963) has investigated the bias associated with this type of estimate and has proposed a bias factor in terms of the rates of exploitation at the time of tagging and recovery. Bailey (1951) showed that in binomial sampling the simple expression given above is in fact the maximum-likelihood estimate of N, or as Cormack (1968) points out, only the integer part of $\hat{N}$. Bailey showed that sample size was critical in that when $m = 0$ the estimate of N reaches infinity. He gave the relative bias in the expectation of $\hat{N}$ as in the order of r^{-1} where $r = Em$ (Expectation of m), and suggested the following as a relatively unbiased estimate

$$\check{N} = \frac{M(n + 1)}{(m + 1)}$$

where the bias is reduced to e^{-r}.

Similarly, the unbiased estimate of the variance of $\check{N}$ is given by

$$\text{Var}(N) = \frac{M^2(n+1)(n-m)}{(m+1)^2\,(m+2)}$$

These equations apply when sampling is direct, ie when the total sample size is fixed. A contrasting approach is the technique of Haldane (1945) known as 'inverse sampling'. Here, resampling is continued until a predetermined number of marked individuals is obtained. Bailey (1951) gives an expression for an estimate of N which is unbiased in most situations. Knight (1965) gives a guide as to the size of m necessary to minimize the variance of $1/\hat{N}$. Inverse sampling has the disadvantage of not allowing summation of separate estimates of sub-divisions of the population concerned.

(b) Multiple Marking

The extension of the capture-recapture technique giving a distinct mark to individuals captured on different days constituted an advance in the study of mobile populations. It increases the proportion of marked members in the population, and can give valuable information on changes in that population, thus allowing assumptions of the model to be tested.

Schnabel (1938) gave the solution to the maximum-likelihood equation for a set of independent samples. Cormack (1973) derived a similar expression using the 'commonsense approach'. His argument is that if the probability of an individual being recorded in a sample, S_i, is given by $\hat{P}_i$, then

$$\hat{P}_i = \frac{m_i}{M_i}$$

where m_i = number of marked individuals in S_i

M_i = total number of marked individuals in the population

Similarly, for the total population, marked and unmarked

$$\hat{P}_i = \frac{n_i}{N_i}$$

$$\therefore \quad \hat{N}_i = \frac{n_i M_i}{m_i}$$

where n_i = number of individuals in S_i

$\hat{N}_i$ total number of individuals in the population.

Immediately after the release of newly marked individuals subsequent to sample S_i, there are $(M_i + n_i - m_i)$ marked individuals in the population. Of these M_{i+1} will be alive at S_{i+1}. Therefore, the survival rate during this time interval is

$$\hat{\phi}_i = \frac{M_{i+1}}{(M_i + n_i - m_i)}$$

For the whole population, the number of individuals alive after this interval is $\hat{N}_i . \hat{\phi}_i$. The number present at S_{i+1} is therefore

$$N_{i+1} = N_i \phi_i + B_i$$

where B_i are the additions to the population during the time interval.

The assumptions of this 'commonsense approach' are inherent in most of the sophisticated mathematical derivations.

Jackson (1937) devised one method involving multiple marks. His 'negative' method involved successive periods of sampling and marking, note being taken of the numbers of marked and unmarked individuals in the final sample only. In contrast, his 'positive' method involved a large number of single marks which were recaptured on a number of later occasions. Both methods take into account birth and death rates.

When animals are marked and released on a number of separate occasions and each individual is marked in such a way as to distinguish each of the occasions on which it was captured, there are a number of possible methods of recording their history. Only two of these will be described in detail as they were used in the present investigation.

Fisher and Ford (1947) arranged their multiple recapture data in arrays referred to as trellis diagrams. Bailey (1951) discussed the modelling of such a complex situation. He assumed an open population with constant birth and death rates. In the case of a large population, where the effects of sampling without replacement could be ignored, he expressed the likelihood as

$$e^L \propto \prod_{j=1}^{k} \prod_{i=o}^{j-1} (N_{ji}/N_j)^{n_{ji}}$$

where n_{ji} are the number of individuals caught on the jth day which were first marked on the ith day. If the total population on the jth day is N_j, N_{ji} were first marked on the ith day, N_{jo} being unmarked. The total number of days considered is k. The newly marked individuals released on the jth day are represented by S_j. The whole population suffer birth and death, though additions to the marked individuals are possible only by the release of newly marked animals. Bailey showed that

$$N_{ji} = S_{i}.e^{-\gamma(j-i)} \qquad (i = 1, \ldots, (j-1))$$

$$N_j = N_1.e^{(\beta-\gamma)(j-1)} \qquad (j = 2, \ldots, K)$$

and $$N_{jo} = N_j - \sum_{i=1}^{j-1} N_{ji}$$

where β and γ are the deterministic birth and death rates respectively.

The solution of maximum-likelihood equations for β, γ and N_1 is difficult but Bailey showed that manipulation of such trellis data becomes feasible when the number of occasions on which catching takes place is reduced to three. This is the familiar 'Triple Catch' situation. Unfortunately the method necessitates ignoring all but the first mark on any animal.

The time intervals between samples 1 and 2 and 2 and 3 are t_1 and t_2 respectively. Using the same notation as given above

$$n_{21} = \frac{N_{21}}{N_2} \cdot n_2 = \frac{n_2 \mu S_1}{x}$$

$$n_{32} = \frac{N_{32}}{N_3} \cdot n_3 = \frac{n_3 S_2}{\lambda x}$$

$$n_{31} = \frac{N_{31}}{N_3} \cdot n_3 = \frac{n_3 \mu S_1}{\lambda x}$$

where $N_2 = x$, $e^{\beta t_2} = \lambda$ and $e^{-\gamma t_1} = \mu$

$$\therefore \hat{x} = \frac{S_2 \cdot n_2 \cdot n_{31}}{n_{21} \cdot n_{32}}$$

The estimate is only unbiased when sample size is large. Bailey derived the following unbiased estimates

$$\check{x} = \frac{S_2(n_2 + 1)n_{31}}{(n_{21} + 1)(n_{32} + 1)}$$

$$\check{\lambda} = \frac{n_{21}(n_3 + 1)}{n_2\ (n_{31} + 1)}$$

$$\check{\mu} = \frac{S_2 \cdot n_{31}}{S_1(n_{32} + 1)}$$

An approximately unbiased estimate of the variance of $\check{x}$ is given by

$$\mathrm{var}(\check{x}) \sim \check{x}^2 - \frac{S_2^{\ 2}\ (n_2 + 1)(n_2 + 2)n_{31}(n_{31} - 1)}{(n_{21} + 1)(n_{21} + 2)(n_{32} + 1)(n_{32} + 2)}$$

The situation encountered in the present research suggested a modified approach.

The condition that all animals should survive is unrealistic, but under the conditions of the investigation described here it is probable that mortality of unmarked fish during the course of a population estimation is negligible. The lakes are closed so that there is no immigration. It is probable, however, that some marked fish do die (see Section 3.3.3). This mortality may be real or apparent (due to an increase or decrease in vulnerability of marked fish to the gear). Therefore, continuing to use the same nomenclature, we can assume a constant, deterministic death rate, γ, is operative on marked animals only. During the time interval $t = t_2 - t_1 = t_3 - t_2$, we have

$$N_2 = N_1 - S_1(1 - e^{-\gamma t})$$

$$N_3 = N_2 - S_2(1 - e^{-\gamma t})$$

$$\text{ie} \quad N_1 = N_2 + (S_1 - S_1\mu)$$

which in recapture terms is

$$N_1 = \frac{S_2 n_{31}}{n_{32}}\left(\frac{n_2}{n_{21}} - 1\right) + S_1$$

In this situation the multiple-mark system serves two purposes; it increases the total number of marked animals in the population and it gives an indication of their behaviour. A value of $\mu = 1$ would suggest total survival of marked members and full integration into the unmarked population. These are the ideal conditions necessary for the functioning of the Lincoln Index model (refer to p. 13). A value $\mu < 1$ could imply death of some marked individuals and/or a decrease in their catchability after marking. A value of $\mu > 1$ suggests an increase in catchability compared with unmarked members. The new expression for N_1 is likely to be a better estimate of population abundance than either the Lincoln Index or Triple Catch (in short term experiments) if the behaviour of marked fish differs from that of unmarked fish.

Whereas Bailey (1951) grouped his multiple recaptures in relation to the time of first marking, the alternative procedure, that of grouping in relation to last capture, is explained in a series of three papers by Leslie and Chitty (1951), Leslie (1952) and Leslie, Chitty and Chitty (1953). A further modification, followed in this work, is given in an Appendix to Leslie, Chitty and Chitty (1953).

Following these authors' nomenclature, R_t animals are caught at time t, consisting of U_t unmarked individuals and M_t individuals last recaptured at time t = x (x = 0,1,2, ..., t − 1; $\sum_x M_t + U_t = R_t$). Assuming a deterministic death rate, if the total number of individuals in the population at the beginning (T = 0) is N_o then $P_{012....(t-1)} \cdot N_o$ exist at time t. (ie P_t is the survival factor over the interval of time t). The sum $\sum_{x=o}^{t-2} M_t$ is defined as n_t (t = 2,3,4,....,T). If Y_t is the total number of marked individuals in the population at time t

$$\psi_{t+1} = P_t(\psi_t + Y_t) \qquad \text{equation (1)}$$

where, allowing for d_t accidental losses $Y_t = U_t - d_t = R_t - S_t$.

The following tabulation therefore is a summary of the expected number of individuals in the population at the sampling time t + 1.

$N_{t+1} - \psi_{t+1}$	U_{t+1}
$\psi_{t+1} - P_t R_t$	n_{t+1}
$\underline{P_r R_t}$	$\underline{m_{t,t+1}}$
N_{t+1}	C_{t+1}
(total population at time t+1)	(Total number of individuals captured at time t+1).

Defining W_t as

$$N_{t+1} = P_t W_t$$

and substituting in the above tabulation gives a log likelihood equation from which Leslie and Chitty (1951) showed that

$$N_{t+1} = C_{t+1}(\psi_t - S_t)/W_t$$

$$m_{t,t+1} = C_{t+1}\ R_t/W_t$$

$$\hat{\psi}_t = \frac{n_{t+1}\ R_t}{m_{t,t+1}} + S_t \qquad (t = 1,2,\ldots.,T-1)$$

equation (2)

and $$\hat{W}_t = \frac{R_t C_{t+1}}{m_{t,t+1}}$$ equation (3)

ie $$\hat{W}_t = \frac{(\hat{\psi}_t + y_t)C_{t+1}}{S_{t+1}}$$

substituting in equation (1) we get

$$\hat{P}_t = \frac{\hat{\psi}_{t+1}}{(\psi_t + y_t)} \qquad (t = 0,1,2,\ldots.T-2)$$

But $$N_t = P_{t-1}\ W_{t-1}$$

$$\therefore \quad \hat{N}_t = \frac{\psi_t C_t}{S_t} \qquad (t = 1,2,3,\ldots.,T-1)$$

N_t being the required estimate of population abundance at time t. Again, this model is basically identical to the Lincoln Index the difference being that the parameters ψ_t, C_t and S_t include marked and unmarked fish corresponding to a number of different sampling occasions.

The appropriate variances are given by

$$V(\psi_t) = \frac{(\psi_t + y_t)^2 \, n_{t+1}}{S_{t+1} \, M_{t,t+1}}$$

$$\hat{V}(P_t) = P_t^2 \cdot \left[\frac{V(\psi_t)}{(\psi_t + y_t)^2} + \frac{V(\psi_{t+1})}{\psi_{t+1}^2} \right]$$

$$\hat{V}(N_t) = N_t^2 \cdot \left[\frac{C_t - S_t}{S_t \cdot C_t} + \frac{V(\psi_t)}{\psi_t^2} \right]$$

The Method B grouping (Leslie, Chitty and Chitty, 1953) here employed has the advantage of calculating the relative parameters from recaptures of animals that are known to survive at least one intersample period. However, in this approach the deterministic death rate calculated from these marked members is assumed to apply equally to unmarked individuals. In this respect it may be no better in practice than either the Lincoln Index or Triple Catch models. One of the advantages of the model, however, is that, unlike the Triple Catch model (see p.17), it can be applied to a large number of recapture periods simultaneously.

(c) Stochastic Models

The use of deterministic models in place of their stochastic (probabilistic) counterparts was once justified on the grounds of simplicity of application. However, Jolly (1965) and Seber (1965) have shown that stochastic models are simpler than deterministic models in this respect. Stochastic models give a more precise estimate of the variance of the estimator than deterministic models which tend to under-estimate this statistic (Moran, 1952). In a population subject to immigration (or birth) or emigration (or death) and growth and maturity, the assumption that all these rates are constant (deterministic) is not valid. A realistic model has to allow for these events in a stochastic manner. This problem was first tackled by Darroch (1958, 1959)

For a closed population over a very short period of a few weeks a deterministic model is adequate, especially where the sample size is relatively large (Cormack, 1968).

The grouping of recaptures according to the time of last recapture (Leslie, Chitty and Chitty, 1953) is described by Moran (1952) as 'semi-probabilistic' (ie semi-stochastic) for, although the probability of survival, P_t, is deterministic the survivors, $P_t.N_t$, are chosen at random.

Jolly's stochastic model (Jolly, 1965) is the most widely used in ecological research, and is the only stochastic model used in the present investigation. This model differs from Jolly's 1963 deterministic model in that instead of assuming a deterministic death rate of exactly μ_i in the interval between the i and (i+1)th sample, we assume ϕ_i is the probability that an animal will survive over that interval. The basic assumptions of this model are the same as for the models discussed above in that each sample is supposedly random, and the S_i animals released from the ith sample after marking have distributed themselves throughout the population so that they have the same probability as unmarked animals of being caught in the (i+1)th sample. So, apart from the stochastic element ϕ_i, the model is simple; the expression for the estimate of the population number at time i being

$$\hat{N}_i = \frac{\hat{M}_i}{\alpha i}$$

where $$\hat{\alpha}_i = \frac{m_i}{n_i} \qquad (i = 2,3,\ldots,L)$$

and $$\hat{M}_i = \frac{S_i Z_i}{R_i} + m_i \qquad (i = 2,3,\ldots,L-1)$$

Where α_i is the proportion and M_i the actual number of marked animals in the population at time i; of the marked animals not caught at time i, Z_i

are subsequently caught; of the S_i animals just released marked from the sample at time i, R_i are subsequently caught; M_i is the observed number of marked animals and n_i the total number of animals caught at time i.

The most important assumption of the model therefore is that the chances of subsequent recapture of animals marked at different times (i = 1,2,3,....L) not caught at time i $(M_i - m_i)$ and of animals actually marked and released at time i (S_i) are the same, ie the chances of all marked animals being caught are the same.

$$\text{ie} \quad \frac{Z_i}{(M_i - m_i)} = \frac{R_i}{S_i}$$

It is therefore a requirement of this model, like the other published models discussed, that marked and unmarked animals behave in the same way. If the marked individuals are not truly representative of the whole population the refinement of the stochastic element offers no advantage.

Where inter-sample time is long and the number of samples large there are strong a priori reasons for choosing a stochastic model. In a three-point sampling survey (as in this investigation) a stochastic model is effectively reduced to a near-deterministic level.

Further evaluation of all these models will be postponed (see p. 28) until some consideration has been given to their practical application.

1.4 The Practical Application of Capture-recapture Models in Fishery Research

Most mathematical models in ecological research assume behaviour patterns in the experimental population which are unrealistic. The main assumptions of some capture-recapture models are listed on pages 13 + 14.

The following practical factors should be taken into account

- loss of marks ((d) on p.14)
- mortality due to marking ((e) on p.14)
- differences in catchability of marked and unmarked individuals ((e) on p.14)

non-randomness of marked fish or of fishing effort (implied in (b) on p.14).

Loss of Marks

The most common methods of marking fish are by: attaching a plastic or metal tag to the jaw of fins; removing a portion of fin; injecting a coloured or fluorescent liquid under the skin; and freeze branding. None of these methods is totally reliable.

Carline and Brynildson (1972) report losses of 2% and 5.7% with Floy anchor tags over a period of 8 months in two trials with brook trout (Salvelinus fontinalis Mitchill). Koshinsky (1972) reports 13% losses with barb-anchored spaghetti dart tags and 92% with monofilament-attached preopercular disc tags over 2 years in pike. Muir (1963) also had to correct his Petersen estimates for tag losses (estimated independently).

Finclipping is probably suitable for only relatively short-term studies. Ricker (1958) describes the almost perfect regeneration of fins in the large crappie (Pomoxis annularis Rafinesque) but noted that fins clipped very close to the base showed imperfect regeneration. LeCren and Kipling (1963) used a complex finclipping system in char (Salvelinus willughbii Gunther) and evaluated the finclipping technique by a sub-cutaneous tag as a second mark. Holes punched in the fins healed in about six weeks. Although regeneration usually resulted in a distorted scar the technique was not considered reliable in long-term experiments. Regenerated fins are recognisable in some instances because the rays are often irregular in the region of the cut (LeCren and Kipling, 1963; Stuart, 1958). Such marks can easily be overlooked by inexperienced observers, for example anglers, who must be relied upon for recapturing marked fish in some investigations. Thorpe (1974) used a similar double-mark system to estimate tag loss in trout in Loch Leven (2.15% tag loss over one angling season).

Many workers have used dyes, injected under the skin, to mark young fish, when other marking techniques are inappropriate. Smith (1970) used fluorescent dyes which were visible for up to 11 months in sticklebacks and minnows. Riley (1966) found that coloured latex injected in the same way lasted two years in plaice (Pleuronectes platessa L.) with no signs of fading.

The Panjet inoculator offers a quick and easy technique for batch-marking large numbers of fish of considerable size range; Hart and Pitcher (1969) found alcian blue panjet marks lasted 14 months on minnows and chub in the laboratory and at least 12 months in the field. My own observations in the field indicate that panjet marks are more distinct in species with smaller scales. Tench, for example, are easier to mark than chub and carp. Good marks are obtained when the dye penetrates the scale pocket beneath the scale itself.

A popular method of marking fish, particularly juvenile salmonids, is by the application of hot or cold branding tools. Batch or individual marks are possible depending on tool design. Fujihara and Nakatani (1967) found both cold and hot brands were retained well on 115-125 mm rainbow trout (Salmo gairdneri Richardson). They noted that tools immersed in a mixture of ethanol and dry ice (-80°C) did not have the disadvantage of slipping on application as did those immersed in boiling water. They found that marks were poorly retained on carp, possibly because of the heavy scales. Everest and Edmundsen (1967) successfully used tools immersed in a mixture of acetone and dry ice (-78°C) on juvenile salmonids. Refestie and Aulstad (1975) obtained up to 92% mark retention after one year in juvenile salmonids using tools immersed in liquid nitrogen (-109°C- -175°C). I consider cold branding inferior to panjeting for the purposes of batch marking fish such as cyprinids which have large scales in comparison with those of salmonids.

Mortality Due to Marking

The simplest assumption that can be made when applying capture-recapture models is that marking does not affect mortality. This is probably rarely true. Deaths may be caused by the mark or tag or merely by handling. Ricker (1958) suggests that differential mortality due to the marks themselves can be tested by comparing returns from different kinds of marks. The survival of brook trout (Salvelinus fontinalis) was found by Carline and Brynildson (1972) to be unaffected by Floy anchor tags. Kishinsky (1972) found dart-tag mortality higher in the second year than in the first year (12.0% and 2.9%) in pike but that disc-tagged pike showed a decreasing mortality from the first year to the second year (5.9% and 1.6%). Kennedy (1970) found almost 100% mortality within one year among dart-tagged sablefish held in tanks and nets, though this result is of doubtful significance to field experiments.

Parker (1955) describes a method which allows for the recruitment of fish into a commercial stock during the course of a capture-recapture experiment. Thorpe (1974) was able to use this method to test for differential mortality in tagged trout. If differential mortality did occur then the rate at which tagged fish were caught would decrease with time. He showed that an apparent differential mortality was due to a seasonal change in the vulnerability of Loch Leven trout to angling. This resulted in more of the April-tagged fish being caught in early summer than fish tagged at other times of the year.

In the present work deaths of some small roach and bream occurred within a few hours of panjeting with indian ink. Subsequent examination showed penetration by the ink into the body cavity of some of these fishes.

A critical examination of the effects of the capture and handling of fish during marking experiments was carried out by Parker et al (1963). They placed particular emphasis on the effects of injury and fatigue and showed a significant correlation between high blood lactate levels and death following hyperactivity. Associated mortality factors are a reduction in oxygen tension and an increase in temperature of the water in the holding tanks (Thorpe, 1974). During the course of the present investigation mortalities of captured fish tended to be greater during the summer months.

It seems, therefore, that marking invariably causes some mortality, and that the extent varies with the marking techniques, the species and size of fish and the climatic conditions. At best only a very approximate estimate of the degree of mortality due to marking can usually be obtained.

Differences in Catchability of Marked and Unmarked Individuals

Mortalities due to marking do not necessarily occur immediately. Before fish die increased sluggishness could increase their chances of capture. Alternatively, if they lie moribund on or near the substrate in fairly deep water the seine net might pass over them. The efficiency of gill nets for sampling also depends upon the activity of fish, therefore, changes in swimming behaviour as a result of marking could affect catchability.

Tags can affect gill net selectivity. Ricker (1958) cites increased vulnerability of Petersen disc-tagged salmon to gill nets. He also reports that jaw tags on blue-gills and sunfishes (*Lepomis* spp.) resulted in these fish being less vulnerable to angling. He made a correction for swimming time of tagged chum salmon (*Oncorhyncus keta* Walbaum) from the area of release to the area of recapture. However, such corrections cannot always be applied.

Leslie (1958) gave details of a statistical test for a null hypothesis of equal catchability of marked and unmarked animals. Here the recapture history of marked individuals is compared with theoretical distributions, Poisson or binomial, assuming sampling to have been random.

Non-randomness of Marked Fish or of Fishing Effort

An assumption of the models already described is that: marked individuals are randomly distributed throughout the population; or that the subsequent sampling is random; or both. It is often possible to check the second assumption; if sampling is done at a number of points in the survey area the proportion of marked and unmarked fish at each site should not be significantly different. Thorpe (1974) was able to employ this method in Loch Leven using fly-fishing to recapture his tagged trout. He was able to show that angling effort was random with respect to the fish population.

Where recapture is carried out by untrained assistants (eg anglers) many additional corrections have to be made. The subject of errors in estimates employing commercial trawlers or anglers has received a great deal of attention reviewed in Ricker (1958) and Dickie (1963). The problem of selectivity for species and sizes of fish either by operators, gear or sampling site can be overcome to some extent by combining different sampling methods. Waters (1960) working on trout in small lakes in Michigan, combined data from traps and from anglers' returns, comparing them with stocking information. He concluded that the best estimates were obtained when the recapture method differed from the method used to obtain the original sample. Beukemia and de Vos (1974) came to the same conclusion by comparing Petersen estimates with different combinations of sampling gear. However, Thorpe (1974) points out that though possibily reducing systematic bias, this method of 'mixed-procedures' does not necessarily eliminate it.

1.5 An Evaluation of Capture-Recapture Models

It is obvious from the discussion of the theory of capture-recapture models (Section 1.3) that although essentially similar, the combination of data from different sample periods and different grouping of multiple marks can give varying estimates of population abundance. Maximum-likelihood estimates, as well as their calculated variances differ with the model used. Therefore, the problem arises of which model gives the best estimate. In practice, particularly where fish are concerned, the data upon which population estimates are based are invariably inadequate. Therefore, evaluation of different models may prove impossible.

To avoid problems of sampling, trap shyness and trap addiction, Carothers (1973) selected the taxicabs of Edinburgh for estimation. The parameters of this 'population' were accurately recorded in independent police records. The most significant observation made was that it was impossible to achieve equal catchability of 'marked' and 'unmarked' individual taxicabs. Carothers suggests that equal catchability is unattainable in natural populations. He found that Jolly-Seber estimates (see p.21) improved in efficiency, (i.e. reduction of the estimated variance) when either the restricted 'birth only' or 'death only' formulae were applied (Jolly, 1965).

The most suitable population for studies of this kind is one designed by the experimenter: a population simulated in a computer can be sampled with ease and the accuracy of the various models checked. Manly (1970) compared Fisher and Ford's (1947) and Jolly's stochastic model (1965) and Manly and Parr's (1968) models in this way. Bishop and Sheppard (1973) similarly compared Fisher and Ford's and Jolly's method. In the last paper various combinations of population size, probability of survival, number of sampling periods and sample size were tried. Where no recaptures were obtained Bishop and Sheppard assumed one recapture, acknowledging a finite population (see p.14). The Fisher and Ford models they employed were the uncorrected maximum likelihood estimate or Lincoln Index and the unbiased estimate of Bailey (1951). They concluded that Jolly's method gave reliable estimates when recapture data were adequate, that is, when the proportion of the population sampled was >0.09 and when the probability of survival was >0.5. They considered Jolly's model to seriously overestimate the survival rate. The simpler Fisher and Ford Model (Lincoln Index) was recommended when the survival rate remains relatively constant during the study period. Unfortunately, Bishop and Sheppard did not investigate the effect of marking mortality.

It is known that the estimated variances of the restricted Jolly model (in which the population is closed to death and immigration) are smaller than those of the general model (see p.21). However, Cormack (1968) points out the dangers of assuming a closed population and quotes Leslie, Chitty and Chitty (1953). In this work dilution (ie immigration of unmarked individuals into the population) occurred during a period when immigration was thought to be impossible. Leslie, Chitty and Chitty had attributed the 'apparent dilution' to a departure from the basic assumptions of the model, marked animals behaving differently from unmarked ones. The variances estimated do not necessarily assist in selecting a model. A variance estimate is dependent on the validity of the model, as emphasized by Cormack (1968). Therefore, unless a new model can be devised specifically for the investigation in hand, it is necessary to know that the basic assumptions of the model chosen are operating.

A consideration of the above factors resulted in the adoption of the methods discussed in Section 2.5(b).

SECTION 2: MATERIALS AND METHODS

2.1 The Programme of Work

The work programme was as follows:

(1) sampling of fish from thirty-nine lakes and calculation of growth rates. This survey was completed in twelve months (November 1971 - November 1972),

(2) further growth and population studies of six selected lakes carried out between November 1972 and June 1973 (Series 1) and repeated between October 1973 and January 1974 (Series 2),

(3) additional studies to elucidate questions arising from (1) and (2) above.

A study of the parasites of these fishes was carried out by Dr. R.A. Sweeting concurrently with the present investigation. As will be discussed later, the parasite fauna of many of the fish studied is thought to play an important part in their population dynamics.

2.2 The Lakes Studied

The gravel-pit lakes studied are within 50 km of London; their locations are shown in Fig. 1 which also shows their code numbers. They range in size from <1 hectare to 40 hectares, and where individual lakes are small they occur in groups, as at Farnborough and Yateley. They have maximum depths from 2 to 8 metres. The majority are less than thirty years old. Some of their physical parameters are given in Table 1.

Older gravel-pit lakes usually have steeply shelving banks. Recent attention to their amenity value has prompted the construction of a more gently sloping profile in some places and an increase in the extent of the littoral zone.

These lakes have a diverse macrophyte flora, mainly restricted to the littoral zone; but shallower waters often have extensive stands of Elodea and Potamogeton spp. The banks and islands of older lakes typically

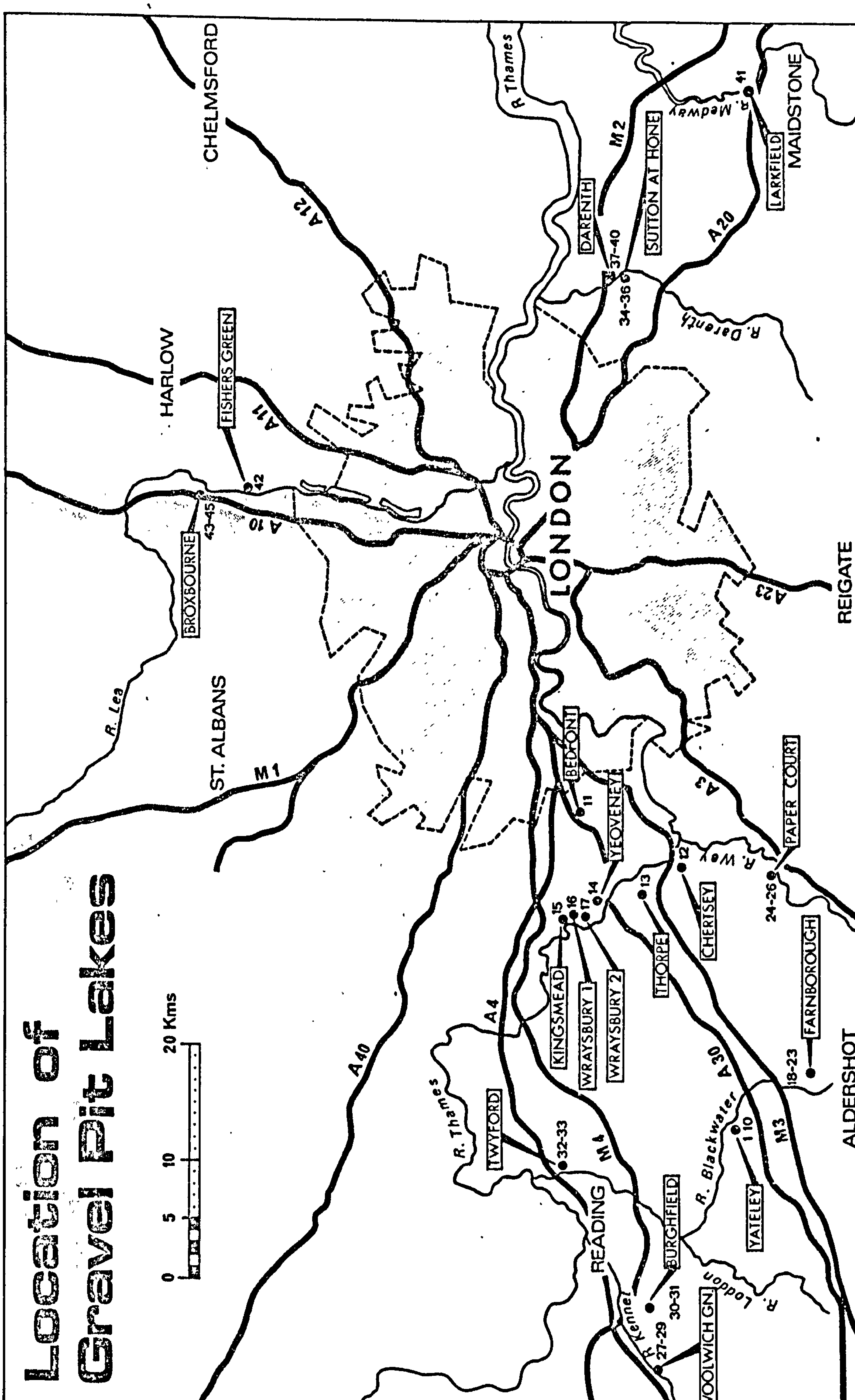

Location of
Gravel Pit Lakes
0
5
10
20 Kms
CHELMSFORD
HARLOW
ST. ALBANS
LONDON
REIGATE
MAIDSTONE
READING
ALDERSHOT
FISHERS GREEN
BROXBOURNE
DARENTH
SUTTON AT HONE
LARKFIELD
BEDFONT
YEOVENEY
KINGSMEAD
WRAYSBURY 1
WRAYSBURY 2
THORPE
CHERTSEY
PAPER COURT
FARNBOROUGH
TWYFORD
BURGHFIELD
YATELEY
WOOLWICH GN
A12
A11
A10
M1
A40
A4
M4
A30
M3
A3
A23
A20
M2
R. Thames
R. Lea
R. Darenth
R. Medway
R. Wey
R. Blackwater
R. Loddon
R. Kennet
42
43-45
37-40
34-36
41
11
12
13
14
15
16
17
24-26
18-23
110
32-33
30-31
27-29

Fig. 1

bear trees and shrubs, e.g. Salix spp.

The lakes do not stratify and are always well oxygenated, with an alkaline or neutral pH. There is some evidence from chemical analyses that differences exist between adjacent waters indicating little or no exchange of water through intervening banks. Again, water levels are not, as might be expected, always the same in all lakes of a group. Rapid level changes, however, indicate that some individual pit basins are highly porous. Long periods of drought during 1972 and 1973 and increased abstraction from river and ground water supplies had the effect of lowering the water level in several lakes (Twyford 32 and 33; Darenth 40).

The six lakes chosen for population studies were Farnborough 18(a), Twyford 32 and 33, Darenth 39 and 40 and Larkfield 41. The reasons for choosing these particular lakes will be discussed later (p.102).

Over the period of study the shape of all but one of the six chosen lakes remained fairly uniform. The exception, Larkfield 41 was continuously fed with pumped water from adjacent workings, but during the interval 18.10.71 - 22.5.73 this inflow was stopped and the water level fell considerably so that it became divided into two small lakes, only one of which was subsequently studied.

The instability of water level between Series 1 and 2 was cause for concern. The summer of 1973 was unusually dry and many lakes suffered a fall in water level at this time (Table 2). This table also shows the areas of the lakes at the beginning of Series 1 and related physical parameters.

The original aim was to produce estimates 12 months apart, but in practice, this was not possible.

TABLE 1 The Code Numbers, Areas and Ages of the Gravel-pit Lakes

Lake	Code Number	Area (hectares)	Age in 1971 (years)
Yateley	1	4.7	8-13
"	2	3.7	5-8
"	3	3.1	8-13
"	4	1.5	13-18
"	5	0.1	13-18
"	6	0.3	13-18
"	7	0.4	13-18
"	8	0.8	13-18
"	9	2.8	2-5
"	10	-	2-5
Bedfont	11	37.5	25
Chertsey	12	34.0	26
Thorpe	13	29.2	31
Yeoveney	14	7.3	11
Kingsmead	15	39.6	28
Wraysbury	16	36.4	33
"	17	33.6	35
Farnborough	18(a)	1.2	15
"	19	1.0	8
"	20	0.7	6
"	21	1.0	5
"	22	1.2	4
"	23	1.6	2
Papercourt	24	8.5	17
"	25	4.5	19
"	26	8.1	25
Woolwich Green	27	6.1	22
"	28	3.4	21
"	29	6.9	25
Burghfield	30	35.2	33
"	31	1.8	33
Twyford	32	6.8	8
"	33	6.2	3
Sutton-at-Hone	34	2.4	16
"	35	1.6	21
"	36	0.8	21

TABLE 1 (Continued)

Lake	Code Number	Area (hectares)	Age in 1971 (years)
Darenth	37	1.2	7
"	38	1.6	13
"	39	4.9	13
"	40	0.16	17
Larkfield	41	8.0	25
Fishers Green	42	28.7	8
Broxbourne	43	11.5	30
"	44	22.9	30
"	45	9.7	11

TABLE 2 Some Parameters of the Six Selected Lakes

Lake	Area During Series 1 (m^2)	Average Depth (m)	Decrease in Depth During 1973 (m)	pH*	Oxygen Saturation* %	Average Temperature* (^{o}C)	Date
18(a)	11,740	1.5	∿0.25	7.5	65	23.0	1.7.73
32	68,300	1.5	∿1.0	6.5	100	22.0	19.6.73
33	61,600	3.0	∿0.25	6.5	100	22.0	19.6.73
39	49,500	3.5	∿0.5	8.2	-	23.0	14.6.73
40	1,623	2.5	∿1.25	7.7	-	23.5	14.6.73
41	27,400	2.5	0.5	7.9	-	20.0	14.6.73

* Readings taken midday of the date given in column 8

2.3 The Fish Studied

There is a dearth of information on the population dynamics of coarse fish in still waters in this country and prior to this study no information existed on gravel-pit lake fishes. The species found during the study are listed in Table 3, these include most of the British coarse fishes. By far the commonest species represented is the roach.

2.4 Field Methods

(a) Sampling for Growth Studies

A regime of weekly visits was established, each lake being visited on at least one occasion.

The majority of the fish sampled were caught using a seine net. The net measured 50 yds (45.8m) in length by 9 ft (2.7m) in depth, with a stretch-mesh of 1 inch (2.5 cm). This was later replaced by a net 50 yds x 12 ft (45.8m x 3.7m) and a mesh of 0.75 inch (1.9 cm). Both nets had a central 12 ft bag. The topography of the lakes limited the use of the net to the littoral region, though small bays and islands were used to increase the range of the net where possible. Occasionally, when the seine caught only a few fish a number of 2m deep gill nets of varying mesh sizes were laid from the surface and recovered the following day. Electro-fishing was not employed during this survey because of the generally poor returns experienced in field trials by the group and because of the limited manpower available.

Samples of up to 30 fish of each size-group represented for each species were taken back to the laboratory for examination. Large specimens were returned to the water after measuring and scale removal where appropriate.

The use of roach scales for age determination for back-calculating growth is well documented (see Section 1.2). However, the validity of the method required testing on gravel-pit lake fish. During the selection of

TABLE 3 Fish Species Inhabiting the Gravel Pit Lakes

CYPRINIDAE	*Rutilus rutilus* L.	roach
	Abramis brama L.	bream
	Scardinius erythrophthalmus L.	rudd
	Alburnus alburnus L.	bleak
	Tinca tinca L.	tench
	Gobio gobio L.	gudgeon
	Leuciscus cephalus (L.)	chub
	Ceuciscus Leuciscus L.	dace
	Cyprinus carpio L.	carp
	Carassius carassius L.	crucian carp
	Phoxinus phoxinus L.	minnow
PERCIDAE	*Perca fluviatilis* L.	perch
	Gymnocephalus cernua (L.)	ruffe
ESOCIDAE	*Esox lucius* L.	pike
COTTIDAE	*Cottus gobio* L.	bullhead
COBITIDAE	*Nemacheilus barbatulus* L.	stone loach
GASTEROSTEIDAE	*Gasterosteus aculeatus* L.	3 spined stickleback

lakes as suitable sites for population estimates Yateley 4 was found to contain a small number of large roach and a large number of fry (1972 year-class). Monthly samples of these fish (commencing in April 1973) were taken by seine net to observe the time of check formation on the scales. As many fish as possible were taken, up to a limit of about 500, and all were anaesthetized in MS222 and their fork lengths measured by pricking on waxed graph paper; the use of graph paper in preference to plain paper greatly facilitated the construction of length-frequency histograms. Where possible at least 100 of these were retained for laboratory examination, the remainder being returned to the lake after recovery. Several very small perch were caught at the same time but these were immediately returned. Pike and tench were also caught; the former were individually tagged initially with jaw tags and latterly with floy anchor tags. Recaptures were recorded.

(b) Sampling for Population Estimates

This was based upon multiple-marking operations on six lakes. Sufficient time was allowed for marked fish to be randomly distributed with unmarked fish. At the same time each population estimate had to be completed within a short time to reduce the possibility of population changes, ie within 3-4 weeks. Where possible, the mark-recapture work was done during Autumn, Winter and early Spring. Thus there was little growth during the mark-recapture period and the lower temperatures increased survival of fish during netting and marking.

Although the theoretical capture-recapture models usually require sampling until a fixed number of individuals are obtained (see p.15), in practice it was necessary to continue sampling as long as daylight permitted. Using the netting technique described on p.38 , fish were caught and transferred into large plastic containers of water. Where substantial numbers of fish were retained the water was changed at short intervals throughout the day, and occasionally oxygenated. Fish were anaesthetized in a solution of MS222 and measured by pricking fork lengths on waxed graph paper. Several measuring boards mounted with the waxed paper were used so that different species could be recorded separately. Measured fish were then marked either by tagging, fin-clipping or pan-jeting depending on size and species. Pike were usually jaw-tagged, though latterly floy-tagging was employed. Tench and carp were normally panjeted, floy tags being used only when time permitted. Fish less than about 8 cm were finclipped, all other fish were panjeted with indian ink. Preliminary trials indicated that indian ink persisted as an easily recognisable mark in roach and tench for at least six months. A batch-marking system was used so that all fish marked on one day received the same mark, a different mark being used for each day. A panjet spot on the left flank of the caudal peduncle was chosen as the day 1 mark and the right flank as the day 2 mark. When a fourth sampling was necessary a third mark, usually on the anterior left flank, was used.

In small fish left and right pelvic fins were clipped as day 1 and day 2 marks and the left pectoral fin was used on the third day. All fish, regardless of previous marks, were given a new mark appropriate to the occasion. Where the proportion of marked fish in the samples was large only three samples were taken and two marks were sufficient. Recaptures were measured on separate sections of waxed graph paper.

After measuring and marking the fish were transferred to and retained for the rest of the day in large tanks or inflatable dinghies filled with water, through which oxygen was bubbled from a large diffuser. This allowed recovery and prevented recapture of fish in subsequent seines. Marked individuals were handled as little as possible.

During the first few months of this work marked fish were returned to the region of the lake where they were caught. However, this procedure became unnecessary when it was shown that only one population of each species existed in each lake. All fish were then returned to the middle of the lake. One week was allowed between sampling occasions. This period was considered adequate for recovery of the fish and integration into the unmarked stock. Equal intersample periods probably reduced sample differences due to the effect of marking and recovery. This is important when using deterministic models.

Although seine-netting was by far the most common sampling technique used, electrofishing was occasionally necessary. Considerable growth of Elodea in Twyford 32 made seine-netting difficult in Series 2, so a 240 volt, 15 ampere, AC/DC generator was used. Although this method is laborious and relatively inefficient in such a large open body of water, the shallowness of the lake enabled a large number of fish to be caught. Gill-nets were used only once, on the final visit to Twyford 33, where extreme difficulty was encountered in catching fish. Perch traps were laid for three weeks at Twyford but no fish were caught.

Dead and dying individuals were removed from the tanks and dinghies before marked fish were returned to the lake. These fish were counted and measured and scales taken for examination. To reduce interference with the population no healthy fish were removed until the last sampling day in each lake in Series 2, when representative subsamples were taken for laboratory examination. Unfortunately, those species or size groups poorly represented in the catches and absent from the final day's catch could not be examined. However, samples of scales were taken for age and growth determination, from very large fish caught on days 1 and 2. On the final day large fish such as carp, pike and tench were weighed in the field.

In Farnborough 18(a) large numbers of 0+ roach (3-7 cm) were caught that were too small to be marked. An estimate of their abundance was obtained from their relative abundance in the seining catches by comparison with capture-recapture estimates of larger fish.

2.5 Laboratory and Analysis Methods

(a) Survey Samples

In the laboratory the fish were numbered, weighed and measured and preserved by deep-freezing. Lengths were measured to the nearest millimetre (standard length, fork length and total length). Fish were weighed on an electric balance to the nearest 0.1 gram.

Gonads and gut contents were examined by Dr. Sweeting during the parasitological examination and do not form part of this thesis.

Scales were taken from the mid-body region immediately below the first spine of the dorsal fin. In cyprinids and pike key scales were taken from the first two rows above the lateral line and from the first two rows below the lateral line in perch (see Section 1.2). Secondary (replacement) scales or scales without clear centres were discarded. In damaged fish it was sometimes necessary to use scales from other regions of the body. Scales were cleaned by immersing in hot water and rubbing between thumb and forefinger. They were then mounted dry between two glass microscope slides. Considerable difficulty was encountered in reading the scales of tench, pike and perch; so cleaned, dried opercular bones were used. Scales were read under a projection microscope, the magnified image (× 15) being measured directly with a transparent ruler on a ground-glass screen. Opercula were examined under reflected light and measured with the aid of an eye-piece micrometer.

For all cyprinids except tench, fork length v. posterior scale radius were plotted separately for each lake. Where opercular bones were used, fork length was plotted against the greatest triangular height of the operculum. The majority of relationships were found to be adequately described by simple linear regression. In other cases the relationship was significantly different from linear and transformations were made to effect linearity. The standard least-squares estimation procedure could not be used because the independent variable was not free from error. Consequently, a modified method due to Bartlett (1949) was employed giving the best-fit linear relationship between the two variables. Although the predicted growth of any one individual fish might not necessarily be accurate, the method probably gives a good estimate of the growth of the year-class (see Section 3.3.2). Back calculations were made by substituting measurements of scale radii to checks in the appropriate regression equations. Year-class growth was calculated as the mean of each back-calculated length-at-age for all individuals of that year-class. Composite growth was also calculated from the means of each set of back-calculated lengths-at-age for all fish irrespective of year-class.

The large quantity of growth data made statistical comparison of separate growth curves for each year-class impracticable. So, comparisons were made on data expressed as the composite year-class means. Some of the shortcomings of this approach to growth have already been described (see p.11).

Comparison of back-calculated lengths-at-age of roach was carried out by means of a number of Student's t-tests as follows:-

If x_{ia} is the mean length of fish at age i years from lake a, and n_{ia} and V_{ia} the appropriate numbers of fish in the sample and variance respectively (already calculated during back-calculation), then the joint variance of the difference between x_{ia} and x_{ib} can be written as

$$S = \frac{(n_{ib} - 1)V_{ib} + (n_{ia} - 1)V_{ia}}{(n_{ib} - 1) + (n_{ia} - 1)}$$

$$t = \frac{(x_{ib} - x_{ia})}{\sqrt{S}\,\sqrt{((1/n_{ib}) + (1/n_{ia}))}}$$

The degrees of freedom are

$$r = n_{ib} + n_{ia} - 2$$

Comparisons of all possible combinations of lengths-at-age were performed on computer (ICL 1900E).

A comparison of the growth in terms of increments between lengths-at-age was carried out as follows:-

If length-at-age is expressed as above, the increment between age i-1 and i can be written as

$$d_{ia} = x_{ia} - x_{(i-1)a}$$

The 'mean' sample size is given by

$$m_{ia} = (n_{ia} + n_{(i-1)a})/2$$

The variance of d_{ia} is then

$$\rho_{ia} = v_{ia} + v_{(i-1)a}$$

The unbiased variance for the t-statistic is

$$S = \frac{(M_{ib} - 1)\rho_{ib} + (M_{ia} - 1)\rho_{ia}}{(M_{ib} - 1) + (M_{ia} - 1)}$$

and

$$t = \frac{(d_{ib} - d_{ia})}{\sqrt{S}\ \sqrt{((1/M_{ib}) + (1/M_{ia}))}}$$

The degrees of freedom are

$$\nu = M_{ib} + M_{ia} - 2$$

The t-test was used in preference to an analysis of variance technique because of the complications of differences in sample size and the number of separate comparisons required.

For the purposes of comparison, it was not considered necessary to know the pattern or rate of roach growth during the year. Comparisons were made simply on the basis of either actual length at a given check or differences between these lengths at successive checks.

(b) Population Estimate Samples

The scales and opercular bones collected during Series 2 (see p.42) were treated as described above for the survey samples. Where possible, fish were aged and their growth back-calculated. Separate scale v. body length regressions were used for each species population. Too few pike and tench were returned to the laboratory to allow age and growth estimation to be made.

As in the case of the survey samples, growth curves were produced by back-calculation for each year-class separately and also for all year-classes combined. Means and associated statistics were calculated assuming a Normal distribution of lengths-at-age. A comparison of growth during intervals of one year and of back-calculated lengths at times of check-formation were made using Student's t-tests as before (p.44).

The holes in waxed graph paper representing lengths of fish of various categories (unmarked, marked day 1 etc.) were counted using a light table. Lengths of fish in Series 1 were divided into 1 cm groups and in Series 2 into 0.2 cm groups. Combining all unmarked individuals of a given species during a series in a given lake provided a length-frequency histogram for the particular population. Length groups were compiled so that each age-class represented could be estimated separately. This was only possible where each age-class was clearly separate in the length-frequency histogram. Where considerable overlapping of lengths-at-age occurred year-classes were combined for estimation of abundance. The following capture-recapture models were applied to the data collected.

(1) Lincoln Index (Bailey Modification, referred to as 'Simple' when applied to day 1 and day 2 data only,

(2) 'Multiple' when applied to days 1, 2 and 3,

(3) Fisher and Ford (Triple Catch),

(4) Triple Catch with mortality of marked fish only,

(5) Leslie (Method B),

(6) Jolly's Stochastic Model (see Section 1.3, p.22).

The analyses were carried out by computer (ICL 1900E) in Fortran IV. The program used for Jolly's method was a modification of Davies (1971). When recaptures were zero a value of 1 was substituted, recognising a finite population. Certain other inadequacies of the data resulted in estimated variances less than zero so that many loops had to be incorporated into Davies' program to avoid termination of the program. All the other models employed required new programs. These programs were written specially for the limited type of data collected during this work.

Instantaneous mortality rate Z was estimated from differences between estimates of population abundance in Series 1 and Series 2.

$$Z = \frac{\ell n\ N_1 - \ell n\ N_o}{\Delta t}$$

where N_1 = numbers of fish at the beginning of the period

N_o = numbers of fish at the end of the period

t = time interval (in years).

As an approximation, $\Delta t = 1$

As previously stated the time interval between estimates was of variable duration so that errors in the estimation of Z for comparative purposes were unavoidable. Z is unlikely to be linearly related to time so that no correction factor is calculable. Details of the time intervals concerned are given in Appendix 2.

Following Chapman (1967), biomass is taken as the total weight (standing crop) of the stock (of given age or size range) at a given time. Therefore, if B_1 is the biomass at the end of a given period and B_0 that at the beginning of the period, the mean biomass during the time interval Δt is $\bar{B} = \frac{B_0 + B_1}{2}$.

As Chapman points out such estimates of mean biomass strictly apply only to periods of short duration (a few weeks). Due to the impracticability of obtaining numerous and regular estimates of population abundance in the six lakes during this study the above expression for mean biomass is applied to the Series 1 and Series 2 data, although the time interval is several months. For comparative purposes at least, I consider it to be a sufficiently good approximation.

Ricker (1946) and Allen (1950) derived expressions for production in terms of instantaneous rates of growth and mortality. However, because of the changing species composition and year class strength in gravel pits from one year to the next, traditional representation of production in the form of an Allen Curve has not been employed. There is no information available on biomass or mortality for any period outside that of this study.

According to Ivlev (1966) production is defined as the total quantity of fish flesh produced in a given area in a given time regardless of whether it all survives to the end of that time. Therefore, if the instantaneous growth rate is defined as

$$G = \frac{\ln \bar{W}_t - \ln \bar{W}_o}{t}$$

where $\bar{W}_t$ = mean weight of fish in the population at time t

$\bar{W}_o$ = mean weight of fish at time o

t = time interval t-o

then the production in Δt is given by

$$P = G\bar{B}$$

The biomass, or total weight of the stock, B_1 was calculated from the relevant length-weight relationship, length-frequency histogram and population estimate. Where possible, separate length-weight relationships were calculated using Bartlett's 1949 method. Using the estimates of abundance given in Appendix 2 and the length-frequency histograms in Figs. 40 to 60 the numbers of fish represented by each column or class interval (mostly 0.2 cm) were calculated by proportion. The weights equivalent to each class interval were obtained by substitution of the mid-class length into the appropriate length-weight regression equation. Multiplying by the abundance estimate for each length group gave the biomass of that group; summation of such biomass estimates over all the length groups represented gave an estimate of the total biomass. Where possible, individual year-classes were identified and treated separately so that the appropriate biomass estimates for the periods Δt apart could be used for estimating production.

The appropriate estimates of G were calculated from the back-calculated lengths-at-age for each year class, having converted these to weights, using the relevant length-weight regression equations. Where biomass estimates applied to two or more combined year-classes, G was taken as the arithmetic mean of the separate Gs for each of these year-classes.

SECTION 3: RESULTS

Results can conveniently be divided into three sections, the first section outlining the validation of the scale reading in roach, the other two sections giving the results of the survey and population estimates respectively.

3.1 Seasonal Growth and Check Formation in Roach in Yateley 4

The mean lengths and related statistics for the 1972 and 1973 year classes of roach are given in Appendix 1. Plate 1 shows scales taken from 1972 year-class fish during May and June 1973, which shows that check formation occurred between 3rd May and 5th June, 1973 in Yateley 4. None of the 100 sets of scales examined in either April or May had formed a check, but all the scales subsequent to June had clear checks. Scale growth (plus growth) was clearly visible on subsequent samples. Fig. 2 shows that growth occurred between April and May, 1973 with an increase in the rate of growth until July, followed by a decline. The majority of the year's growth occurred between the beginning of May and the end of September. Comparison of the mean lengths of the monthly samples using the t-test described in Section 2.5 shows significant increases ($P < 0.05$) in all but the two final samples. In contrast, there is a highly significant ($P < 0.01$) decrease in mean length between the November and December samples. All samples prior to December were large and were taken in a few seines but, in December, many seines were necessary. The January sample required three successive days of netting to catch 100 fish. A total of 6 roach was caught in the following three months after which the programme was terminated. The decrease in length of roach between November 5th and December 6th might be due to predation as will be discussed in Section 4 - the pike present were estimated using Jolly' stochastic model, the results which are given in Table 4. As will be discussed in Section 4 the cestode *Ligula intestinalis* may cause mortality of the host directly or by increasing vulnerability to pike predation. Table 5 shows a decrease in the percentage of ligulosed roach in Yateley 4 in successive monthly

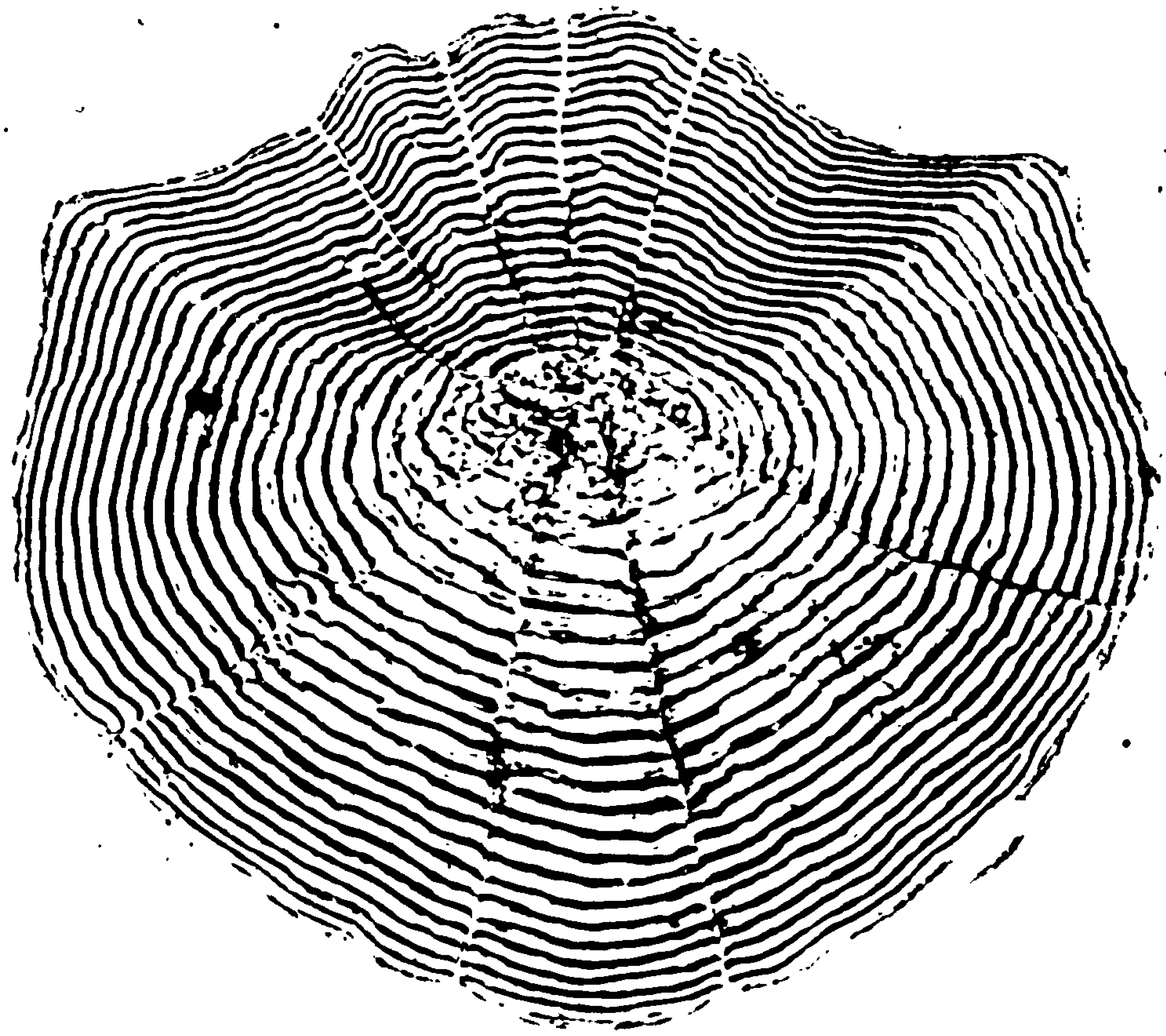
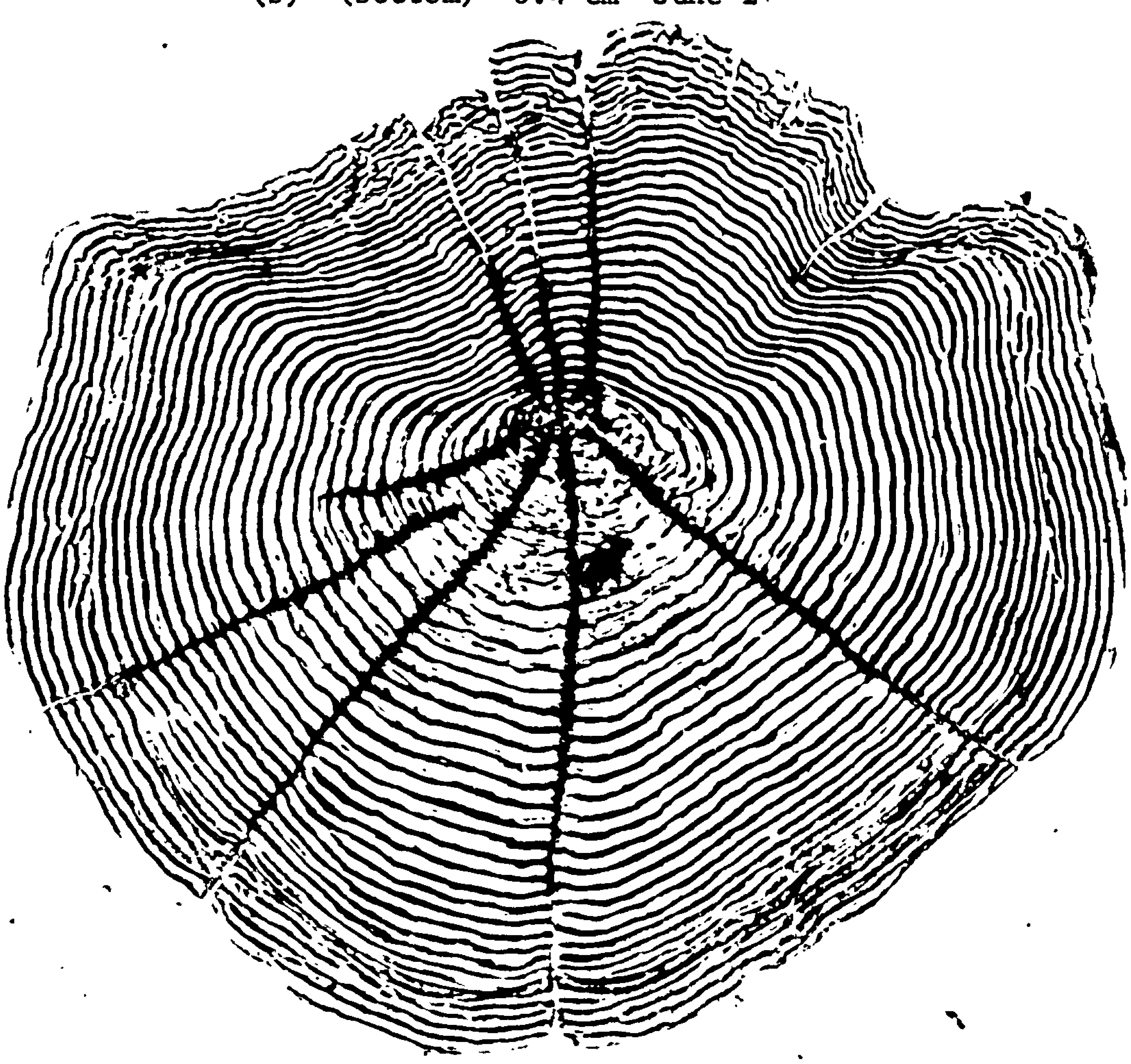


Plate 1 Scales from the 1972 Year-class Roach in Yateley 4

(a) (top) 6.1 cm May 0+

(b) (bottom) 6.4 cm June 1+



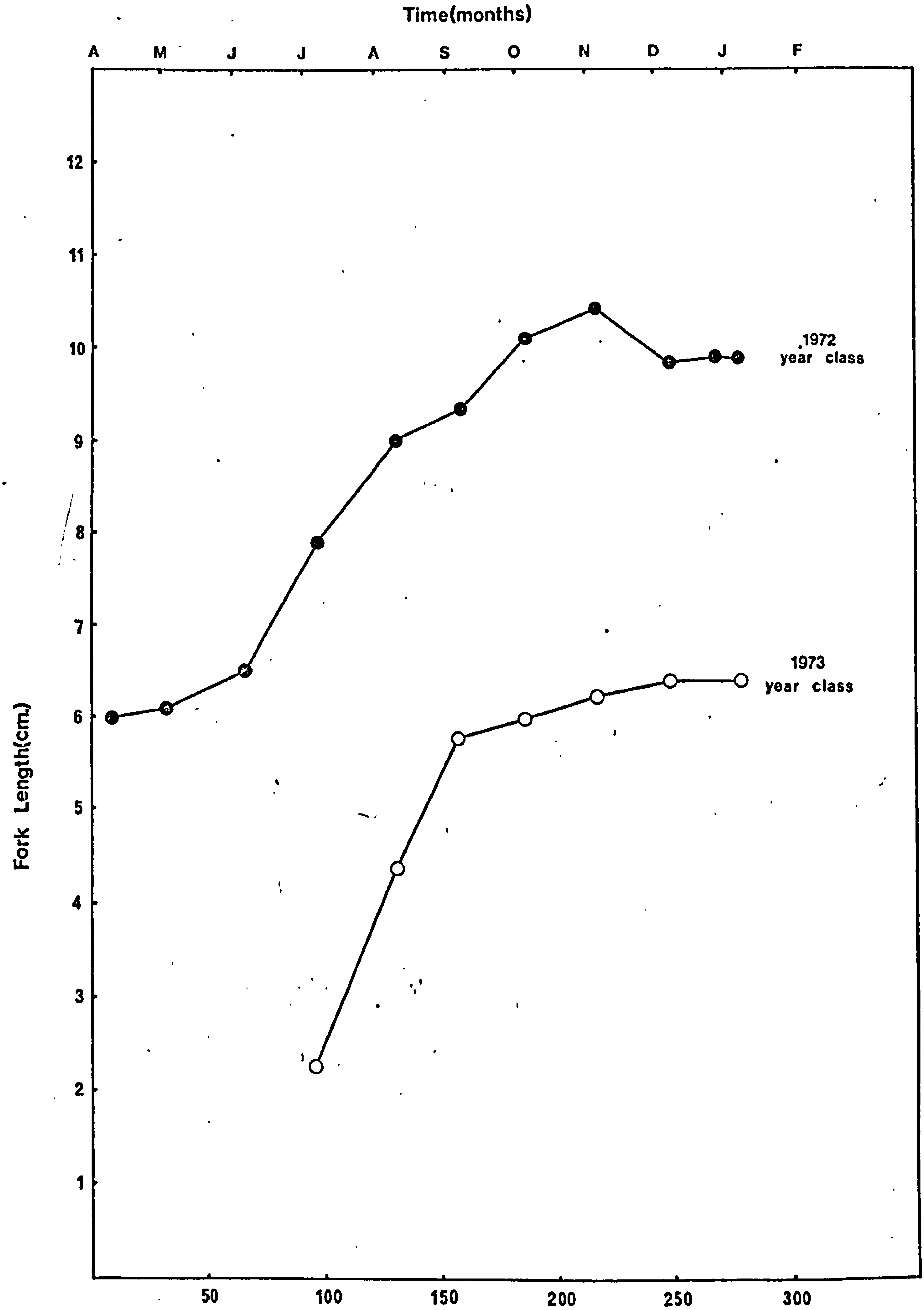


Fig. 2 The Growth of Roach in Yateley 4

TABLE 4 Jolly's Stochastic Model Output for Pike in Yateley 4

Date	Proportion Marked	Abundance Estimate (N)	S.E (N).
3. 5.73	0.43	21	7.3
1. 6.73	0.67	25	7.6
13. 9.73	1.00	12	0.0
4.10.73	0.56	47	18.6
5.11.73	0.75	66	40.1
6.12.73	0.43	242	246.1

TABLE 5 The Degree of Infestation of 1972 Year Class Roach by *Ligula intestinalis* in Yateley 4

Month	Degree of Infestation (%)	
	Non Ligulosed	Ligulosed
1973		
April	8	92
May	11	89
June	37	63
July	40	60
August	40	60
September	55	45
October	59	41
November	82	18
December	* 68	32
1974		
January	75	25

* all data except December sample based on 100 fish

samples indicating higher mortality of infected fishes.

The 1973 year-class showed very rapid growth during July and August 1973, falling off during the autumn. All mean values of length of successive samples are significant ($P < 0.05$) when compared by t-test.

Examination of the scales and mean lengths of monthly samples of the 1972 year-class roach indicate that formation of marks on the scale corresponding to descriptions of annual rings from the literature occur at the onset of growth in May. Furthermore, the heavy Ligula burden in 89% of these fish had not caused the formation of any additional or 'false rings'.

3.2 Survey

The returns (Table 6) indicate that roach is the commonest fish in the gravel pits studied. The samples from some lakes are inadequate for calculation of growth rate, either because too few fish were caught or because all fish caught belonged to the same age group (0+ or 1+). Scale v. body length regressions (Table 7) and back-calculations were carried out for the remaining samples; growth curves of these are shown in figs. 3 to 32 and the sample statistics are given in Appendix 1.

All fish caught between September and May were considered to have completed the current season's growth, whilst growth curves for those caught before September were drawn for the period prior to the time of formation of the last check. Annual check formation was taken as occurring during May, slight plus growth in samples taken during May and June was treated as representing the current season's new growth. (See Section 3.1).

Several species in many lakes were found to be parasitised by *Ligula intestinalis*, as shown in Table 8.

TABLE 6 The Numbers of Fishes Caught and Examined During the Survey

Lake Number	Roach	Bream	Tench	Bleak	Gudgeon	Rudd	Chub	Crucian Carp	Perch	Pike	Others
1			3						24	11	
2	36*		3					1	1	3	
3(a)	26*		4						13	4	eel
(b)	48*		4			1		1	19	7	
4	72*		9					2	9	6	
5	67*		2					1	18	1	stickleback, carp
6	6*			5					4	4	
9	57*		1			6			23	5	
10											None
11	60*				8*					1	
12	54*	2		25*					2	1	
13	59*	10*		20					11	3	ruffe
14	1	7	6	2					4	10	eel
15	6*	3	7	2		41*			2	3	
16	12*		1						10	8	
17	45*	18*	2	1*				4	2	1	bullhead, stickleback hybrid (R-B)
18	50		14		1	5			25		stickleback
19	1*		5		3*	1		3	23		hybrid (R-R)

TABLE 6 Continued

Lake Number	Roach	Bream	Tench	Bleak	Gudgeon	Rudd	Chub	Crucian Carp	Perch	Pike	Others
20	3*		2		16*	20		2	21		
21			3			2			16		
22			2						10		
23											None
24											None
25											None
26	7*		3						2		
27	10	1							8		
30	32*			2			2		4	4	
31	4*						2*			1	
32	2*								45	8	dace
33									50	2	stickleback
34	12*		10			1					minnow
35	21*	9*				5			1		
36	27	1	3			38			8		carp
37	3	4									
38	49*	4	4								minnow, dace carp
39	27*	2	4			6*	4*			1	carp

TABLE 6 Continued

Lake Number	Roach	Bream	Tench	Bleak	Gudgeon	Rudd	Chub	Crucian Carp	Perch	Pike	Others
40	24*	12	6		1*	16			8	1	minnow, dace carp
41	13	36*	7			1			8	22	carp, dace
42	31*	25	1	30*	24*				8	6	stone loach, bullhead
44	40*								1	1	

* Denotes parasitisation by <u>Ligula intestinalis</u>

R-R = Roach - Rudd hybrid

R-B = Roach - Bream hybrid

TABLE 7 Linear Regression Statistics for Fork Length (cm) x Posterior Scale Radius or operculum size (arbitrary units)

Lake	Species	A	B	t	n
Yateley 3a + b	Roach	1.657	0.266	5.02	71
Yateley 5	Roach	2.110	0.240	0.391	51
Yateley 9	Roach	1.690	0.260	1.690	39
"	Rudd	0.373	0.282	0.948	4
Bedfont 11	Roach	1.700	0.267	1.125	59
Chertsey 12	Roach	1.297	0.283	0.738	27
"	Bleak	1.398	0.314	2.534	16
Thorpe 13	Roach	1.905	0.251	1.157	58
"	Bleak	5.566	0.184	1.011	19
"	Bream	2.232	0.317	0.013	9
Kingsmead 16	Rudd	0.677	0.263	1.251	26
Farnborough 18(a)	Roach	2.079	0.242	1.003	47
"	Perch	2.157	0.121	0.344	21
Twyford 32	Perch	1.234	1.331	0.573	17
Twyford 33	Perch	1.850	1.234	1.590	49
Sutton-at-Hone 34	Roach	1.567	0.291	0.044	11
" 35	Roach	2.040	0.261	1.094	20
" "	Rudd	1.324	0.268	7,333	4
	Bream	3.458	0.311	1.582	5
" 36	Roach	2.031	0.244	1.552	26
Darenth 39	Roach	1.455	0.257	2.023	32
"	Rudd	1.660	0.232	0.831	5
Darenth 40	Roach	2.001	0.248	1.006	24
"	Rudd	1.524	0.234	1.551	16
	Bream	2.094	0.324	0.539	25
Larkfield 41	Roach	2.762	0.241	0.590	11
	Bream	0.119	0.397	1.217	32
Fishers Green 42	Roach	2.765	0.226	0.161	30
	Bleak	5.298	0.196	0.075	29
	Bream	1.259	0.368	0.473	24
Farnborough 18(b)	Tench	1.236	0.218	-0.712	19

A, B = regression coefficients

t = Student's t-test for deviations from linearity

N = sample size

TABLE 8 The Occurrence of *Ligula intestinalis* in Fishes Caught During the Survey

Species	Number of Lakes out of 39 in Which Found	Number of Lakes where *Ligula* was Present
Roach	32	26
Bream	14	4
Bleak	9	3
Gudgeon	7	4
Rudd	13	2

(a) Roach

The majority of the roach caught were found to be young (< 4 years). In fact, very few lakes contained roach of more than 6 years of age. Exceptions to this were the Sutton-at-Hone pits (34, 35 and 36) where fish of age 7+, 8+ and 9+ were caught. (See Figs. 3-16).

The growth of roach during the first year of life, i.e. up to the formation of the first check, was compared using the t-test as described for Yateley 4 roach comparing the mean lengths of fish at age 1 year in all lakes. Table 9 shows the relevant t-values and degrees of freedom. Most means are significantly different at the 5% level. Many are very highly significant ($P < 0.01$). The mean length for Darenth 38 is significantly larger than for all the other lakes. Taking Darenth 38 as a standard, the first year increments provide a league in decreasing order of magnitude as shown in the top line of Table 10. Table 11 shows the t-values and degrees of freedom for the increment between the times of formation of the first and second check, i.e. the second year of life. Here the number of significantly different comparisons is less than for the first year of life. The order of lakes in this case is given in the second line of Table 10. The differences between these two leagues indicate that the growth achieved in the first year of life does not necessarily affect that in the second year. When the two leagues are compared with one based on mean lengths achieved at the end of the second year of life (third line in Table 10), a greater similarity of order is obtained in comparison with the second league. In the third league, Darenth 39 has changed position from fifth to first, and other lakes have also changed position in the series. The differences in growth increments become less significant as the fish get older. This is probably due to a combination of a decreasing growth rate with age, larger variance of length-at-age within any one year-class and increasing variance between year-classes. The third to fourth year increments are not significantly different at the 5% level, neither are those of the fifth to sixth, sixth to seventh nor

TABLE 9 Student's t-values and degrees of Freedom for Roach 0-1 year increments (for explanation see text)

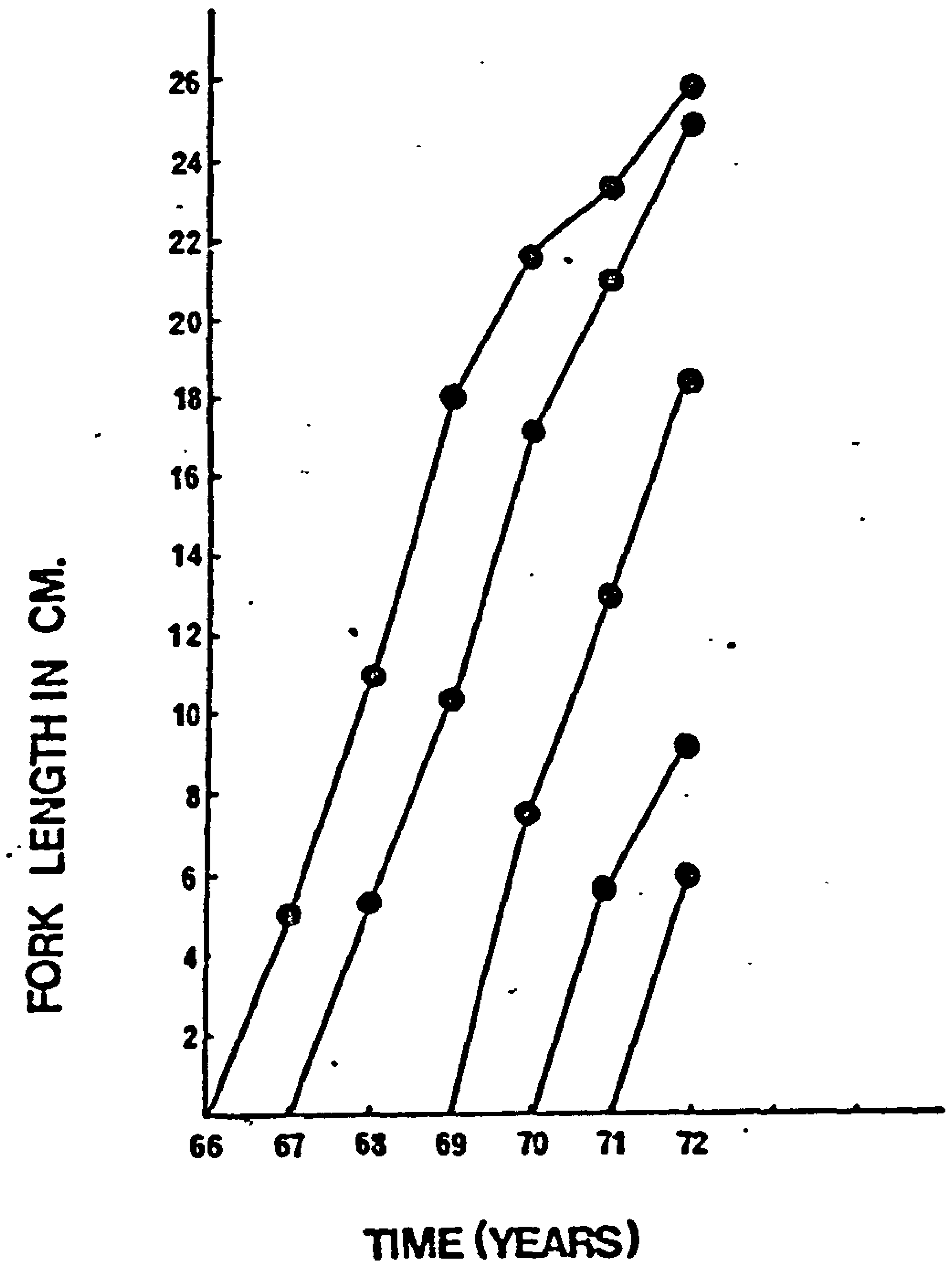
	3a+b	5	9	11	12	13	18(a)	35	36	38	39	40	41	42
3a+b		2.45 118	11.33 110	1.44 127	10.64 98	2.55 129	-3.16 118	2.36 91	2.23 94	-7.54 78	1.02 118	-0.31 99	-1.22 75	12.04 72
5			12.42 86	-1.08 103	12.11 74	-0.32 105	-7.13 94	0.93 67	0.57 70	-13.85 54	-2.48 94	-2.26 75	5.86 72	4.98 53
9				-11.19 95	1.54 66	-15.03 97	-18.81 86	-9.38 59	-10.32 62	-21.86 46	-18.87 86	-9.28 67	-6.17 64	-6.35 50
11					10.70 83	0.97 114	-5.08 103	1.51 76	1.28 79	-9.65 63	-0.68 103	-1.39 84	5.33 81	2.14 67
12						-14.65 85	-17.44 74	-9.35 47	-10.22 50	-19.81 34	-18.33 74	-8.70 55	-6.87 52	-6.54 38
13							-8.03 105	1.39 78	0.96 81	-16.93 65	-2.60 105	-2.41 86	7.46 83	2.70 69
18(a)								6.48 67	6.49 70	-9.09 54	6.41 94	2.10 75	12.01 72	6.37 58
35									-0.38 43	-14.63 27	-3.69 67	-2.15 48	4.54 45	1.23 31
36										-14.90 30	-3.25 70	-2.06 51	5.19 48	1.60 34
38											21.83 54	5.99 35	22.98 32	14.64 18
39												-1.22 75	12.04 72	5.28 58
40													4.98 53	2.34 39
41														-2.46 36
42														

TABLE 10 A Comparative League of Lakes in Order of the Magnitude of Growth Increment

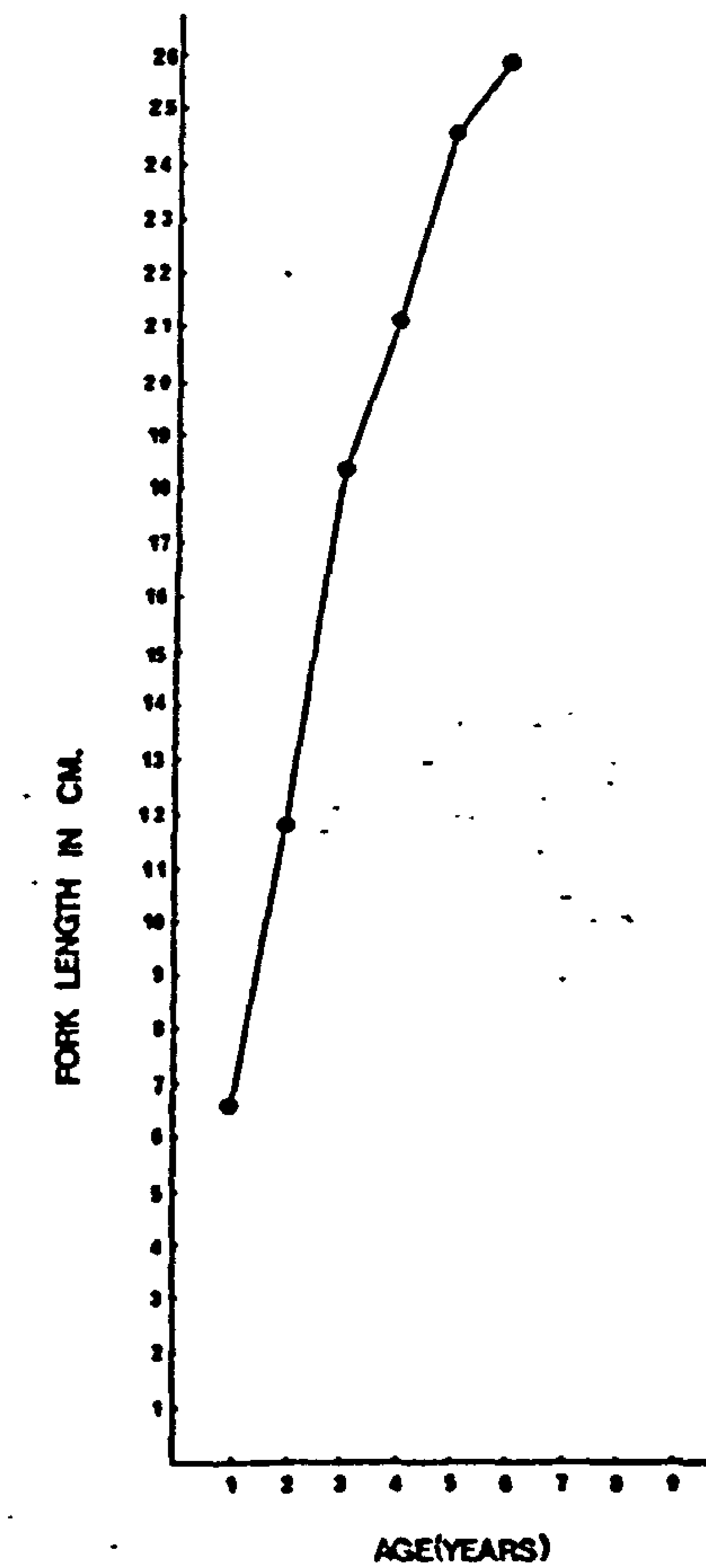
Incremental Period (years)														
0-1	38	40	3a+b	18(a)	11	5	35	42	36	13	12	39	9	41
1-2	3a+b	35	41	42	39	12	9	40	11	13	38	36	18(a)	5
0-2	38	3a+b	39	40	35	11	19(a)	41	13	36	42	9	5	12

TABLE 11 Student's t-values and Degrees of Freedom for Roach 1-2 Year Increments (for explanation see text)

	3a+b	5	9	11	12	13	18(a)	35	36	38	39	40	41	42
3a+b		6.39 105	3.28 93	3.76 110	2.75 80	4.96 103	5.63 105	1.51 78	5.38 81	5.25 85	2.56 87	3.75 85	1.85 55	2.19 47
5			-3.09 82	-2.47 98	-3.09 68	-1.94 91	-0.65 94	-4.67 67	1.15 69	0.08 74	-4.48 76	-0.87 73	-1.00 65	-0.03 44
9				0.30 86	-0.06 56	1.46 79	2.25 82	-1.54 55	3.33 57	2.88 62	-0.88 64	1.19 61	1.25 53	1.85 55
11					-0.32 73	0.96 96	1.81 98	-1.57 71	2.66 74	2.12 78	-1.05 80	0.09 78	0.87 69	1.33 72
12						1.52 66	2.16 68	-1.61 41	3.48 44	3.28 48	-0.88 50	1.12 48	1.33 39	2.03 42
13							1.10 91	-3.23 64	2.67 67	1.90 71	-2.71 73	0.33 71	0.32 62	0.89 65
18(a)								-3.59 67	1.51 69	0.64 74	-3.31 76	-0.39 73	-0.46 65	-0.06 67
35									4.66 42	4.81 47	1.01 49	2.10 46	2.49 38	3.34 40
36										-1.05 49	-4.73 51	-1.34 49	-1.58 40	-1.41 43
38											-4.67 56	-0.79 53	-1.02 45	-0.68 47
39												1.85 55	2.19 47	3.10 49
40													-0.03 44	0.27 47
41														0.36 38
42														

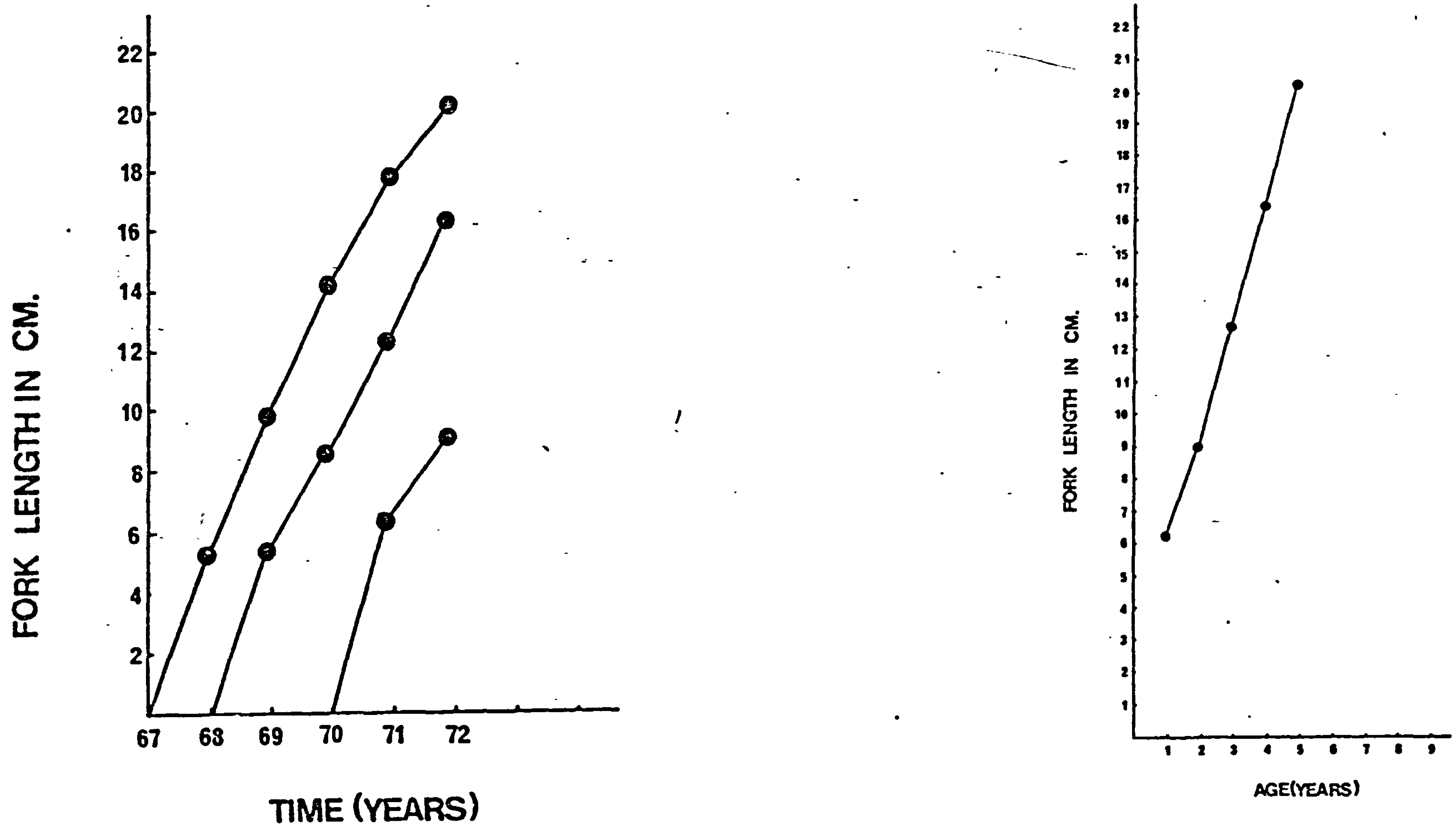


(a) Separate year-classes



(b) Composite year-classes

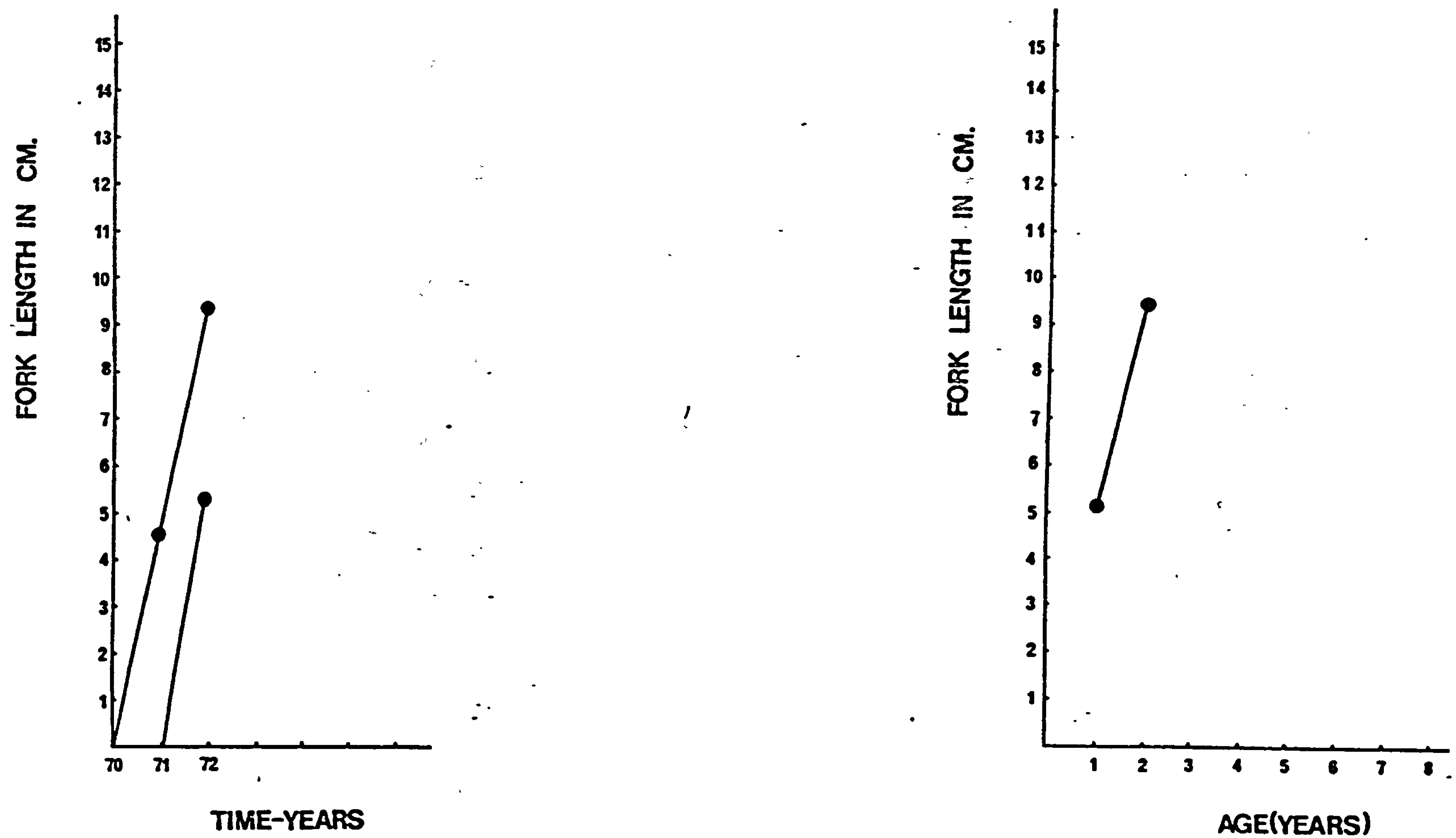
Fig. 3 Back-calculated Growth of Roach in Yateley 3a + b



(a) Separate year-classes

(b) Composite year-classes

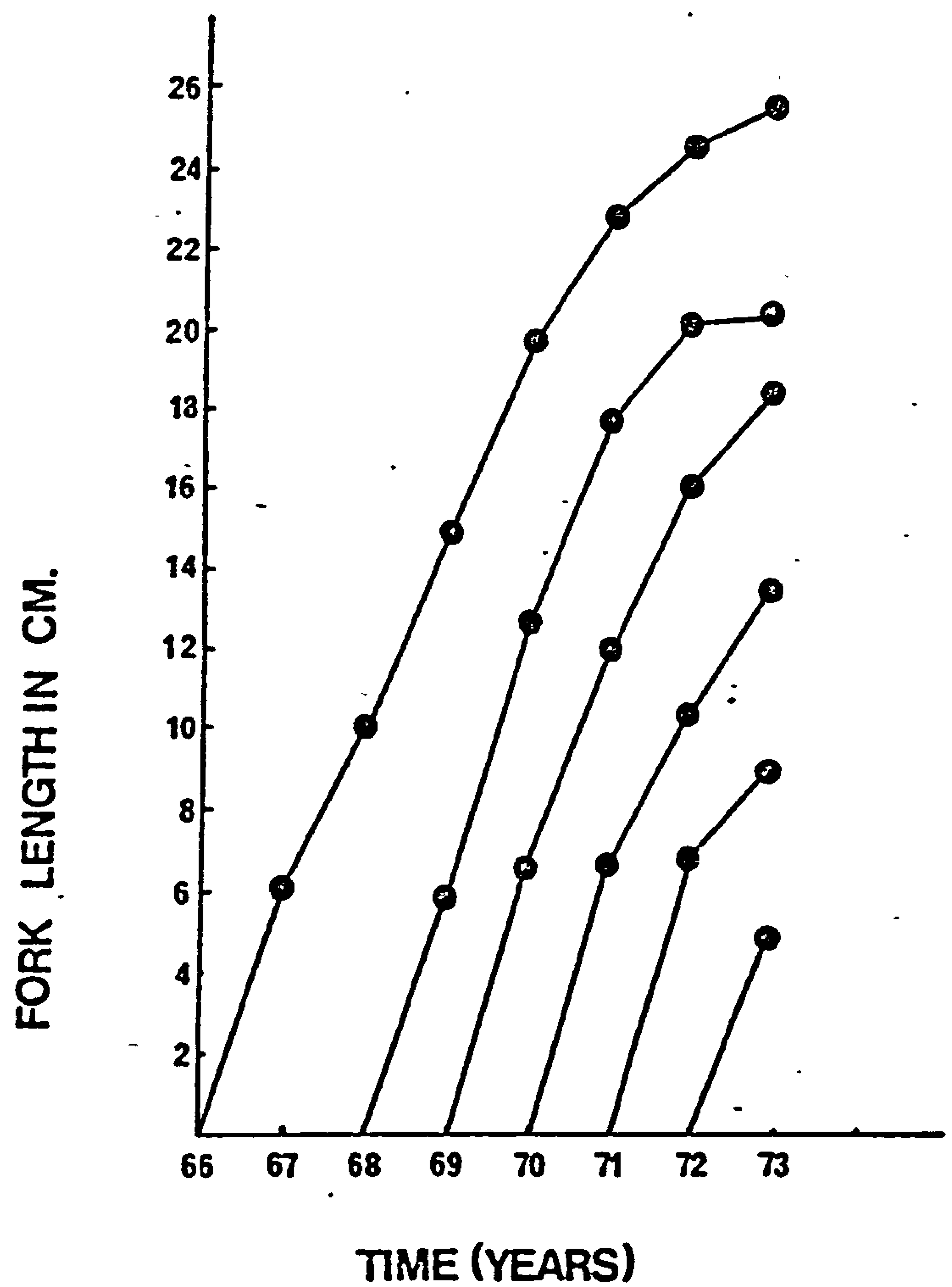
Fig. 4 Back-calculated Growth of Roach in Yateley 5



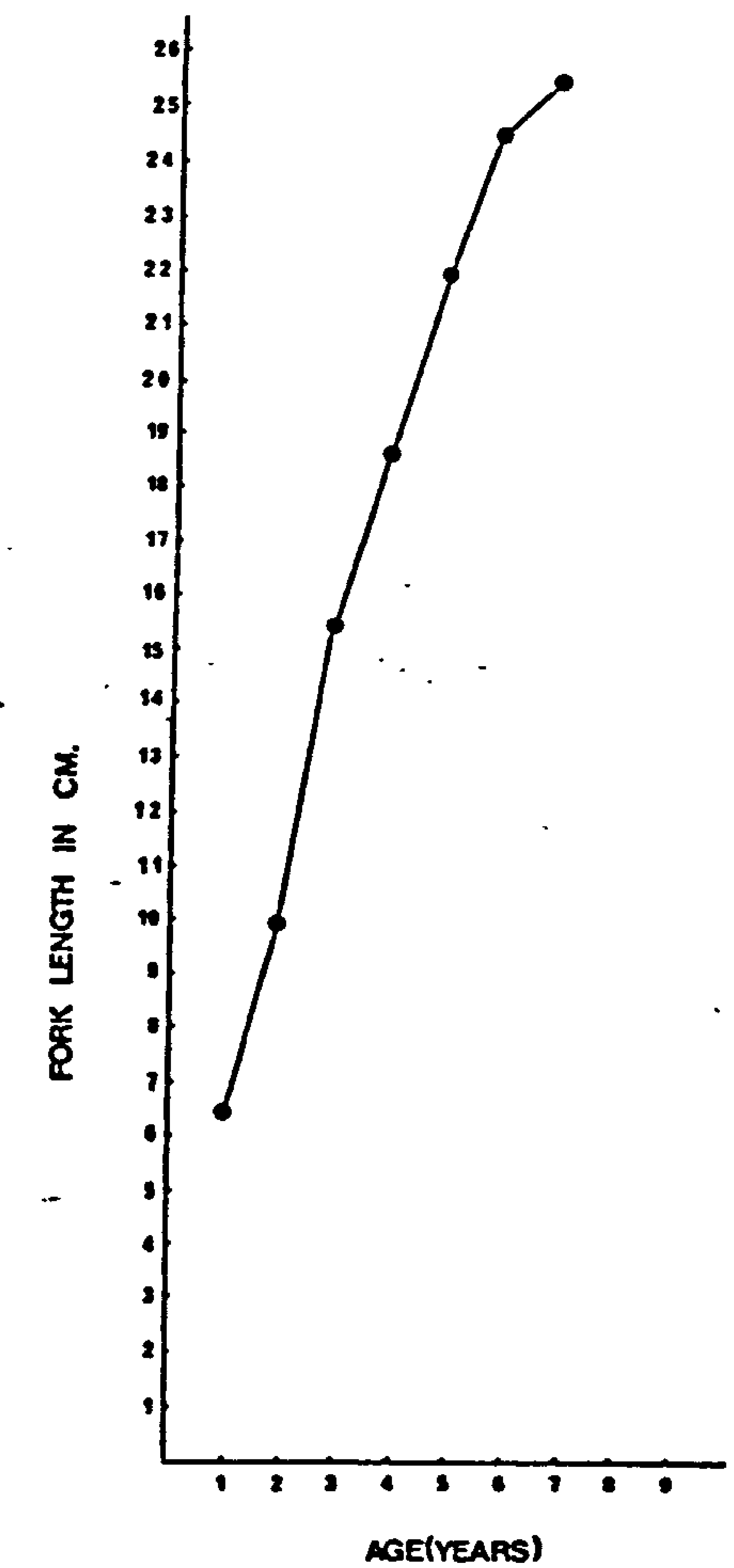
(a) Separate year-classes

(b) Composite year-classes

Fig. 5 Back-calculated Growth of Roach in Yateley 9

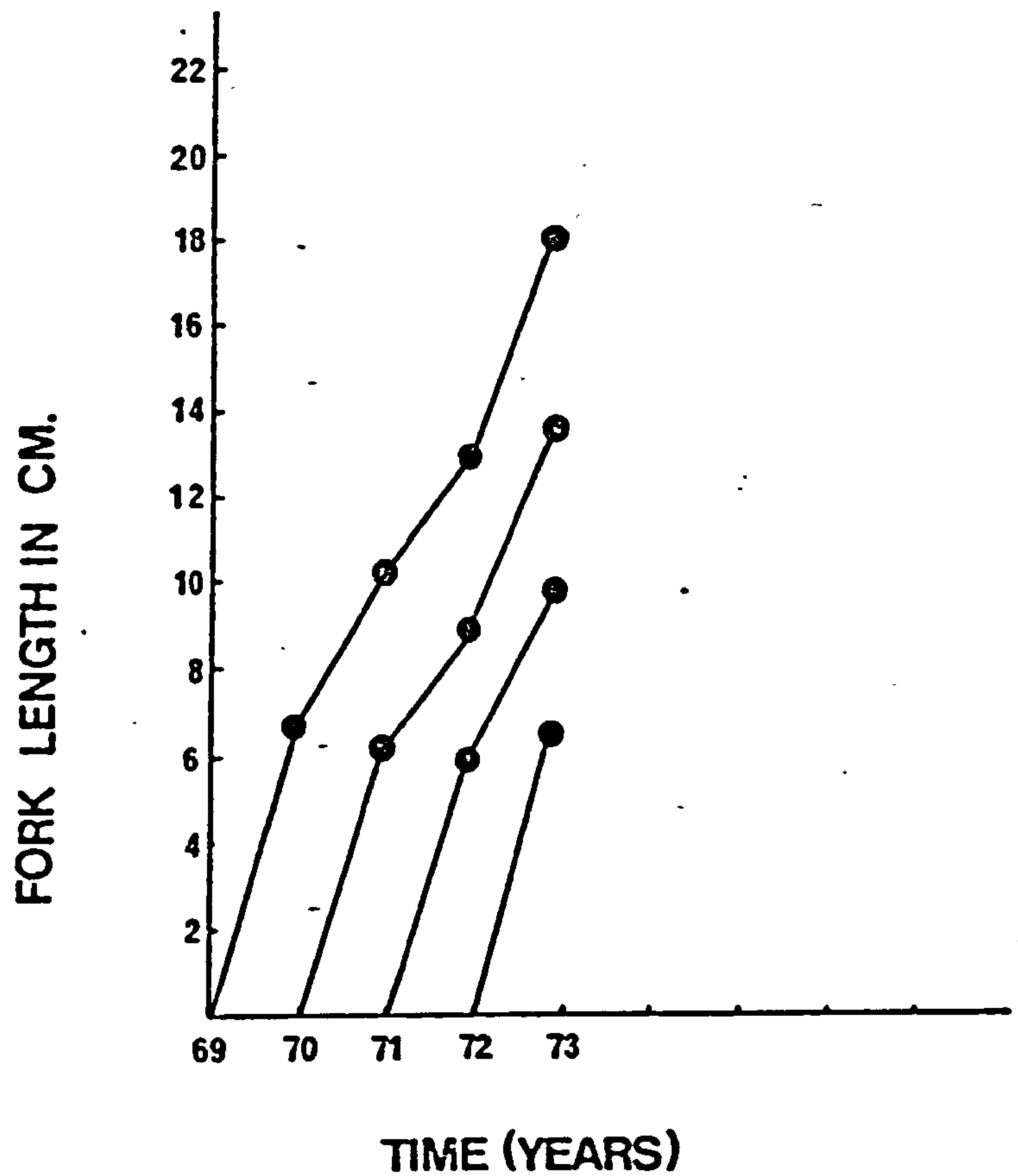


(a) Separate year-classes

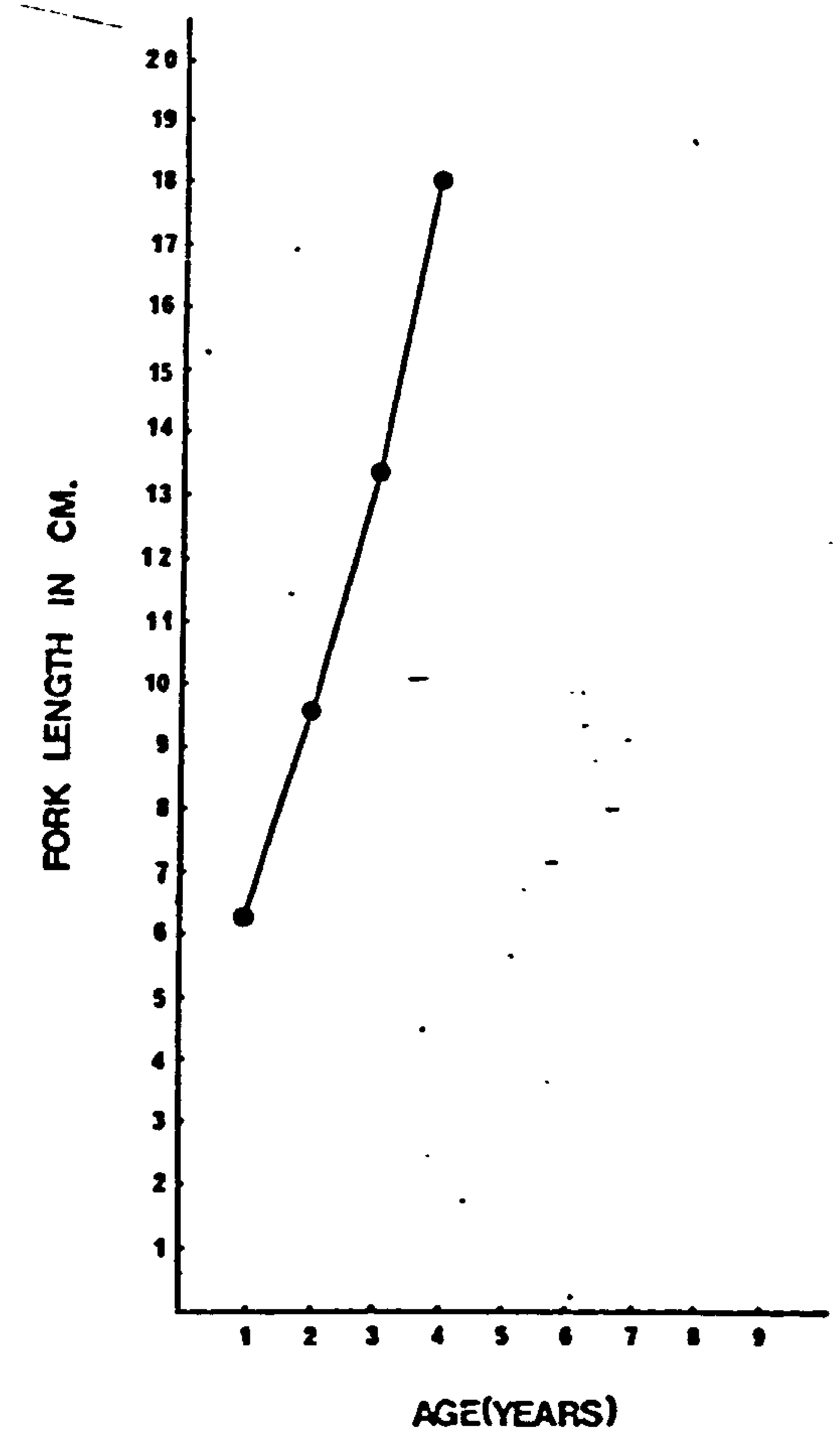


(b) Composite year-classes

Fig. 6 Back-calculated Growth of Roach in Bedfont 11

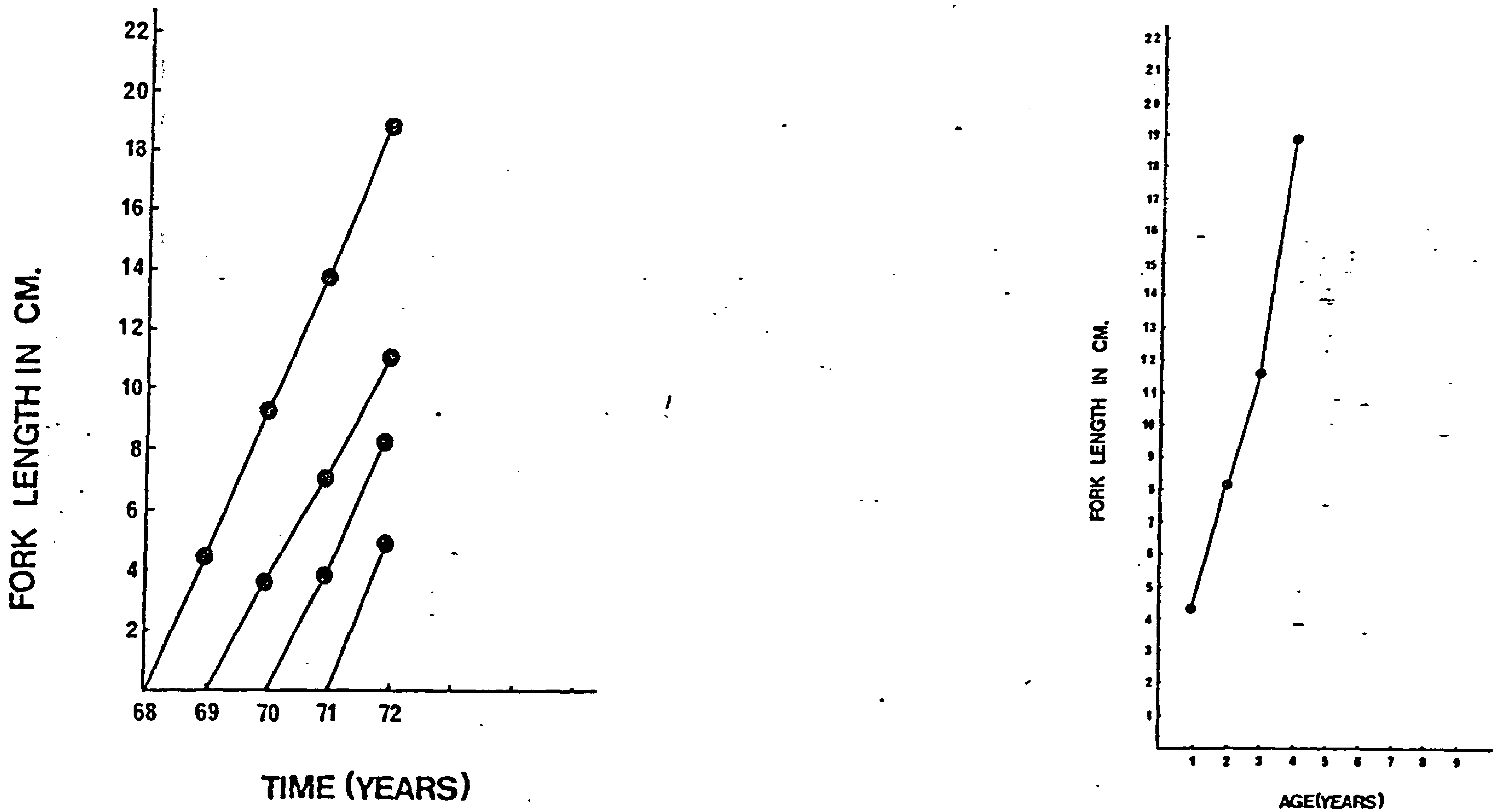


(a) Separate year-classes



(b) Composite year-classes

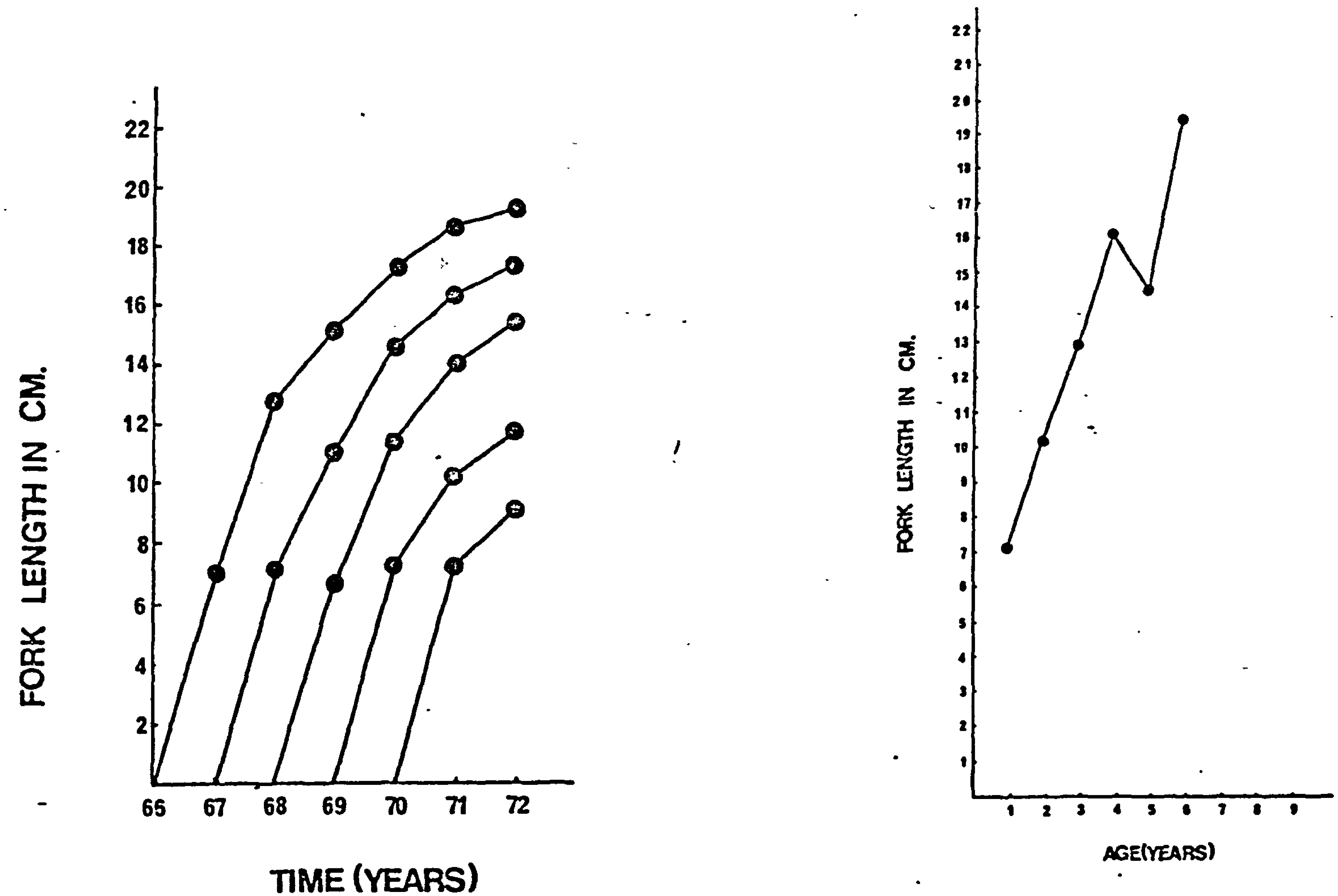
Fig. 7 Back-calculated Growth of Roach in Chertsey 12



(a) Separate year-classes

(b) Composite year-classes

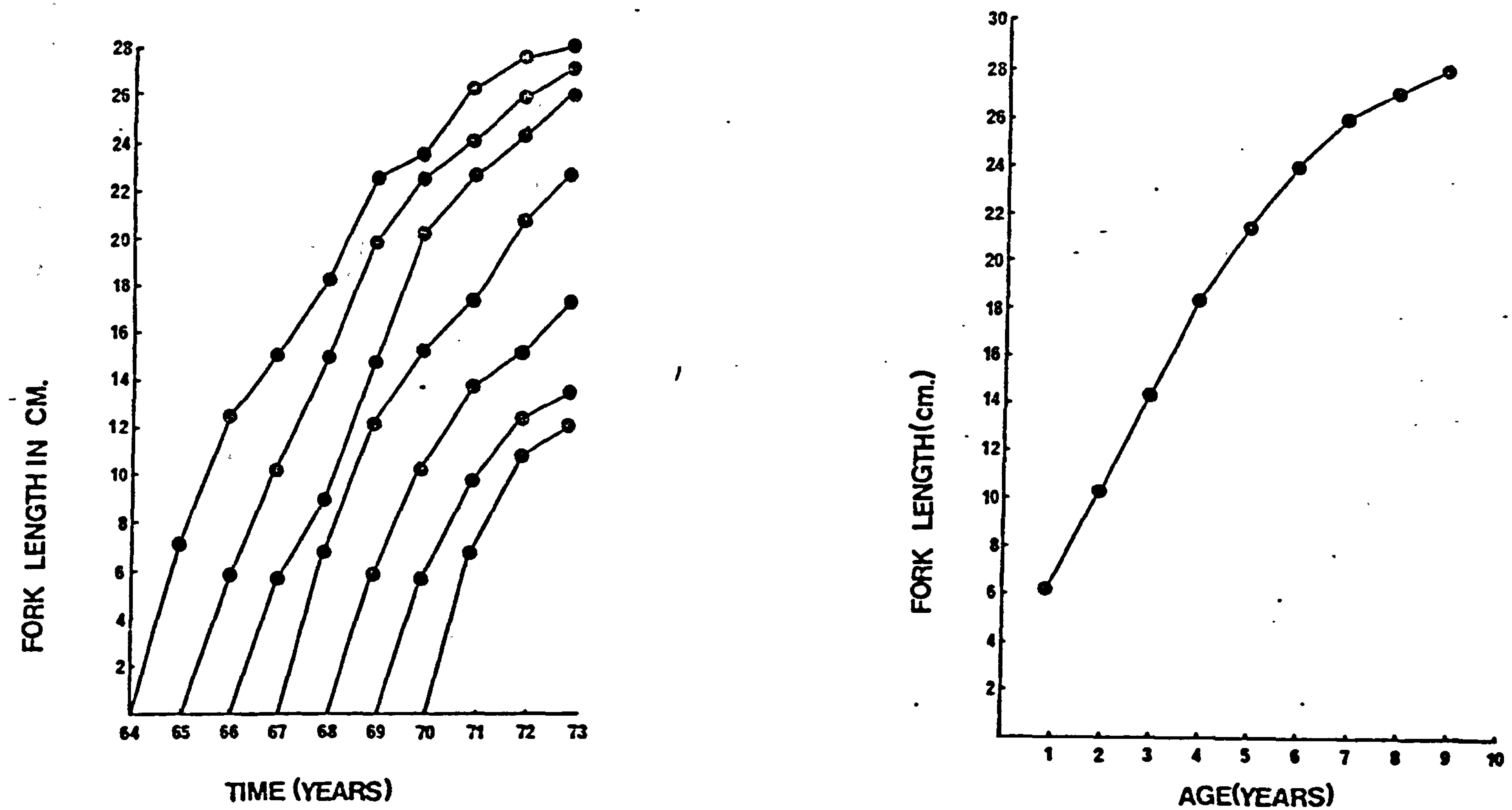
Fig. 8 Back-calculated Growth of Roach in Thorpe 13



(a) Separate Year-classes

(b) Composite Year-classes

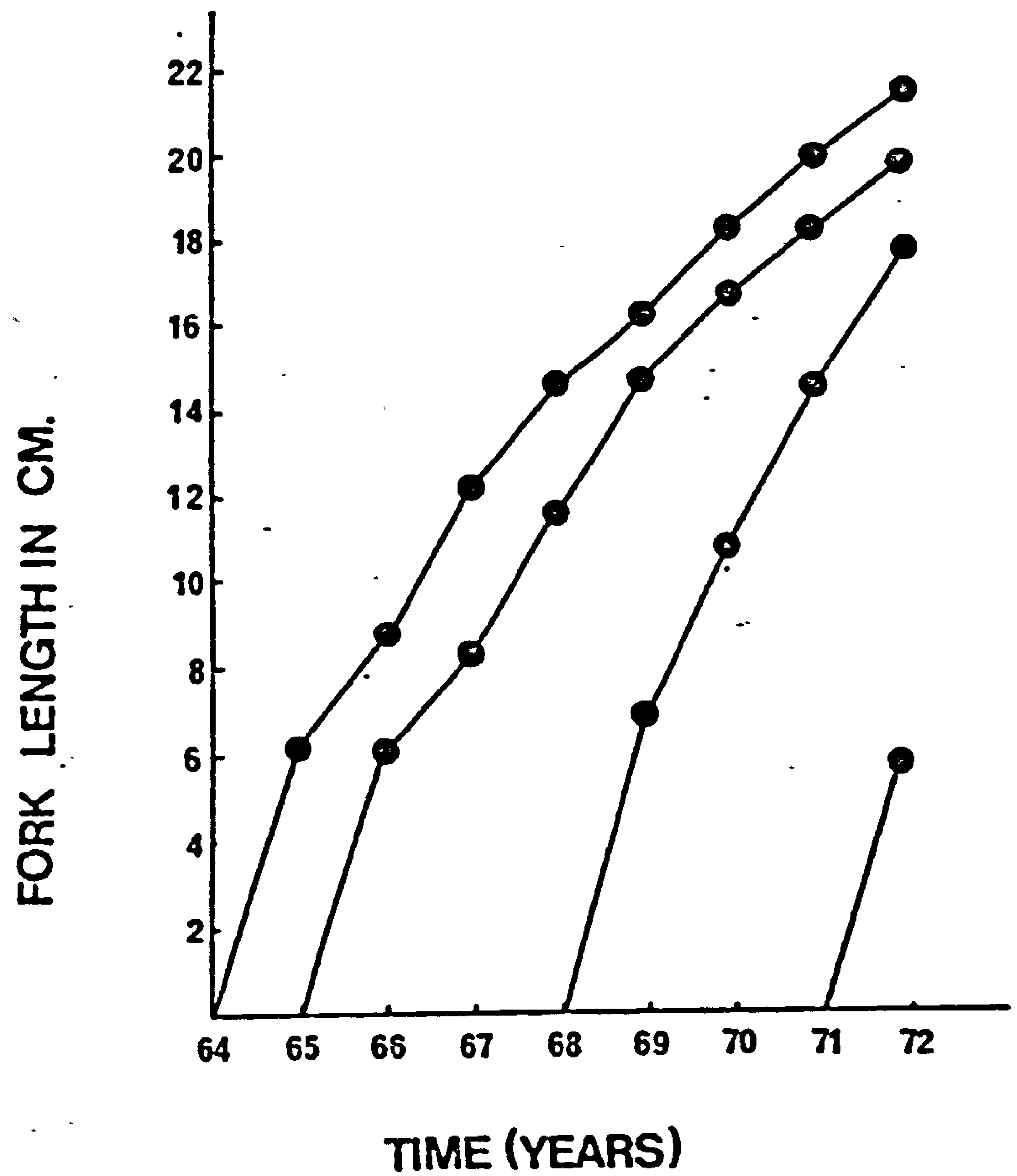
Fig. 9 Back-calculated Growth of Roach in Farnborough 18(a)



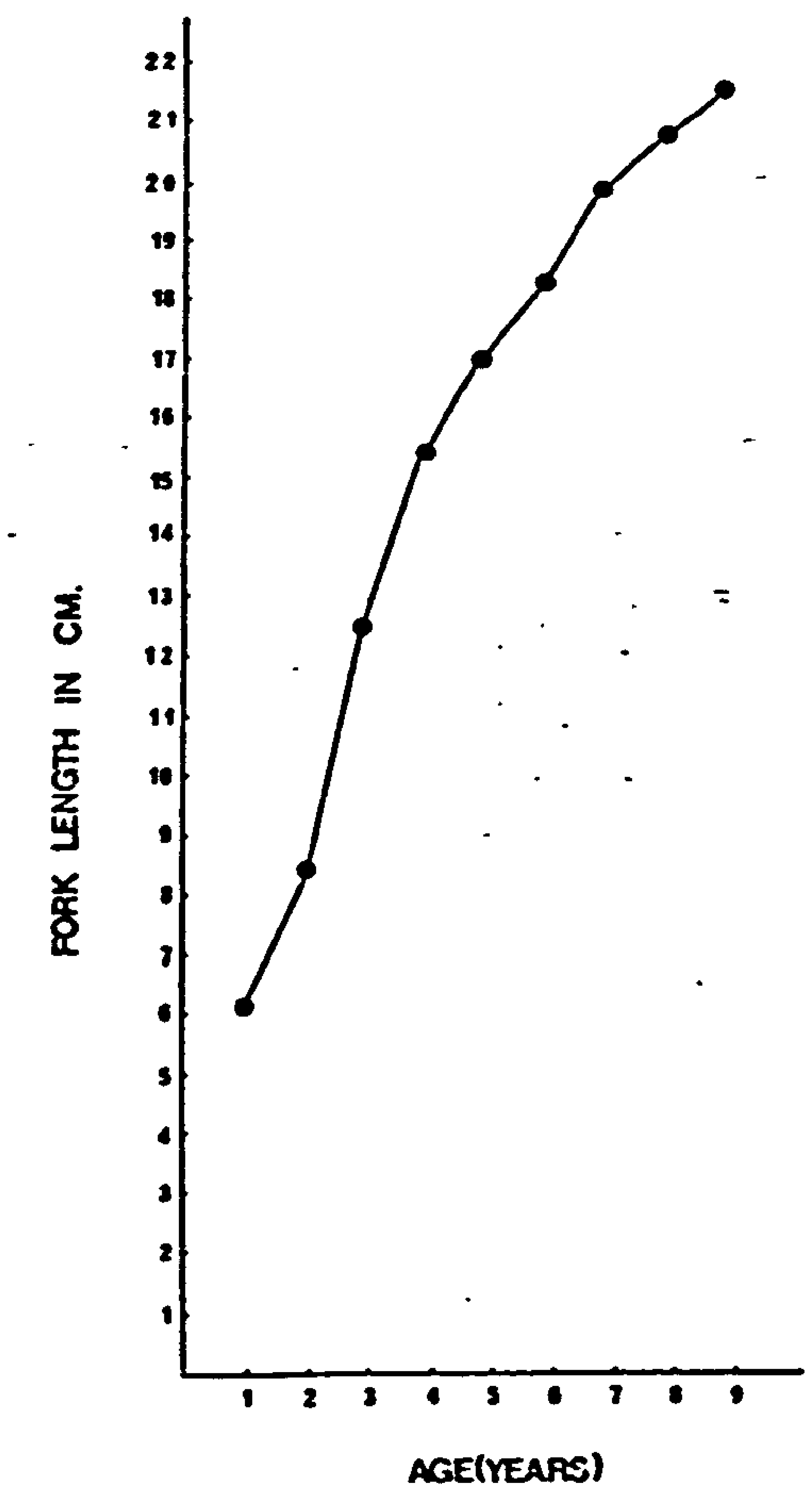
(a) Separate Year-classes

(b) Composite Year-classes

Fig. 10 Back-calculated Growth of Roach in Sutton-at-Hone 35

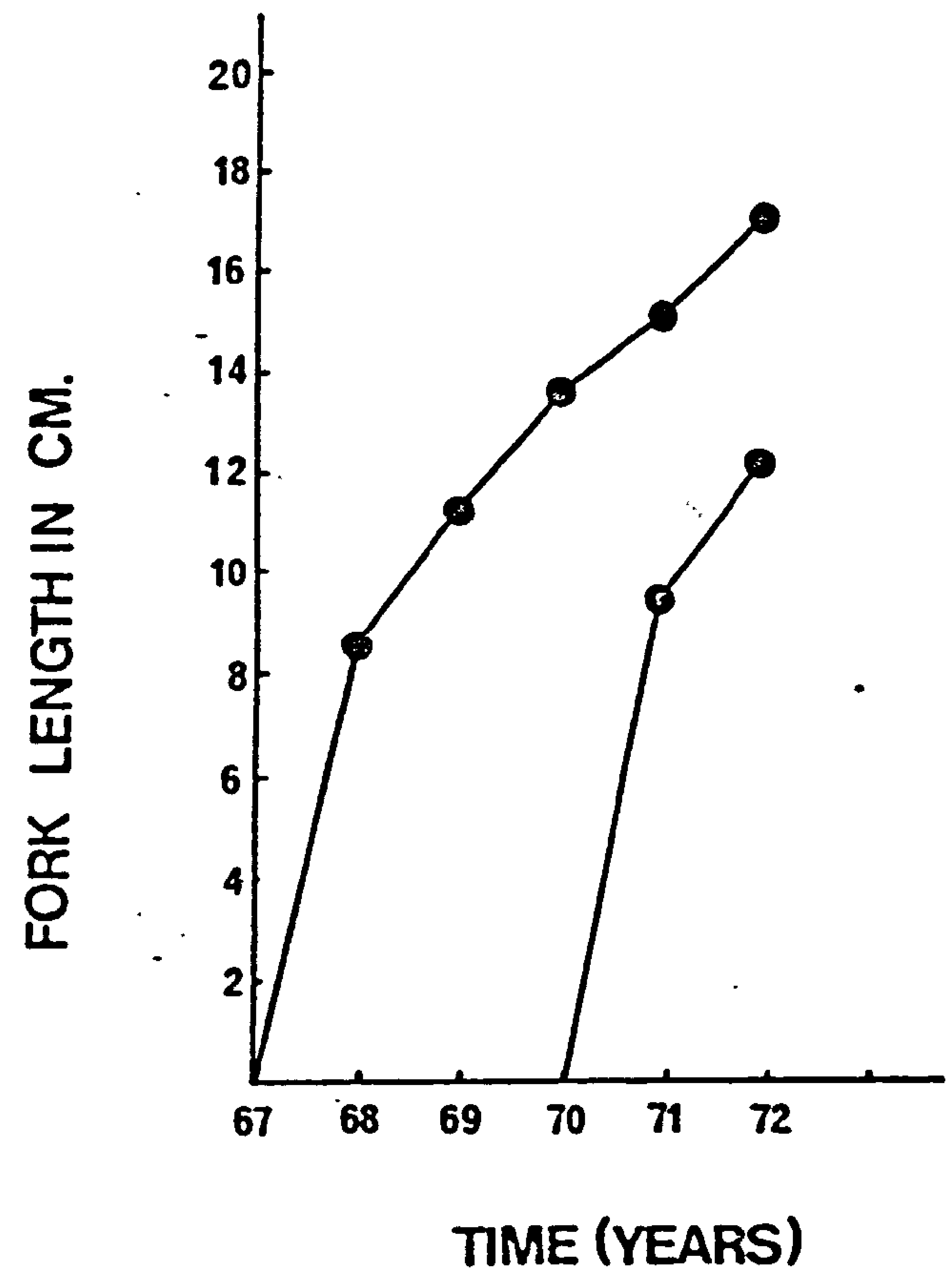


(a) Separate Year-classes

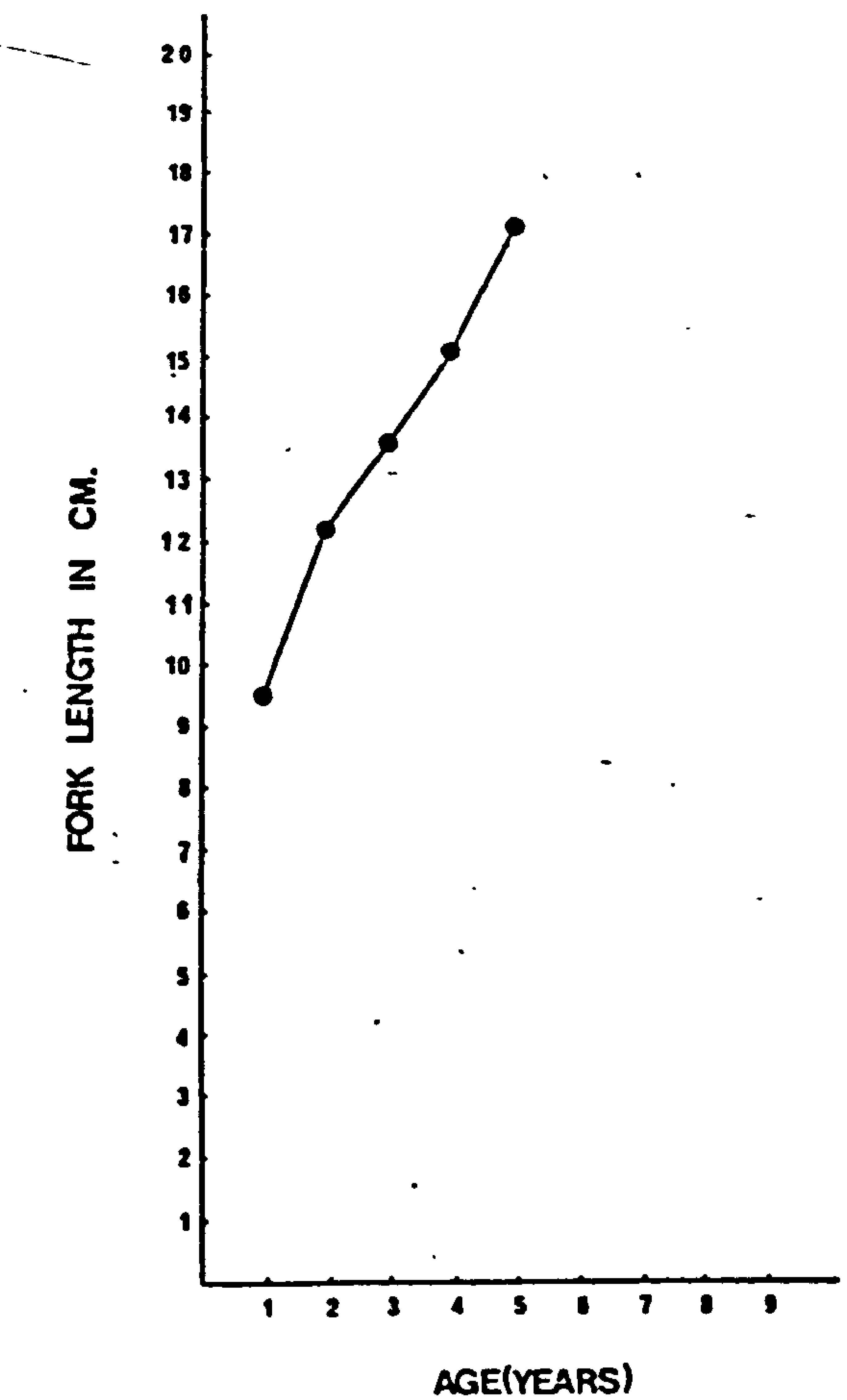


(b) Composite Year-classes

Fig. 11 Back-calculated Growth of Roach in Sutton-at-Hone 36

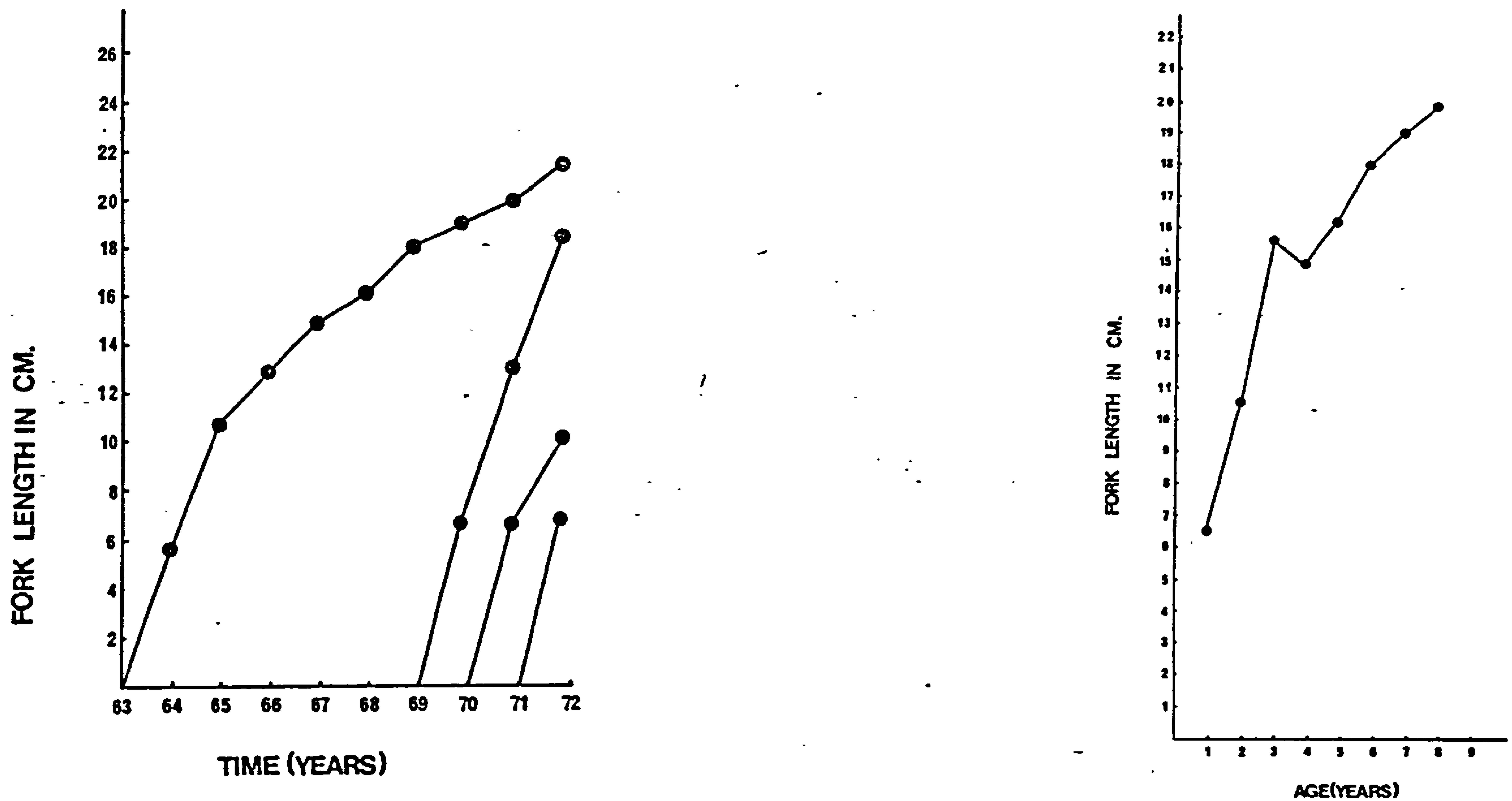


(a) Separate Year-classes



(b) Composite Year-classes

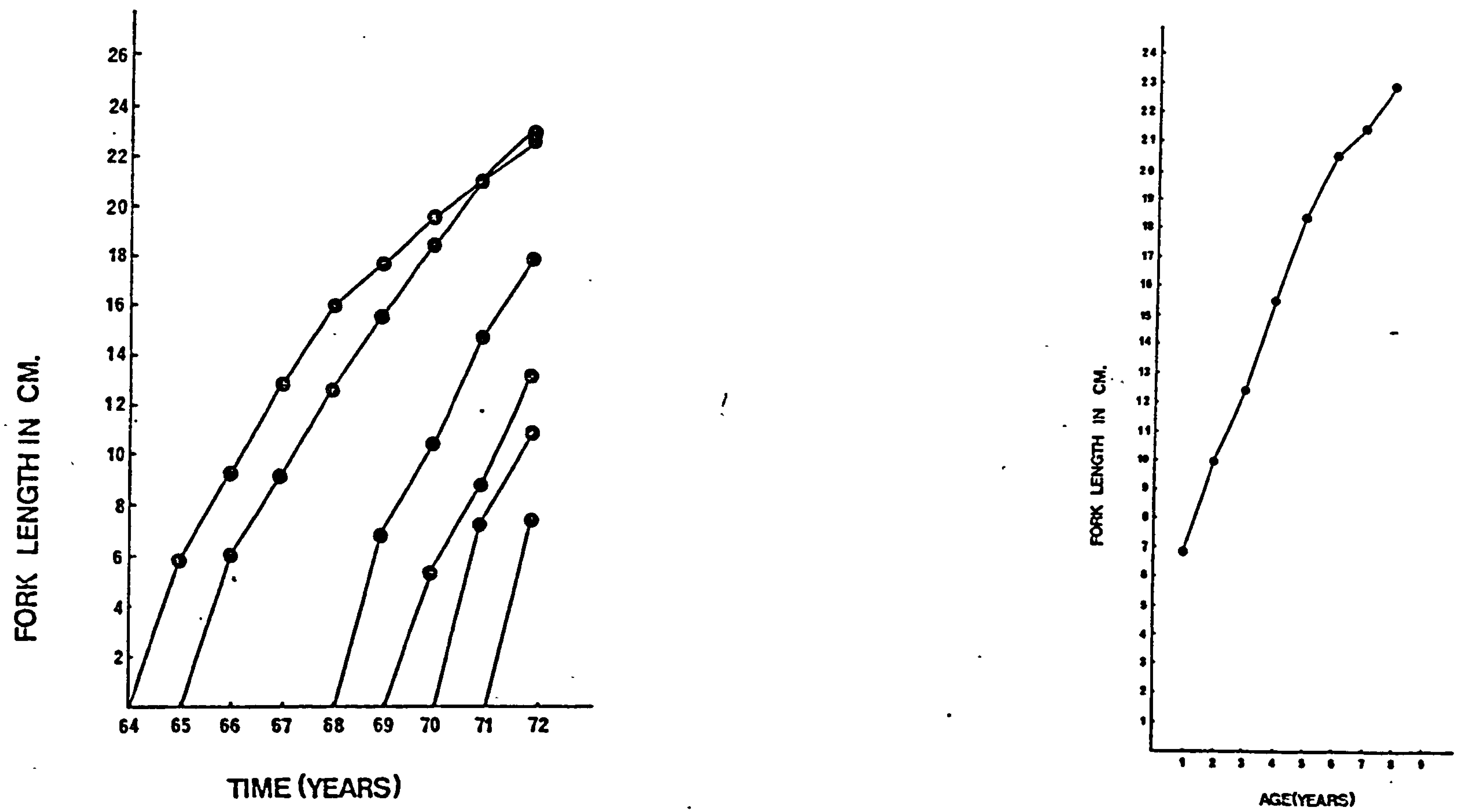
Fig. 12 Back-calculated Growth of Roach in Darenth 38



(a) Separate Year-classes

(b) Composite Year-classes

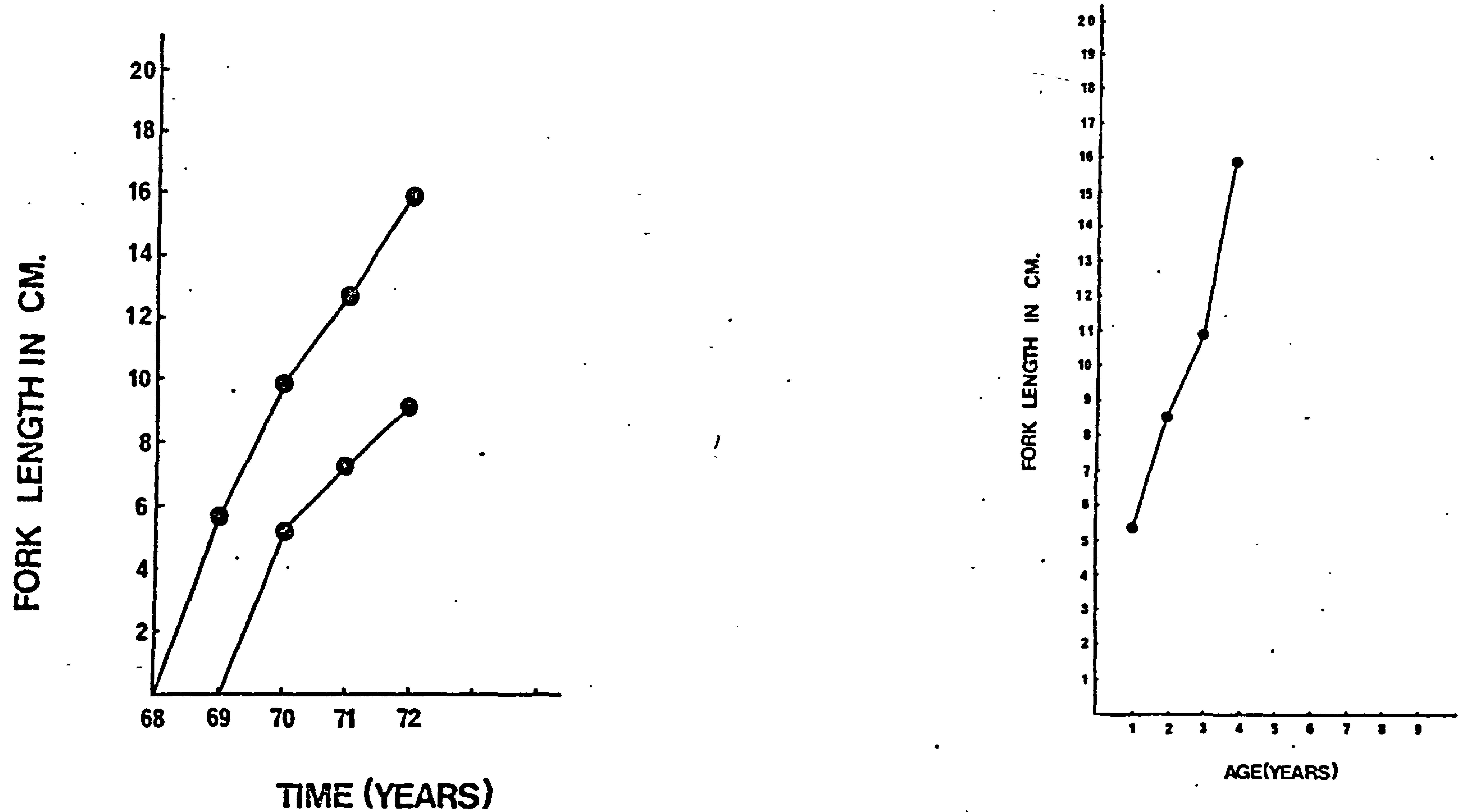
Fig. 13 Back-calculated Growth of Roach in Darenth 39



(a) Separate Year-classes

(b) Composite Year-classes

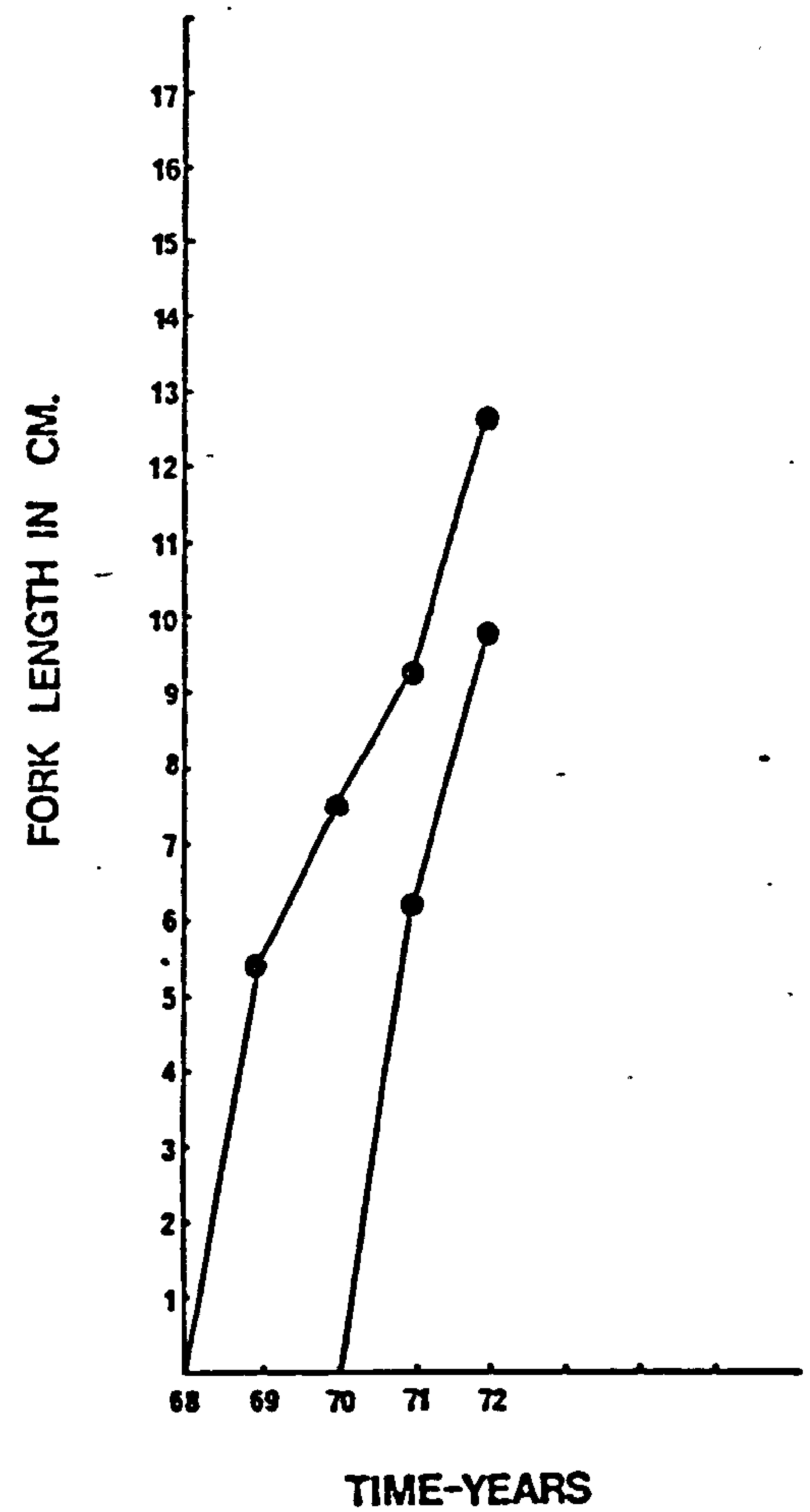
Fig. 14 Back-calculated Growth of Roach in Darenth 40



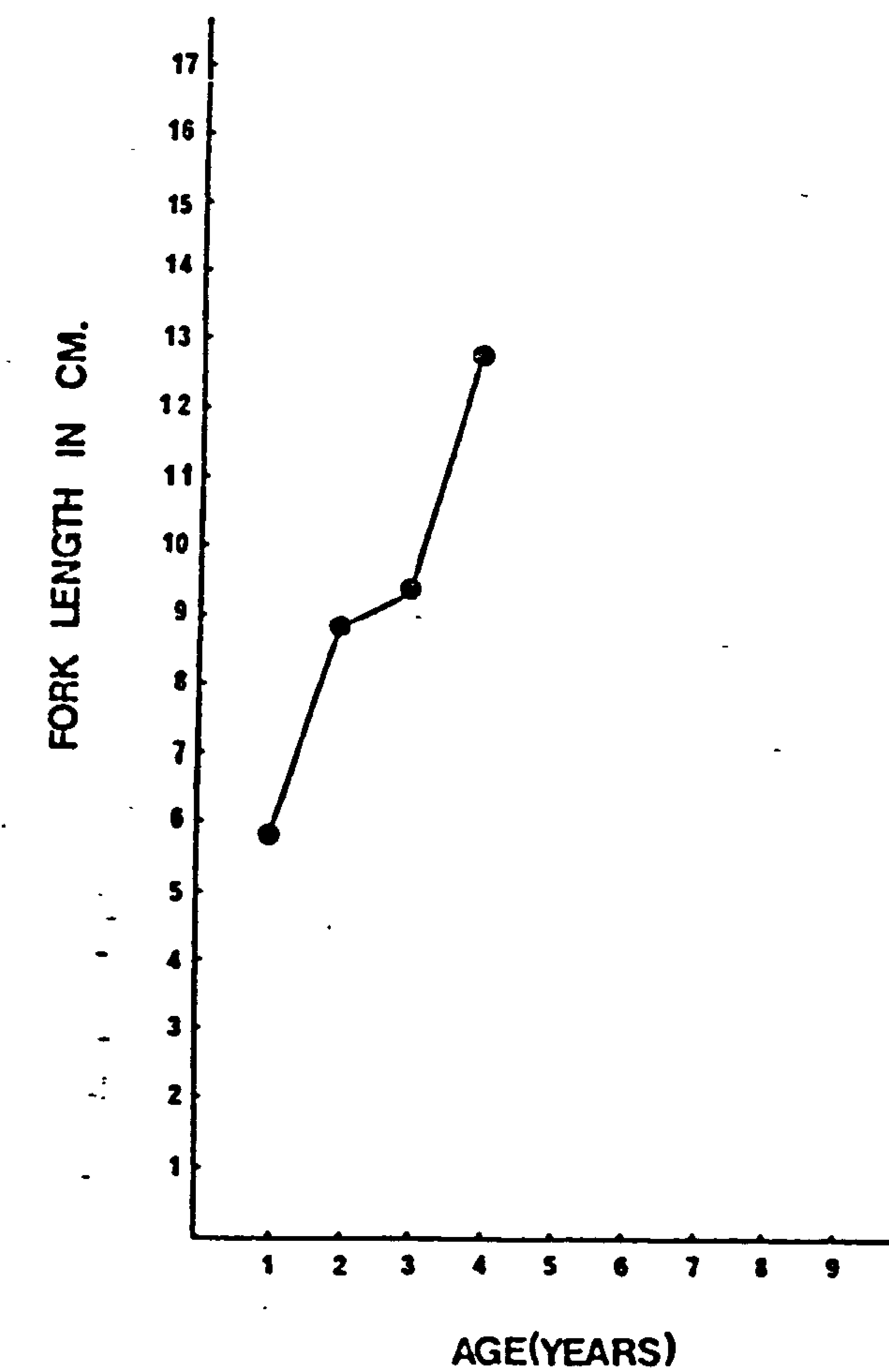
(a) Separate Year-classes

(b) Composite Year-classes

Fig. 15 Back-calculated Growth of Roach in Larkfield 41



(a) Separate Year-classes



(b) Composite Year-classes

Fig. 16 Back-calculated Growth of Roach in Fishers Green 42 seventh to eighth years. In the fourth to fifth year group there are two cases only of significant differences ($P < 0.05$), namely between Farnborough 18(a) and Sutton-at-Hone 35, and Sutton-at-Hone 36 and Fishers Green 42.

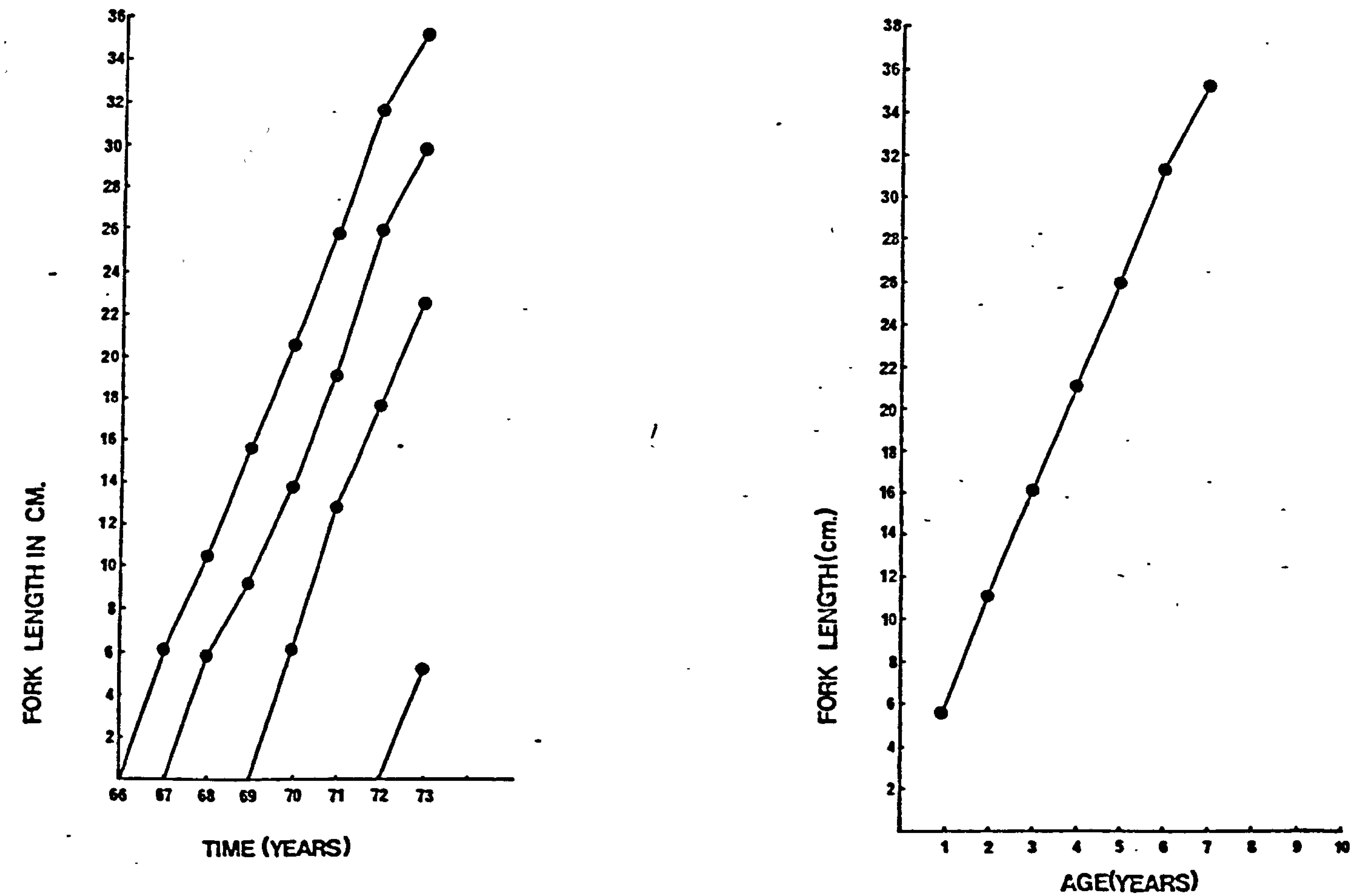
(b) Bream

The bream was the second most abundant fish in the gravel pits surveyed. It did not occur in as many lakes as the roach, but bream, when present, were sometimes more numerous in the samples. Figs. 17-21 show the maximum age of bream caught to be 8 years. Wraysbury 17 and Fishers Green 42 bream have the fastest growth rates, reaching 34-35 cm in 7 years (Figs. 17,21). Larkfield 41 bream reach 29 cm in this time (Fig.20) and Darenth 40 fish, 30 cm in 8 years (Fig. 19). At Sutton-at-Hone the oldest bream were only 5 years of age and 21 cm in length (Fig. 18). Bream over 50 cm were caught during the sampling described in Section 2.4(b). One fish of 45.5 cm from Fishers Green 42 was tentatively aged at 12 years, and one of 50.5 cm from Darenth 39 at 10 years. Kennedy and Fitzmaurice (1968) chose to differentiate between the majority of bream and 'specimen' fish of over 7 lb (3.175 kg), about 50 cm, the latter having a different growth pattern to smaller fish.

Netting experience in gravel-pit lakes indicates that large fish are infrequently encountered in the samples, although they were seen on other visits and in anglers' catches. This may be due to such factors as low probability of meeting the gear, increased ability with age to avoid the gear and possibly some degree of learned avoidance behaviour. Beuekema and de Vos (1974) showed that carp rapidly learned to avoid a seine net.

(c) Rudd

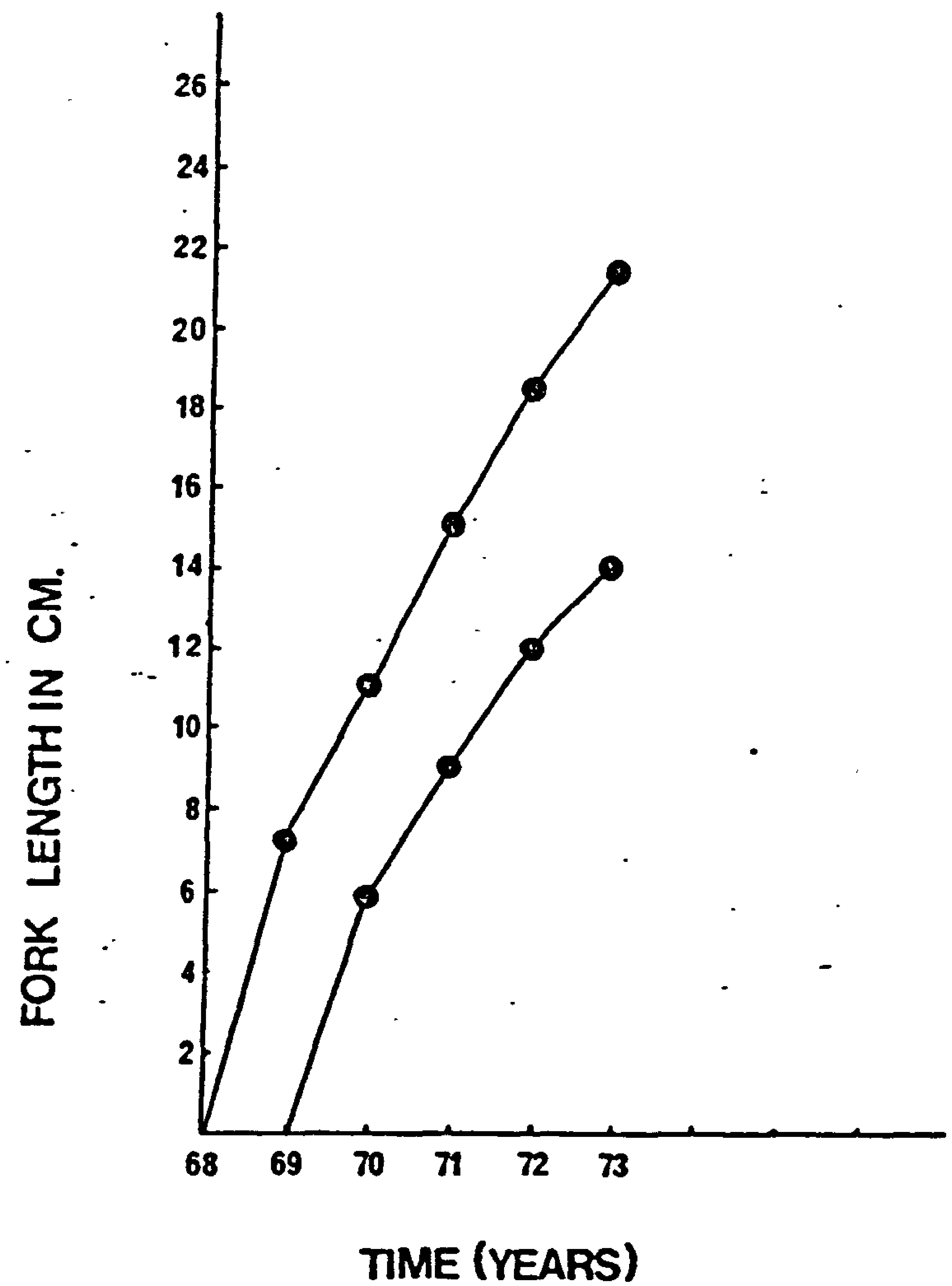
Catches from the gravel pits indicate that rudd are less common than roach or bream in all but two lakes, Kingsmead 15 and Sutton-at-Hone 36. The former is a large lake (39.6 ha) where catches during one day's seining would not be expected to be representative of the fish community,



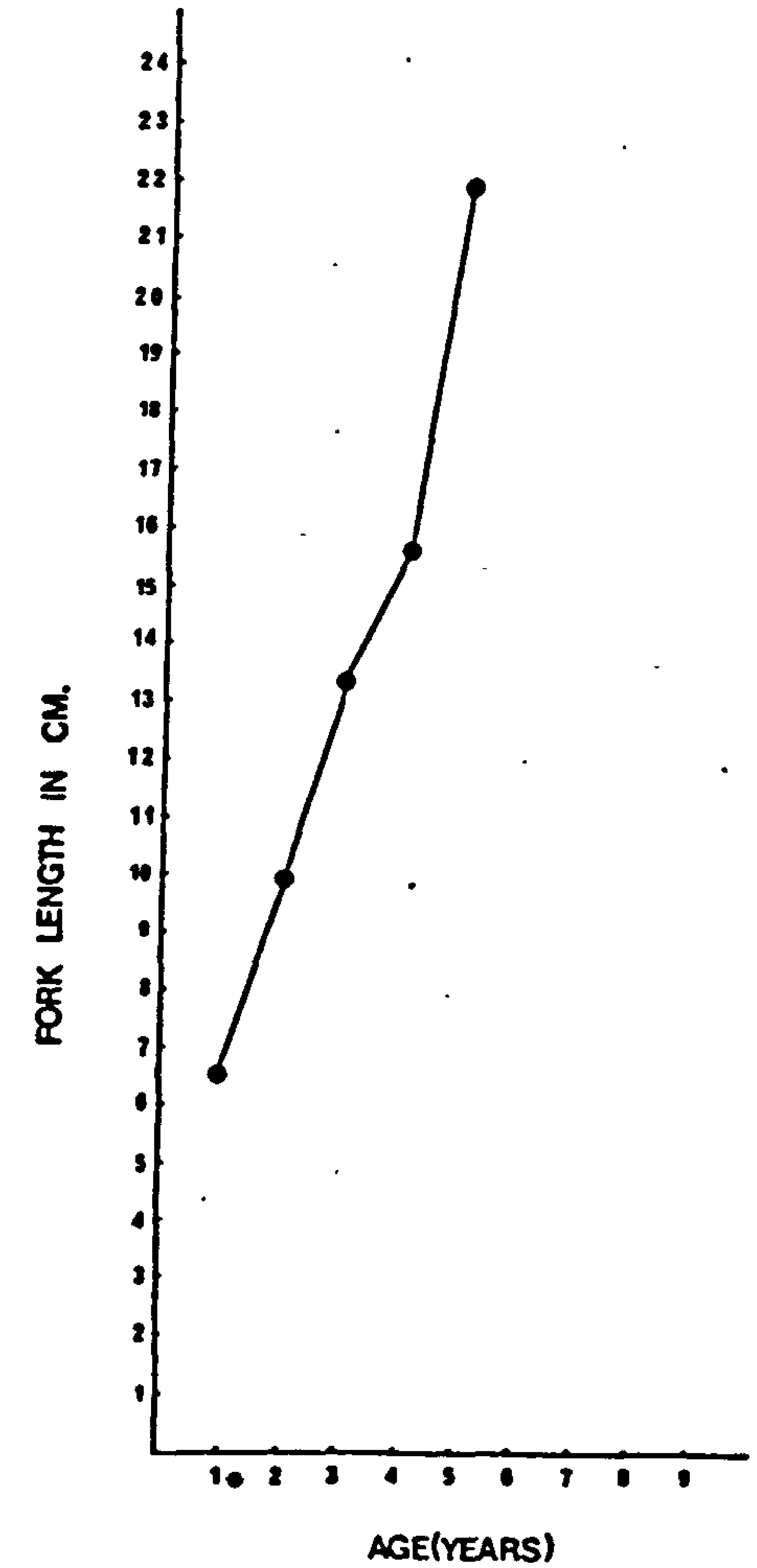
(a) Separate Year-classes

(b) Composite Year-classes

Fig. 17 Back-calculated Growth of Bream in Wraysbury 17

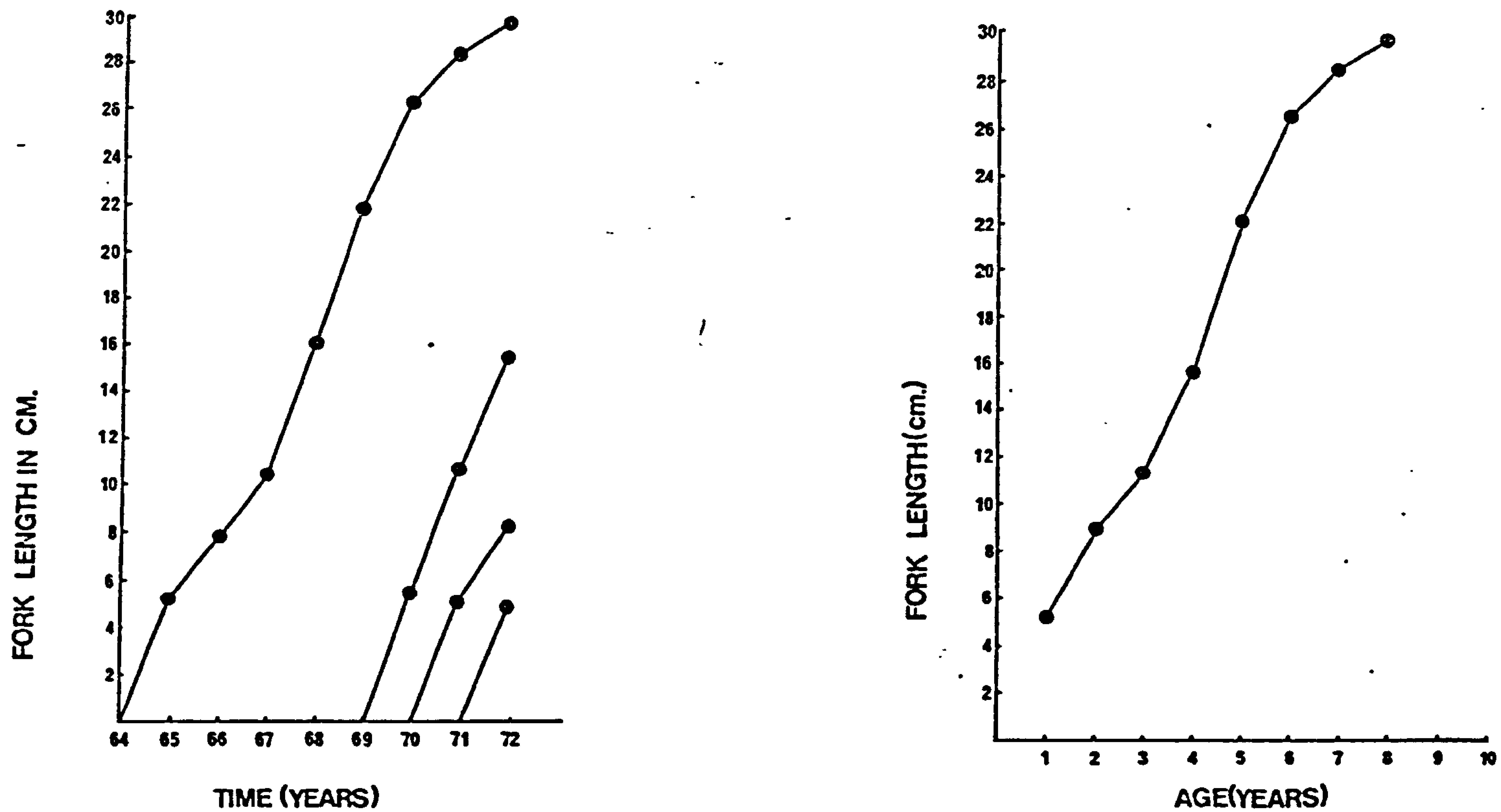


(a) Separate Year-classes



(b) Composite Year-classes

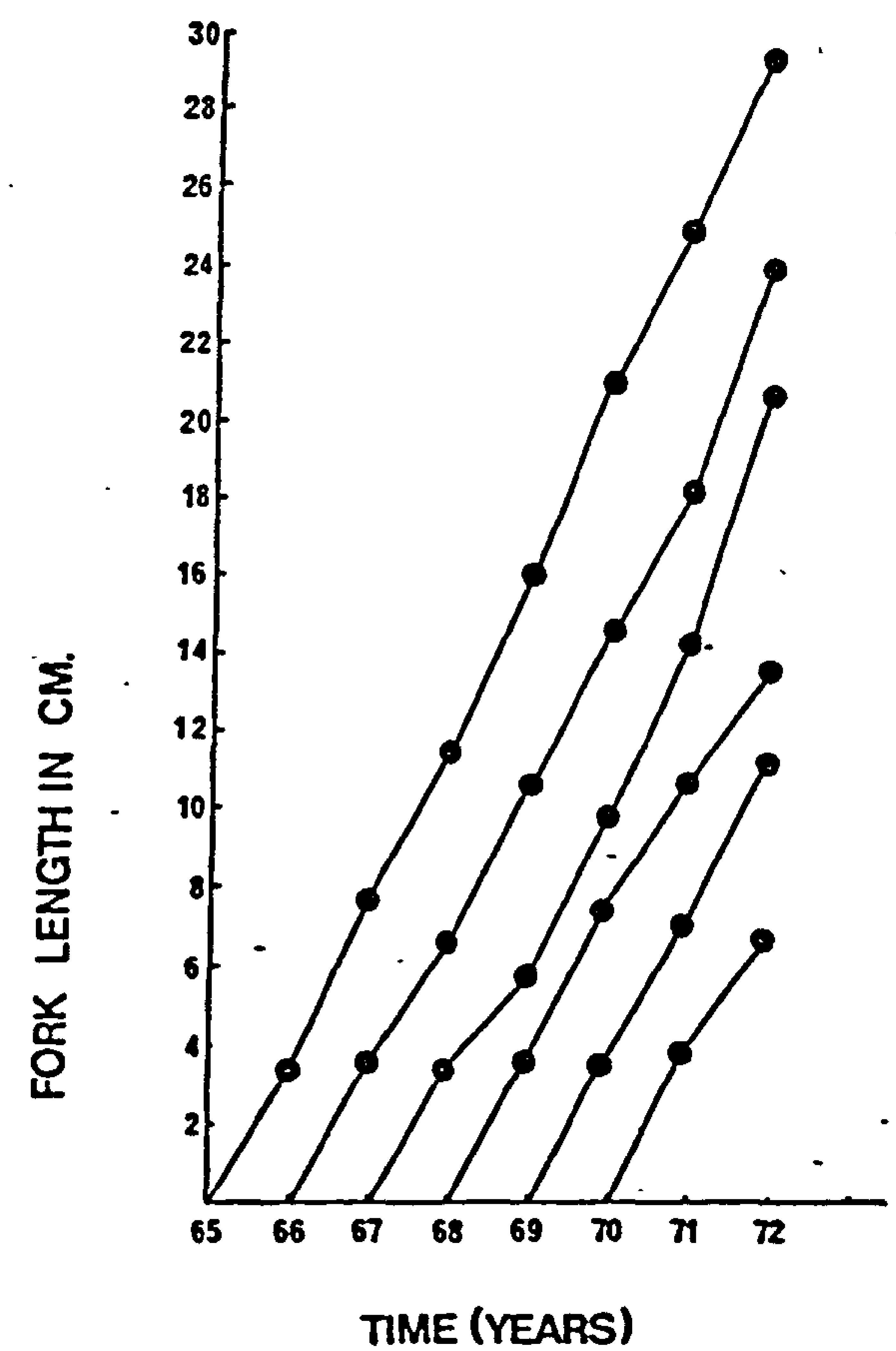
Fig. 18 Back-calculated Growth of Bream in Sutton-at-Hone 35



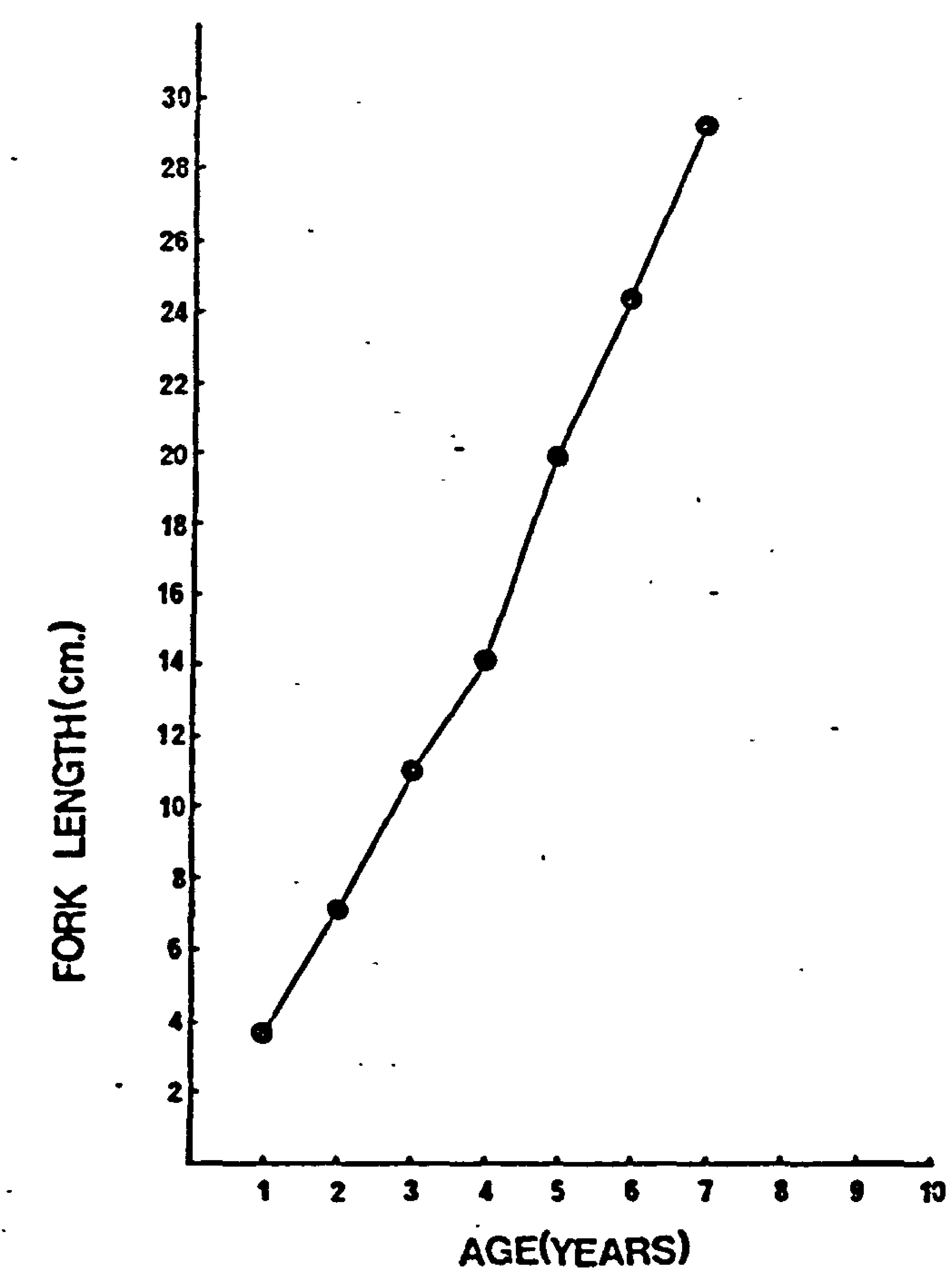
(a) Separate Year-classes

(b) Composite Year-classes

Fig. 19 Back-calculated Growth of Bream in Darenth 40

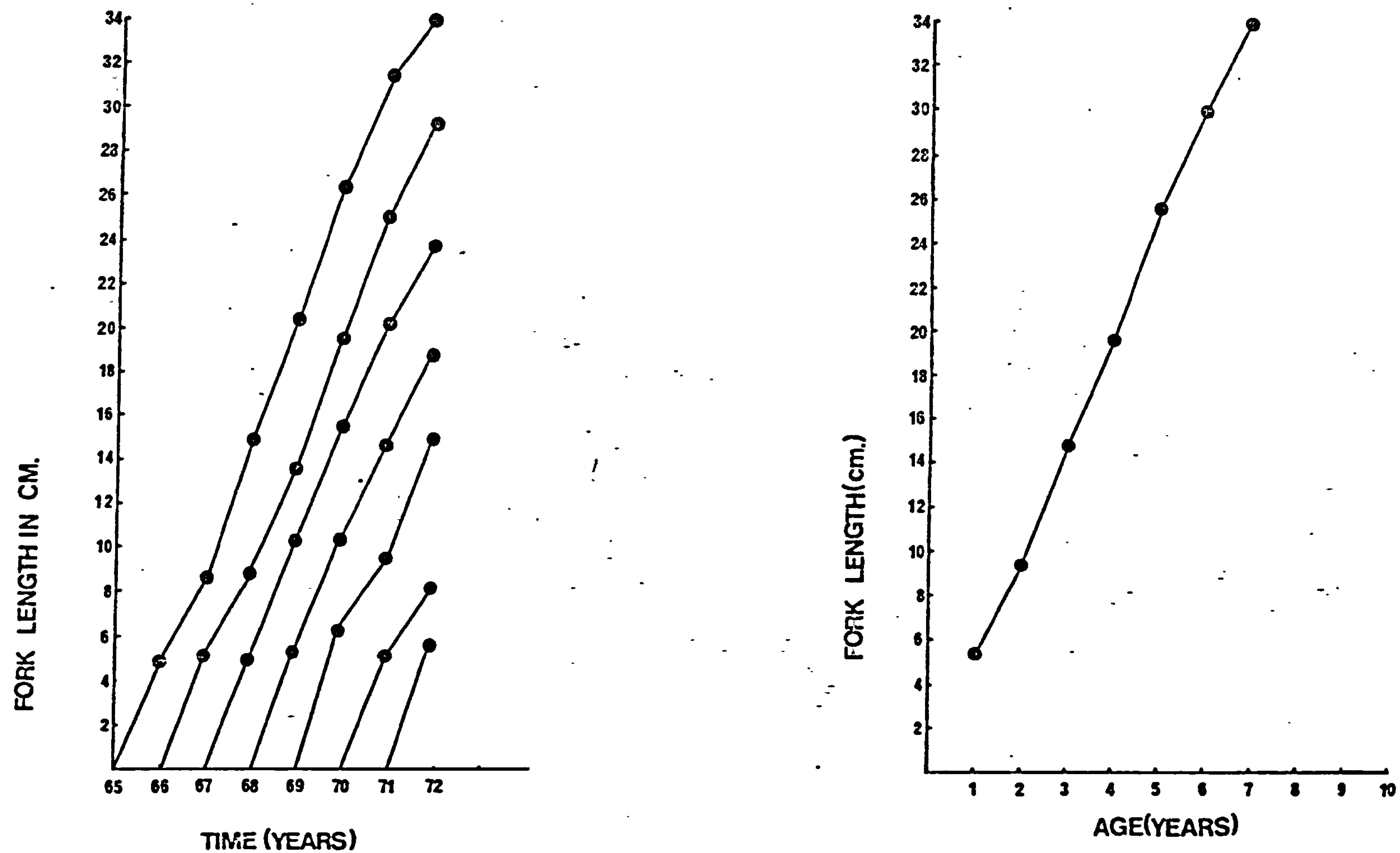


(a) Separate Year-classes



(b) Composite Year-classes.

Fig. 20 Back-calculated Growth of Bream in Larkfield 41



(a) Separate Year-classes

(b) Composite Year-classes

Fig. 21 Back-calculated Growth of Bream in Fishers Green 42 though many rudd and tench were caught. Sutton-at-Hone 36 in contrast is a very small lake (0.8 ha) with a high fish density. Survey catches indicated that rudd was the most numerous species present; this was subsequently verified by netting in July 1973.

Figs. 22-26 show that the growth achieved in the first year varies from 2.9 cm in Yateley 9 to 5.6 cm in Sutton-at-Hone 36. Lengths at 2 years-of-age vary from 6.4 cm in Darenth 39 to 9.9 cm in Sutton-at-Hone 36. The 1967 year-class of rudd in Sutton-at-Hone 36 grew very well, overtaking both the 1964 and 1965 year-classes.

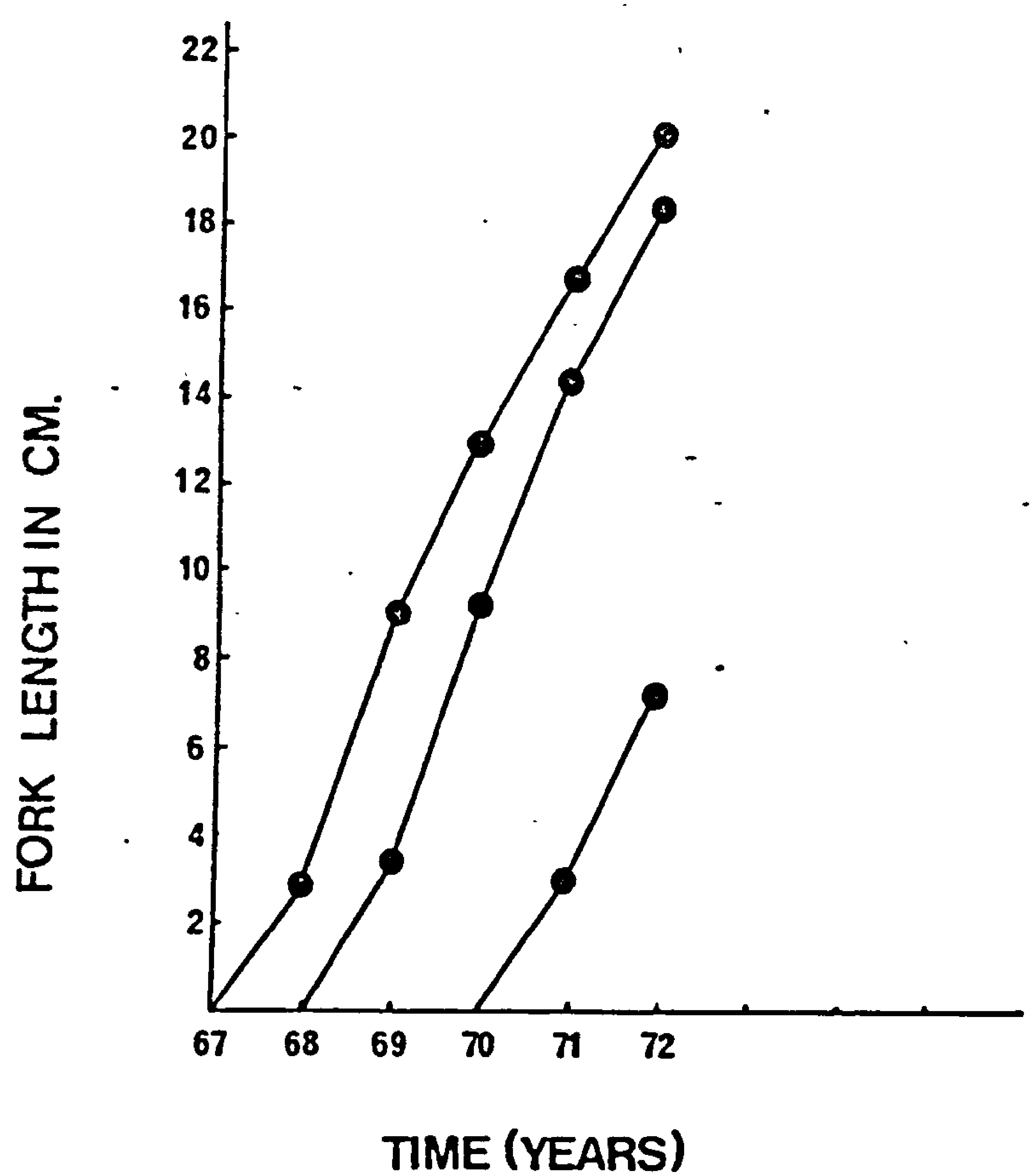
The most notable character of the rudd examined was the proximity of the first check mark to the scale centre in relation to subsequent checks, as shown by the back-calculated lengths in figs.22-26. There is no evidence available to explain this phenomenon.

(d) Bleak

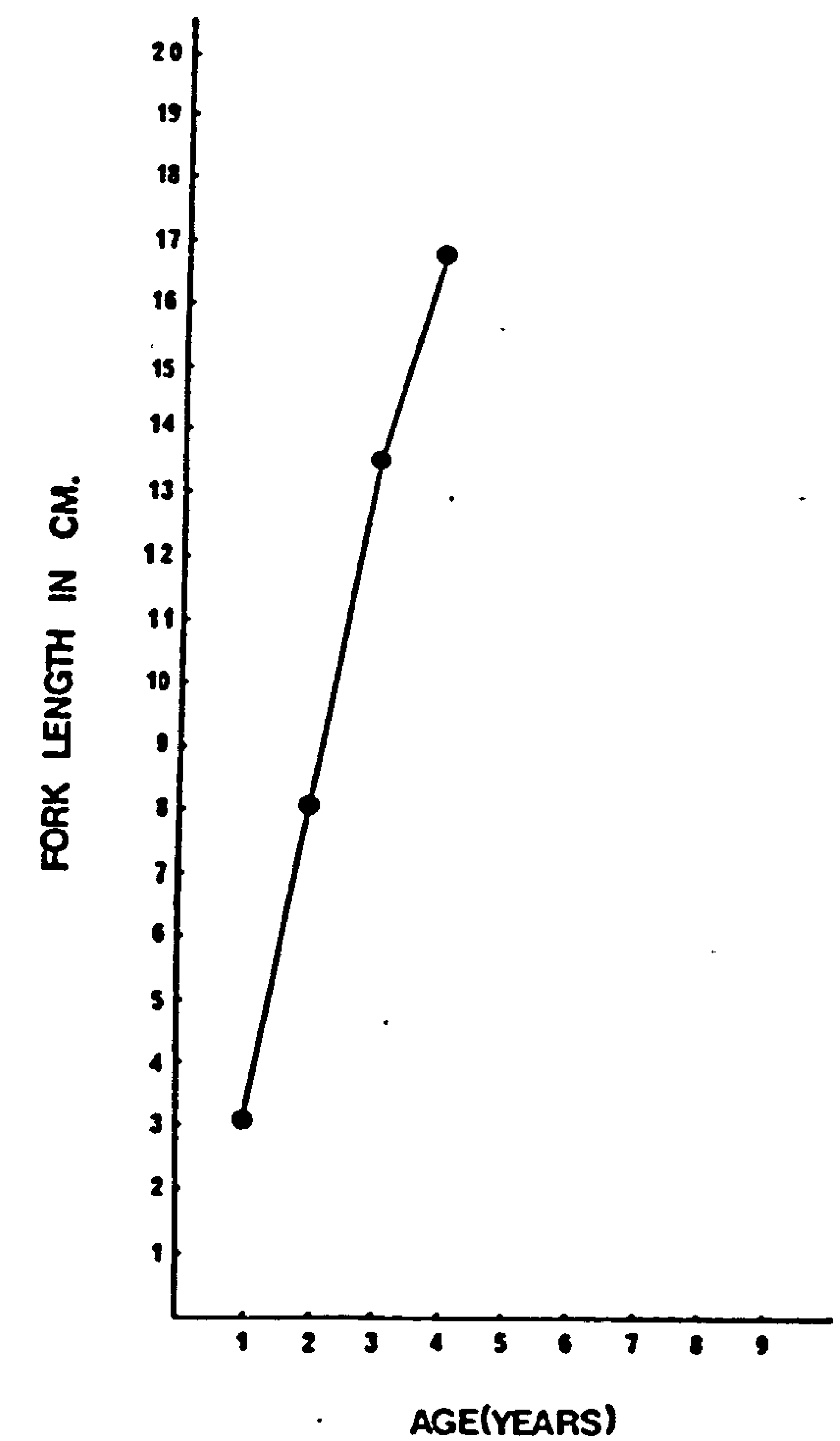
Bleak were caught in large numbers in only two gravel pits (Chertsey 12 and Fishers Green 42), both of which are large. Bleak occurred in large shoals, individuals ranging in size from 5 to 15 cm. Figs. 27 and 28 show that the fish caught were less than 3 years old.

Bleak are commonly found in flowing waters and their occurrence in small lakes is possibly a result of accidental introduction from neighbouring streams, or as a result of livebaiting by anglers in pursuit of pike. The presence of large shoals of bleak suggests that once introduced they breed successfully in gravel-pit-lakes.

River Thames bleak (Williams, 1967), in conditions of high density, grew up to 9.5 cm in 3 years, a rate similar to those of Chertsey 12 (Fig. 27). Much faster growth is shown by bleak from Fishers Green 42 (Fig. 28). Both lakes 12 and 42 are very large gravel pits and have streams running through them. Unfortunately, there is no information available on the relative densities of the fish communities in the two lakes.

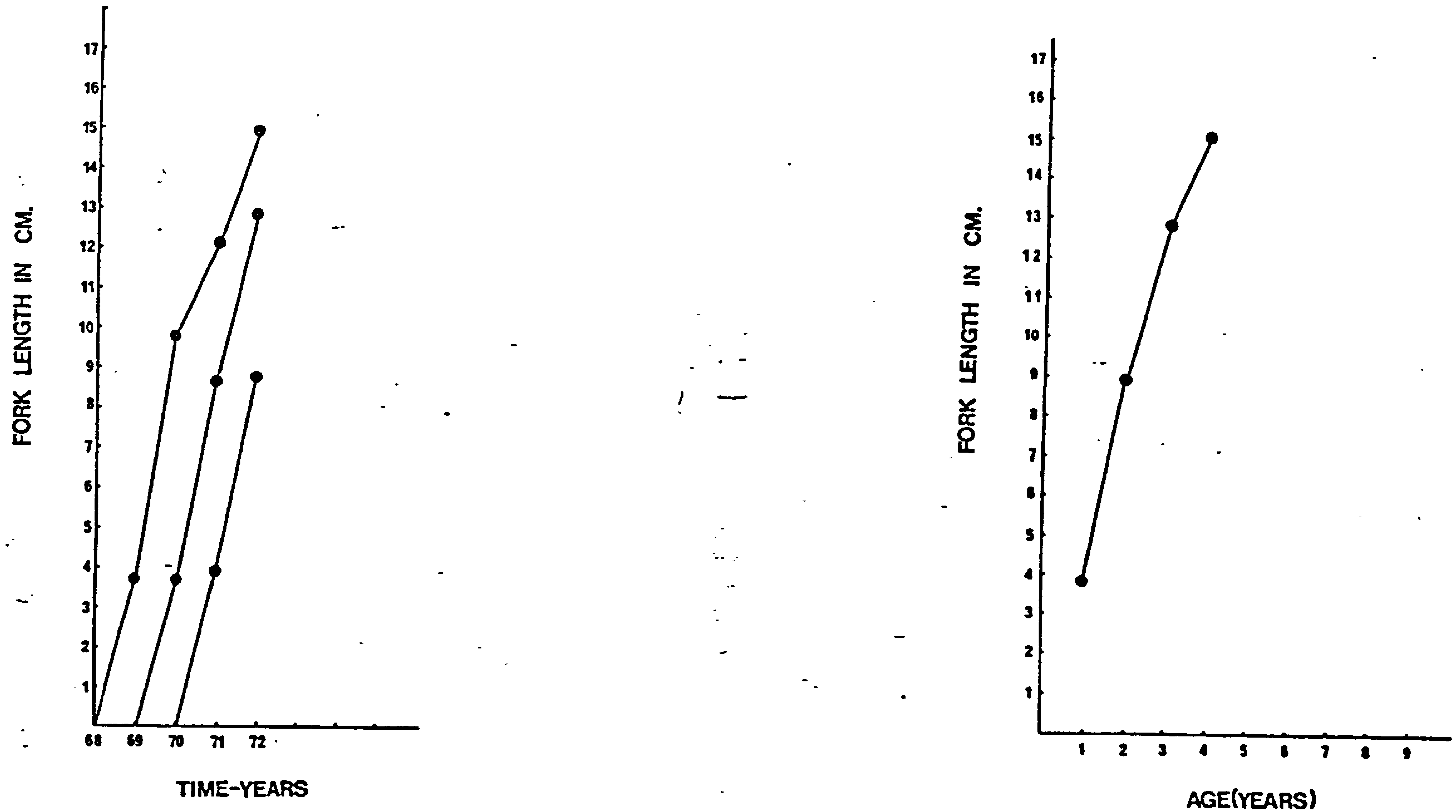


(a) Separate Year-classes



(b) Composite Year-classes

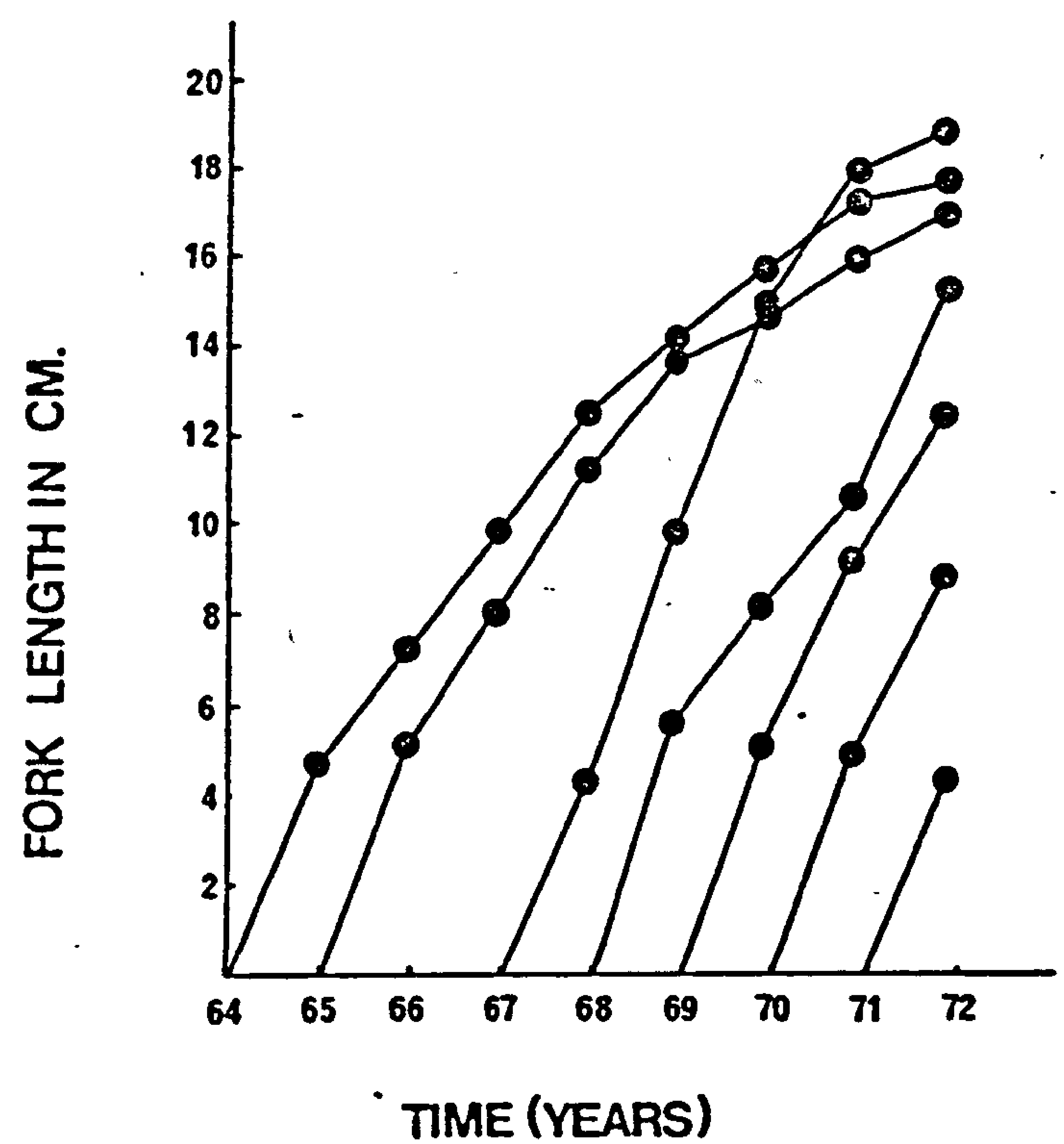
Fig. 22 Back-calculated Growth of Rudd in Yateley 9



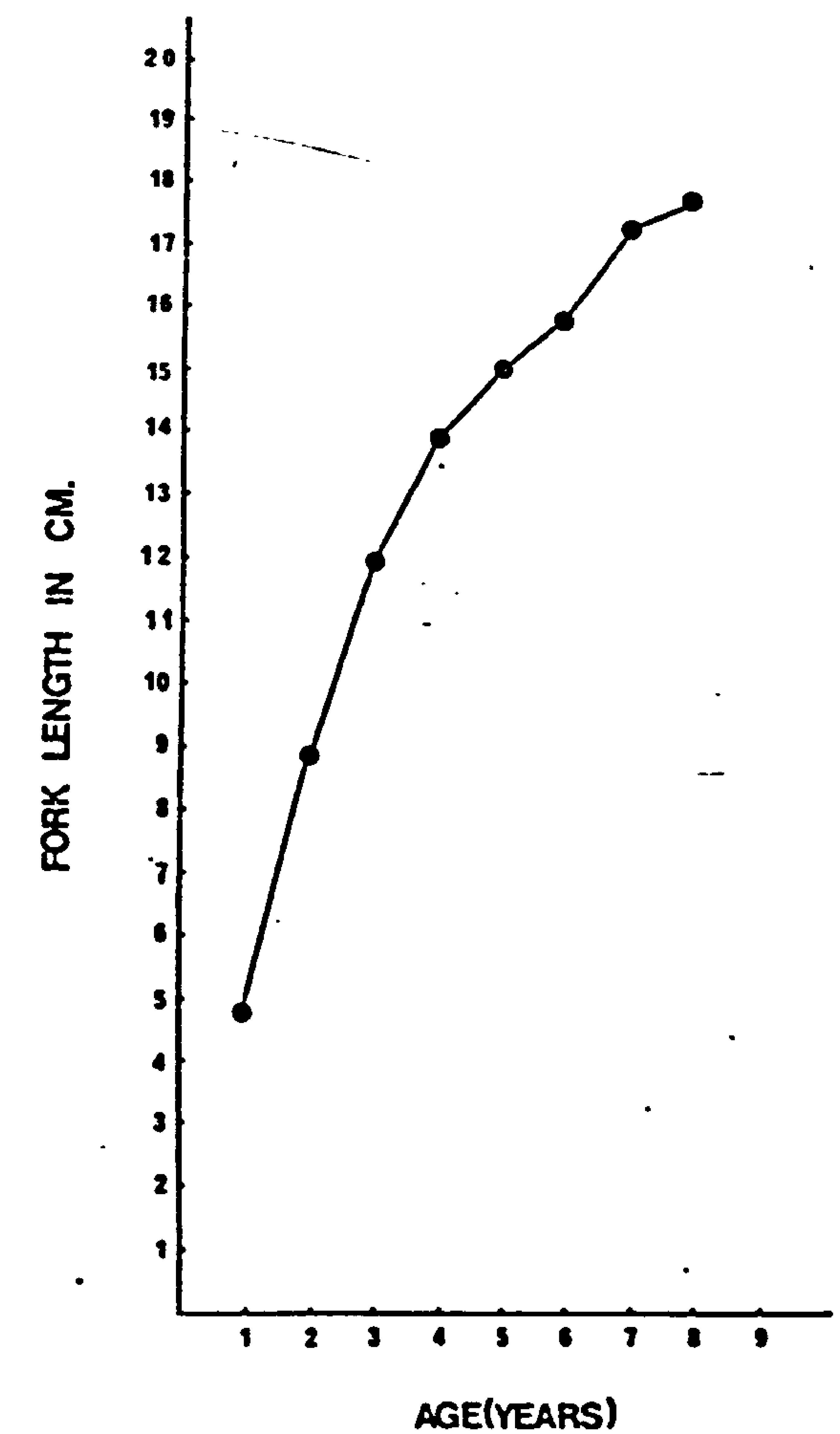
(a) Separate Year-classes

(b) Composite Year-classes

Fig. 23 Back-calculated Growth of Rudd in Kingsmead 15

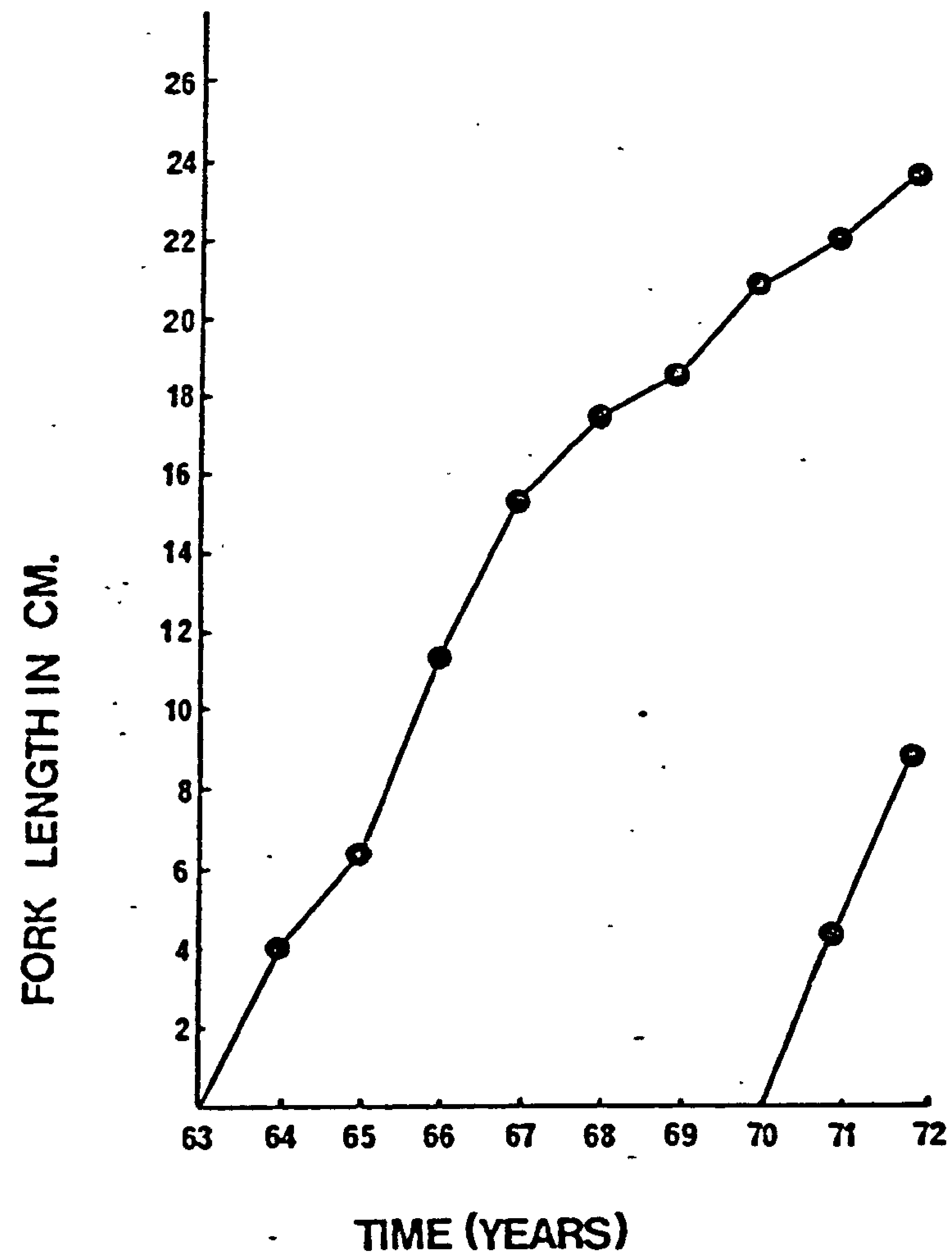


(a) Separate Year-classes

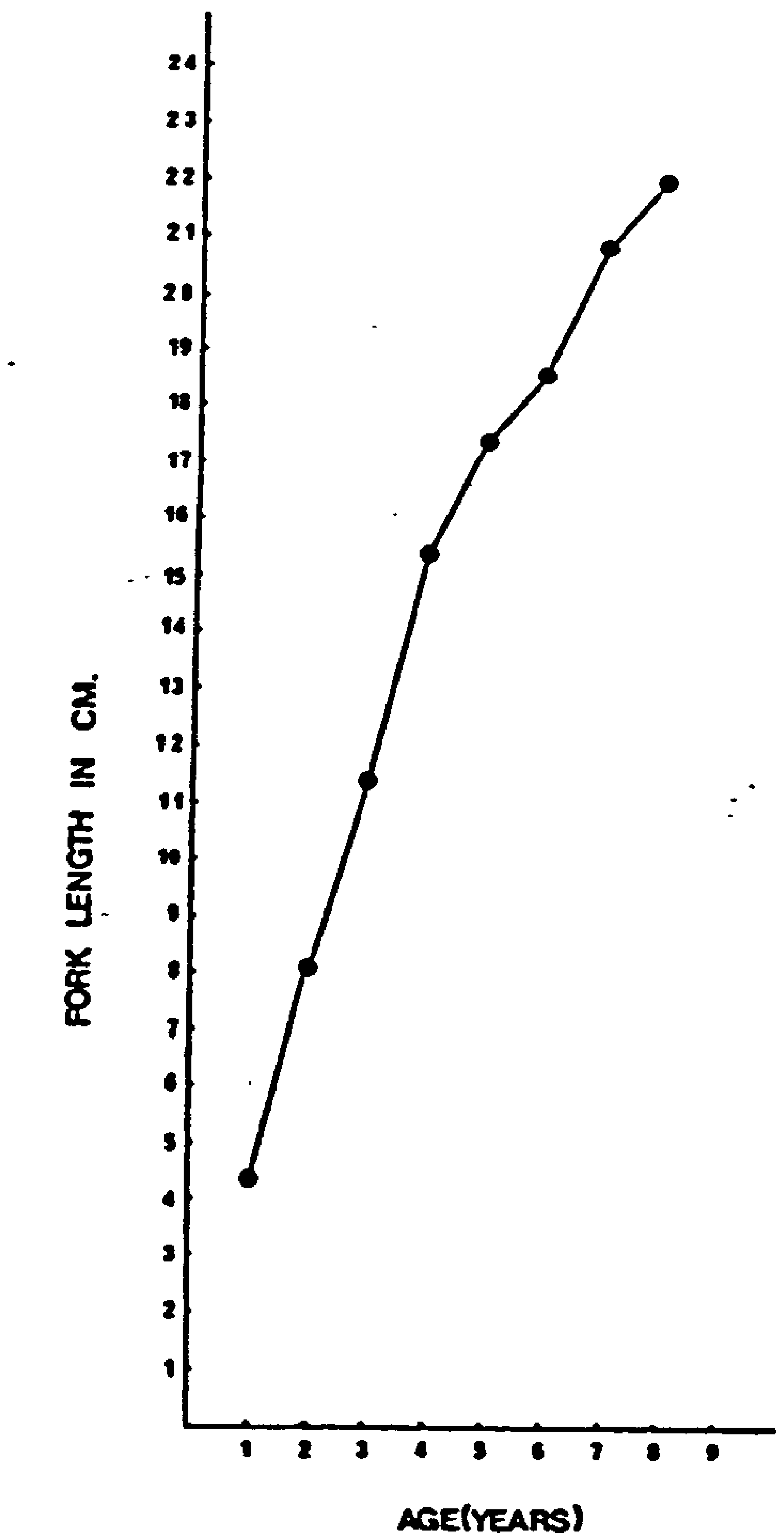


(b) Composite Year-classes

Fig. 24 Back-calculated Growth of Rudd in Sutton-at-Hone 36

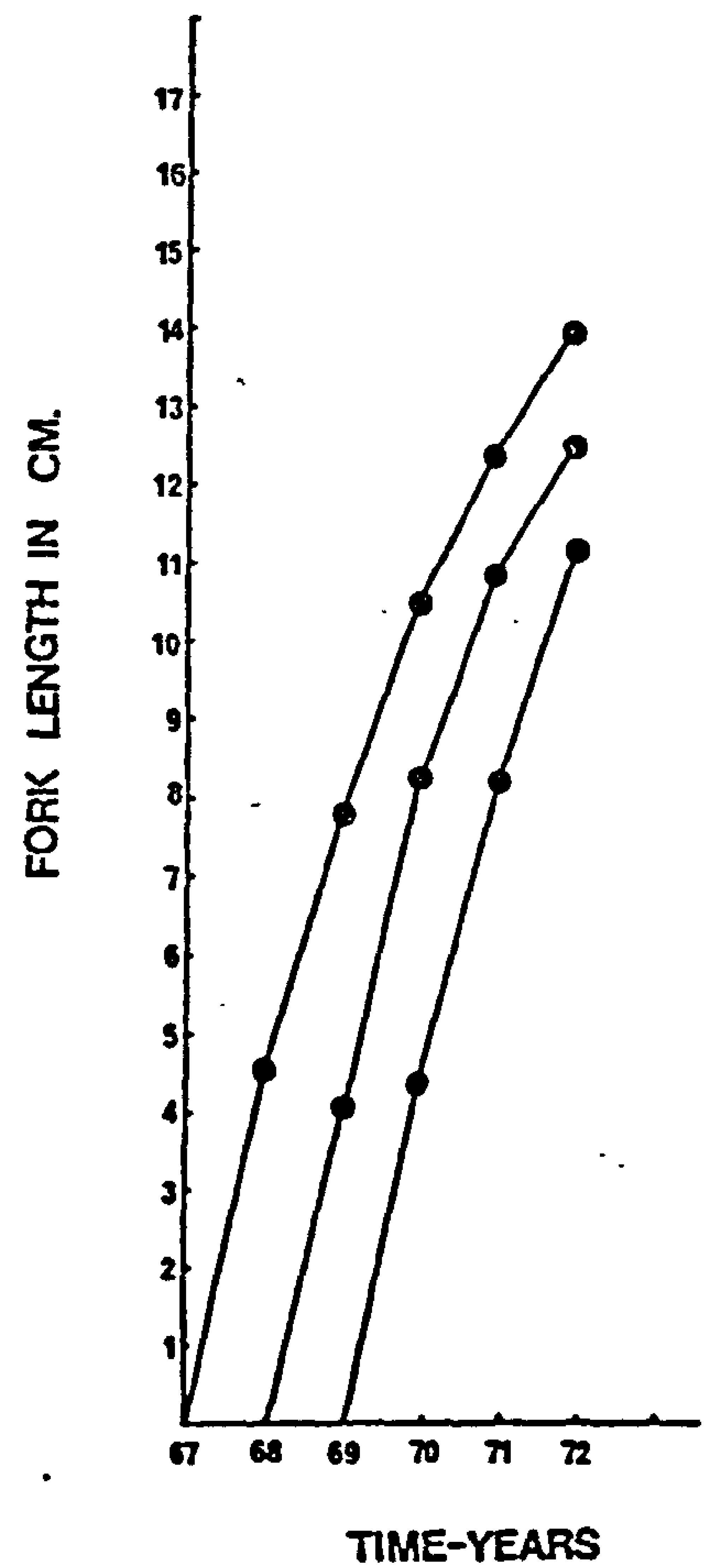


(a) Separate Year-classes

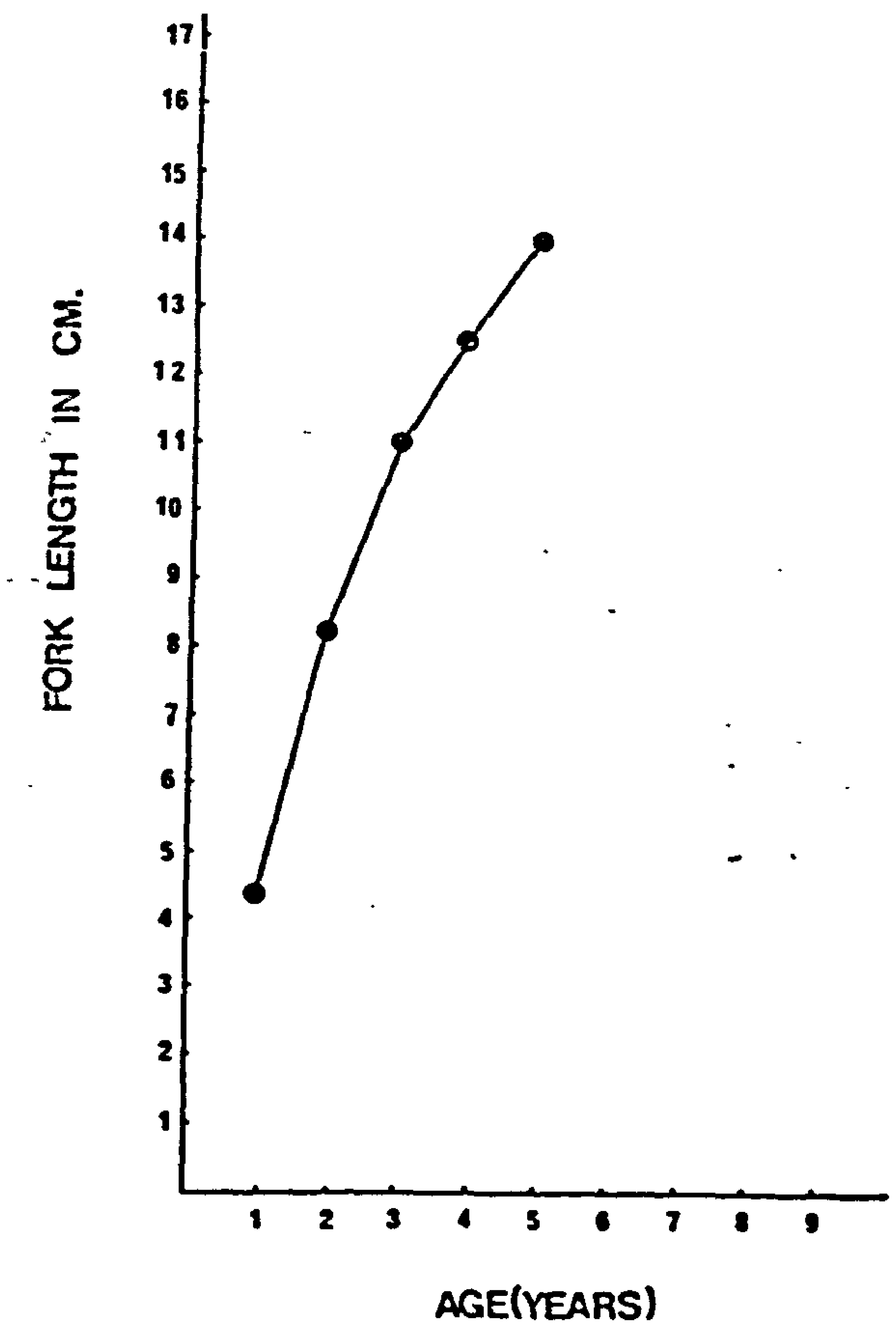


(b) Composite Year-classes

Fig. 25 Back-calculated Growth of Rudd in Darenth 39

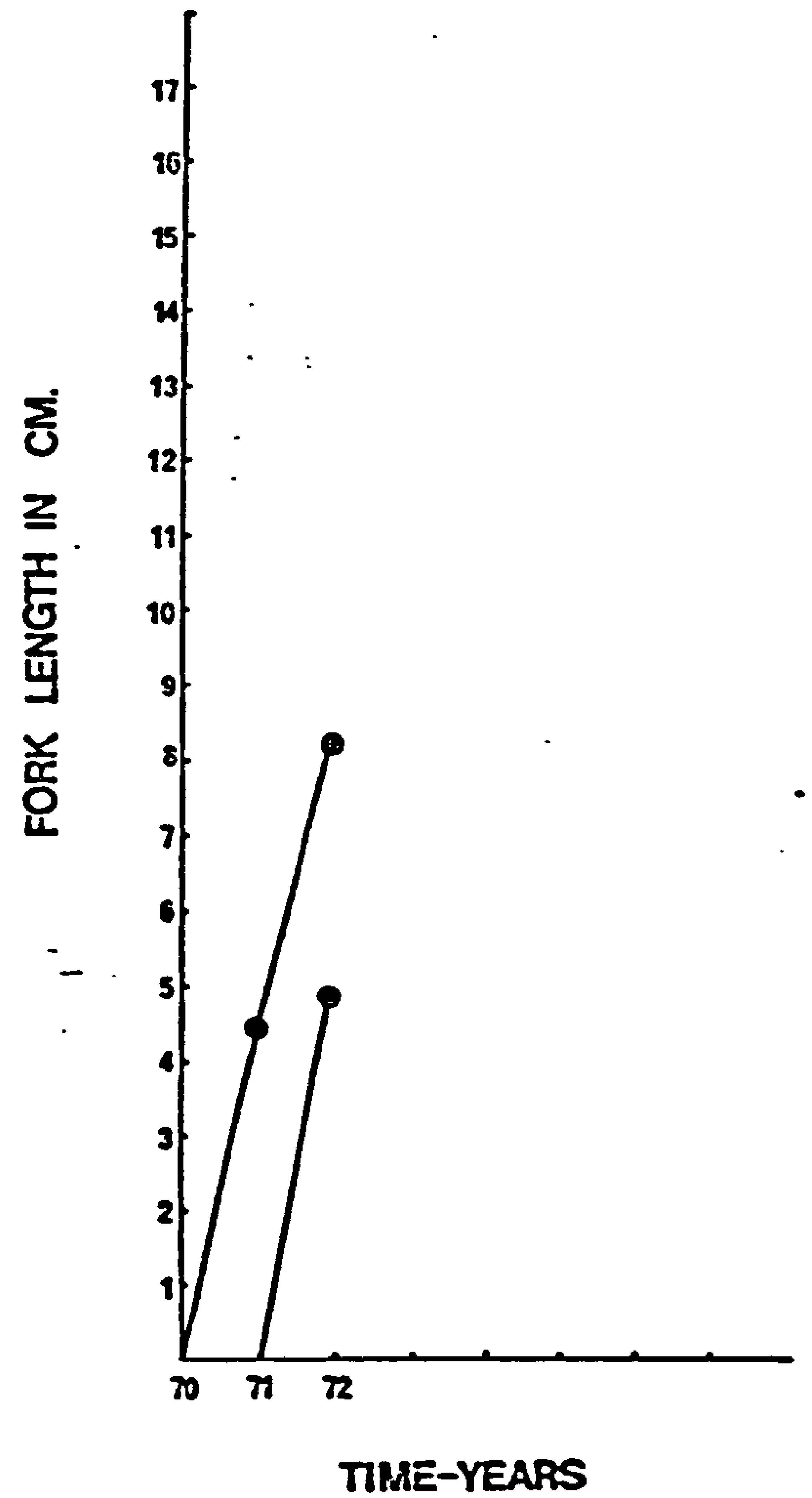


(a) Separate Year-classes

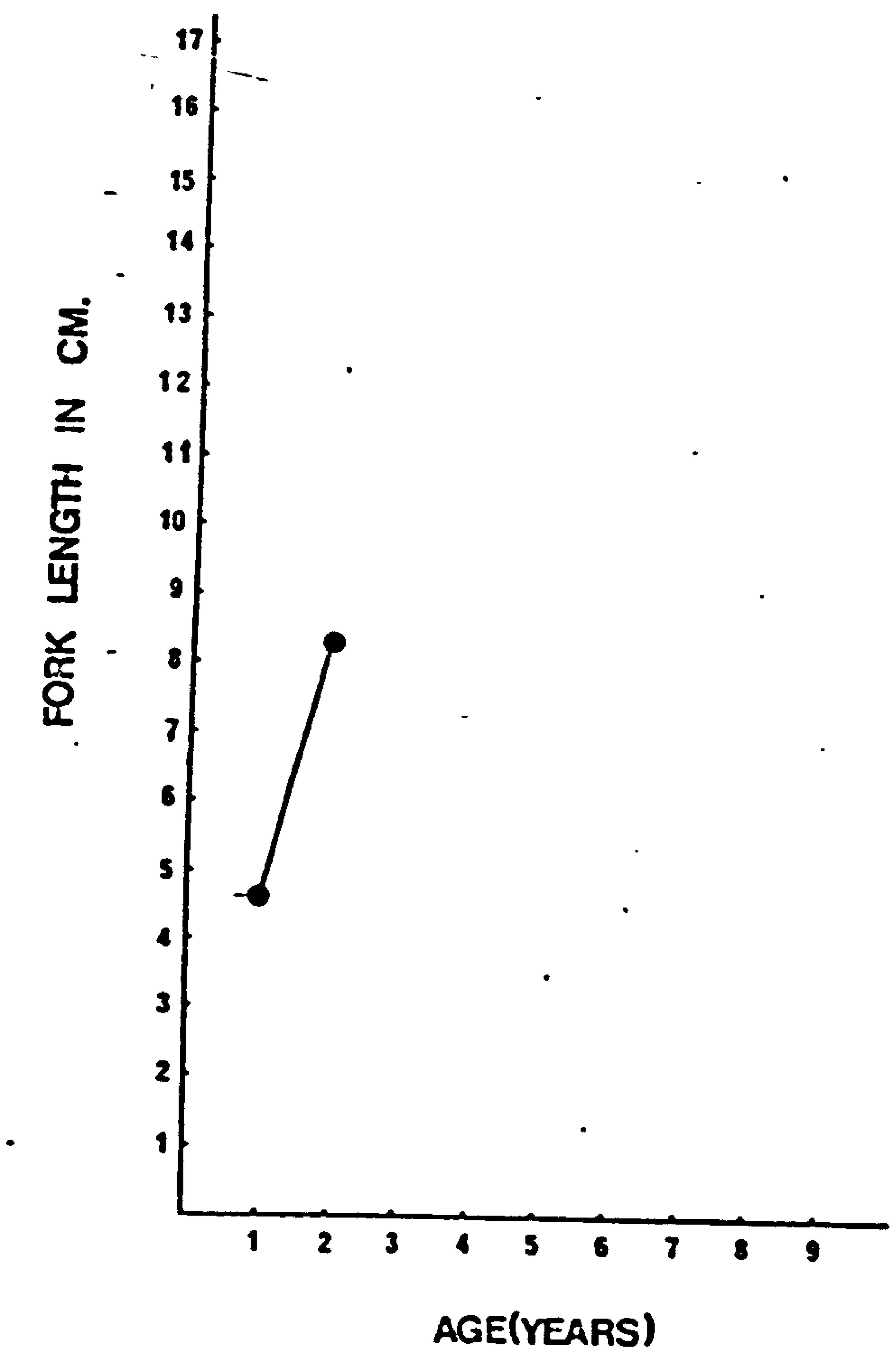


(b) Composite Year-classes

Fig. 26 Back-calculated Growth of Rudd in Darenth 40

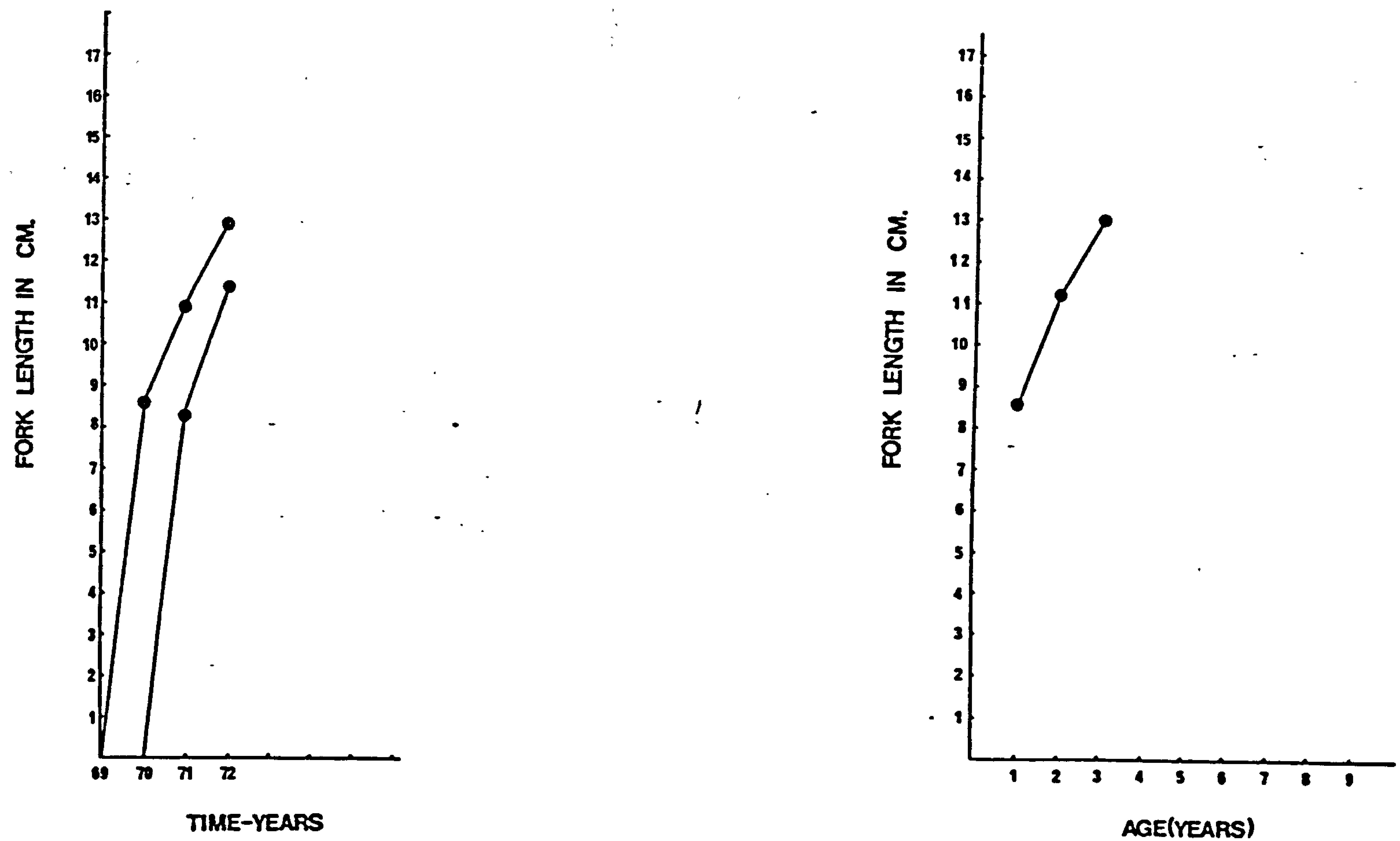


(a) Separate Year-classes



(b) Composite Year-classes

Fig. 27 Back-calculated Growth of Bleak in Chertsey 12



(a) Separate Year-classes

(b) Composite Year-classes

Fig. 28 Back-calculated Growth of Bleak in Fishers Green 42

(e) Perch

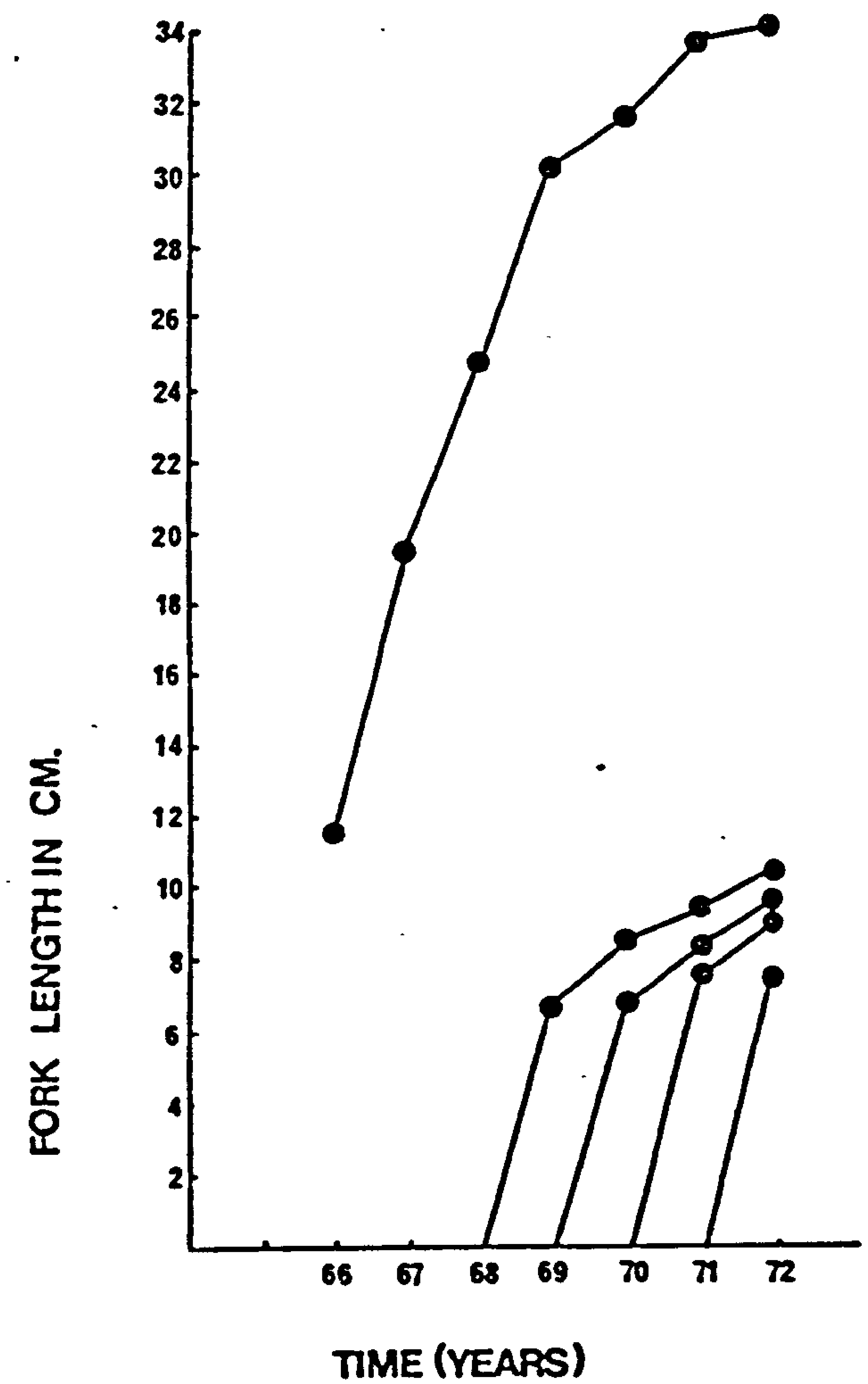
Though widespread in distribution in Britain and Europe, the perch is rarely a dominant species in those gravel-pit lakes surveyed. It was found in samples from 29 out of 39 lakes (Table 6) and was represented by large numbers of small fish, of age 0+ and 1+; larger, older fish rarely occurring, at least in the seine net catches. In only three lakes, (Farnborough 18(a), Twyford 32 and 33, were large, older fish taken in the seine net, and in the last two perch dominate the fish fauna.

Figs. 29-31 show the growth curves for perch from Farnborough 18(a), Twyford 32 and Twyford 33. The growth achieved in the first year varies from 6.3 cm in Twyford 32 to 8.1 cm in Twyford 33, and that in the second year from 8.5 cm in Farnborough 18(a) to 12.6 cm in Twyford 32. One perch of 34.0 cm was caught in Farnborough 18(a) and aged at 7+; it was the largest and oldest perch caught during the survey.

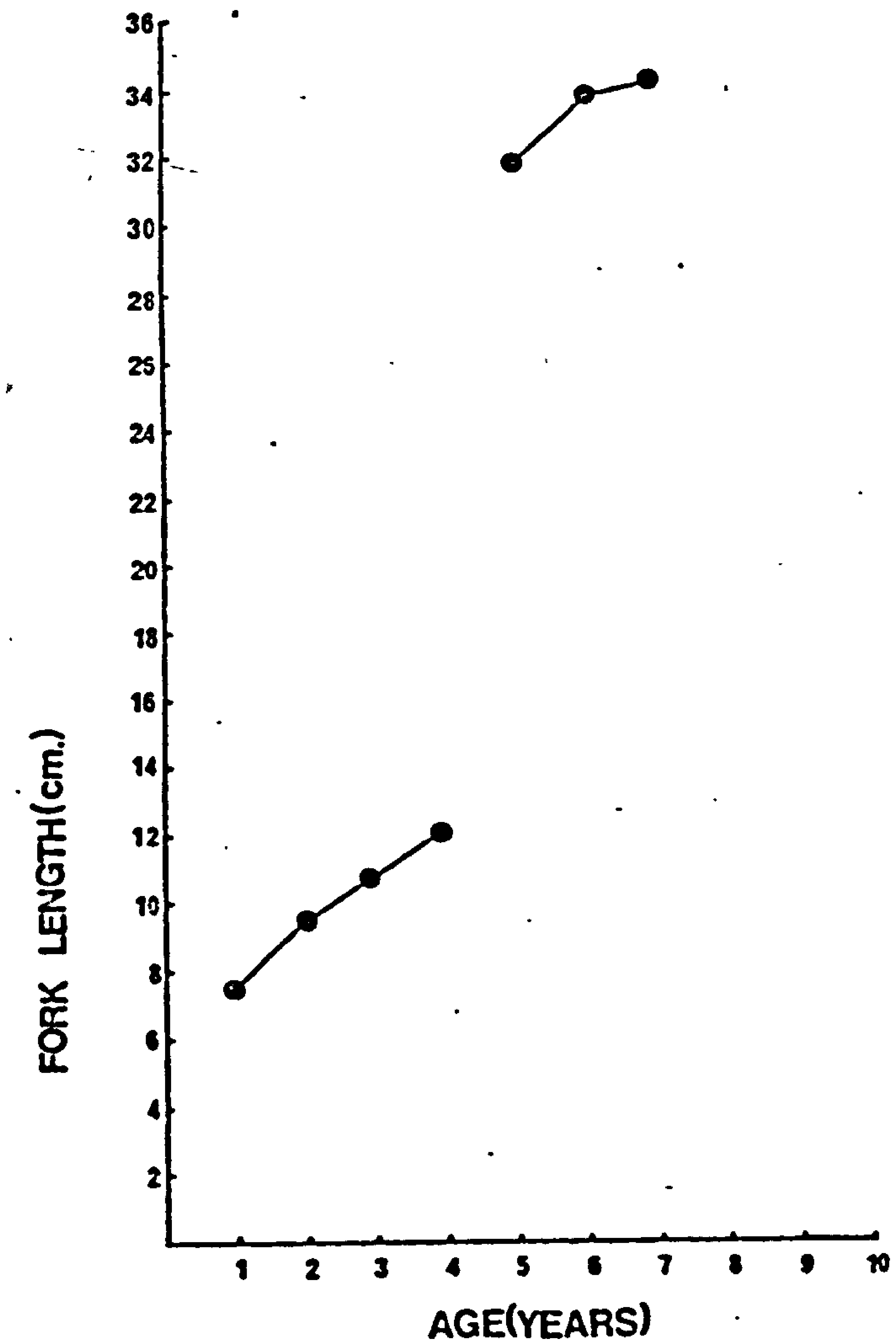
(f) Pike

Difficulty in reading the scales and the necessity to return most of the pike resulted in there being insufficient data for accurate growth rate estimation. Pike are present in the majority of gravel-pit lakes but occur in large numbers only in the presence of large perch populations (Table 6), as discussed on p.101. In Twyford 32 and 33 pike and perch were the commonest species caught; perch is by far the commonest food of the pike (Toner and Lawler, 1969).

Though variable, the growth rate of pike in the gravel pits is of the order: age 1 - 20 cm; age 2 - 30 cm; age 3 - 40 cm; age 4 - 50 cm. These lengths-at-age are similar to those described as 'medium' by Frost and Kipling (1959) for Windermere pike. Compared with Irish pike they are slow-growing (Healy, 1956), similar to Barnagrow lake. Some Irish pike grow to as much as 27 cm in their first year and reach up to 50 cm at two years of age.

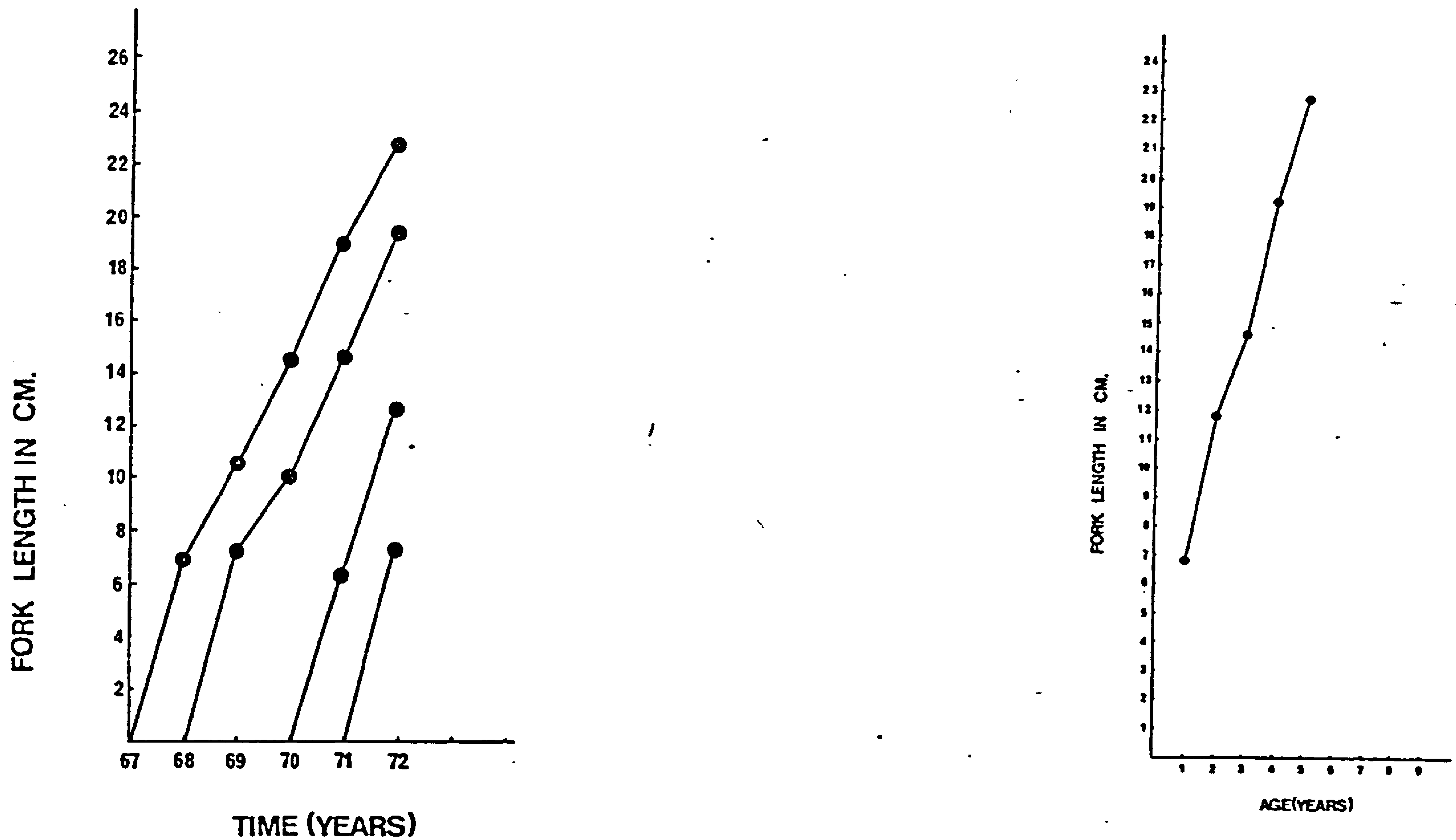


(a) Separate Year-classes



(b) Composite Year-classes

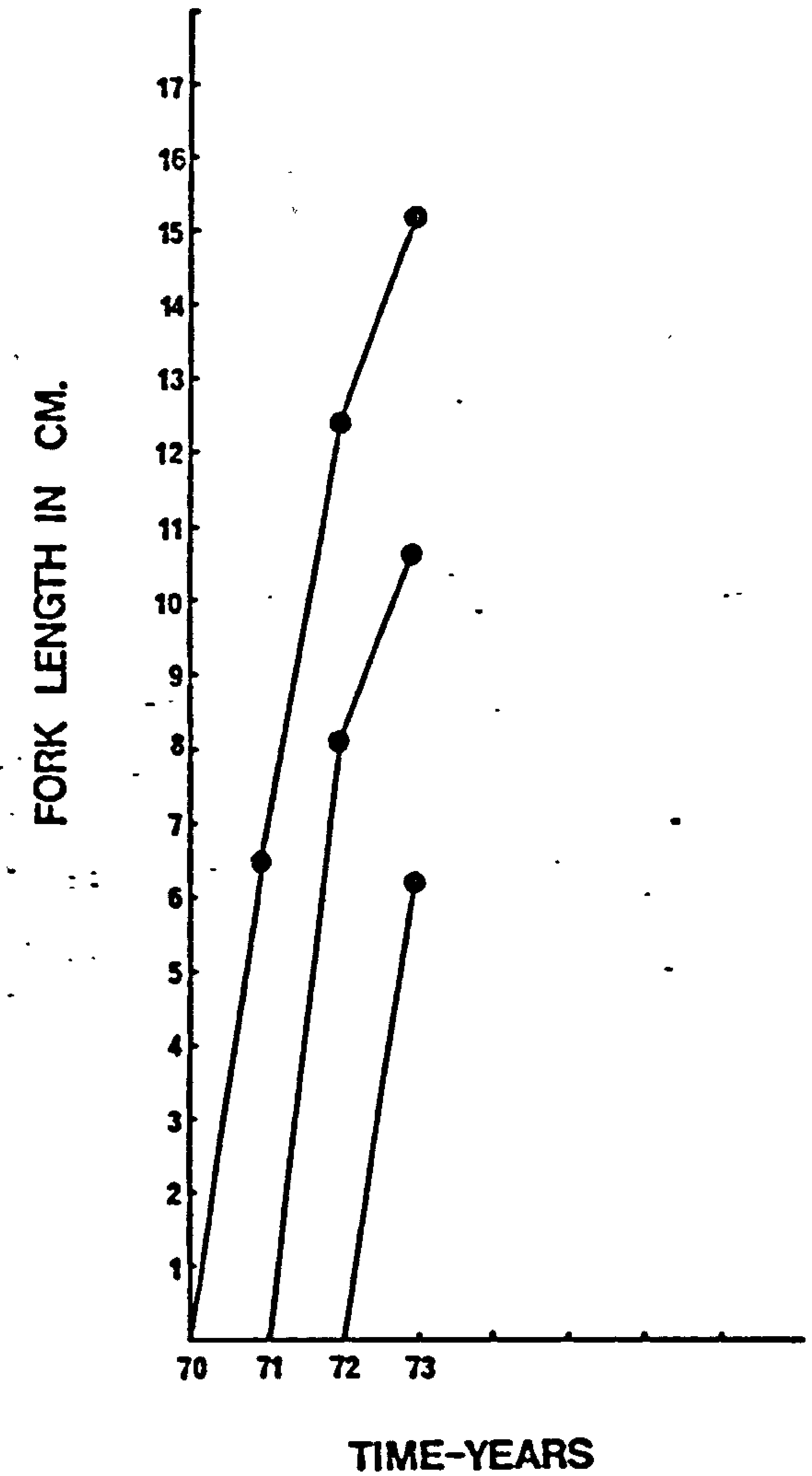
(Fig. 29 Back-calculated Growth of Perch in Farnborough 18(a)



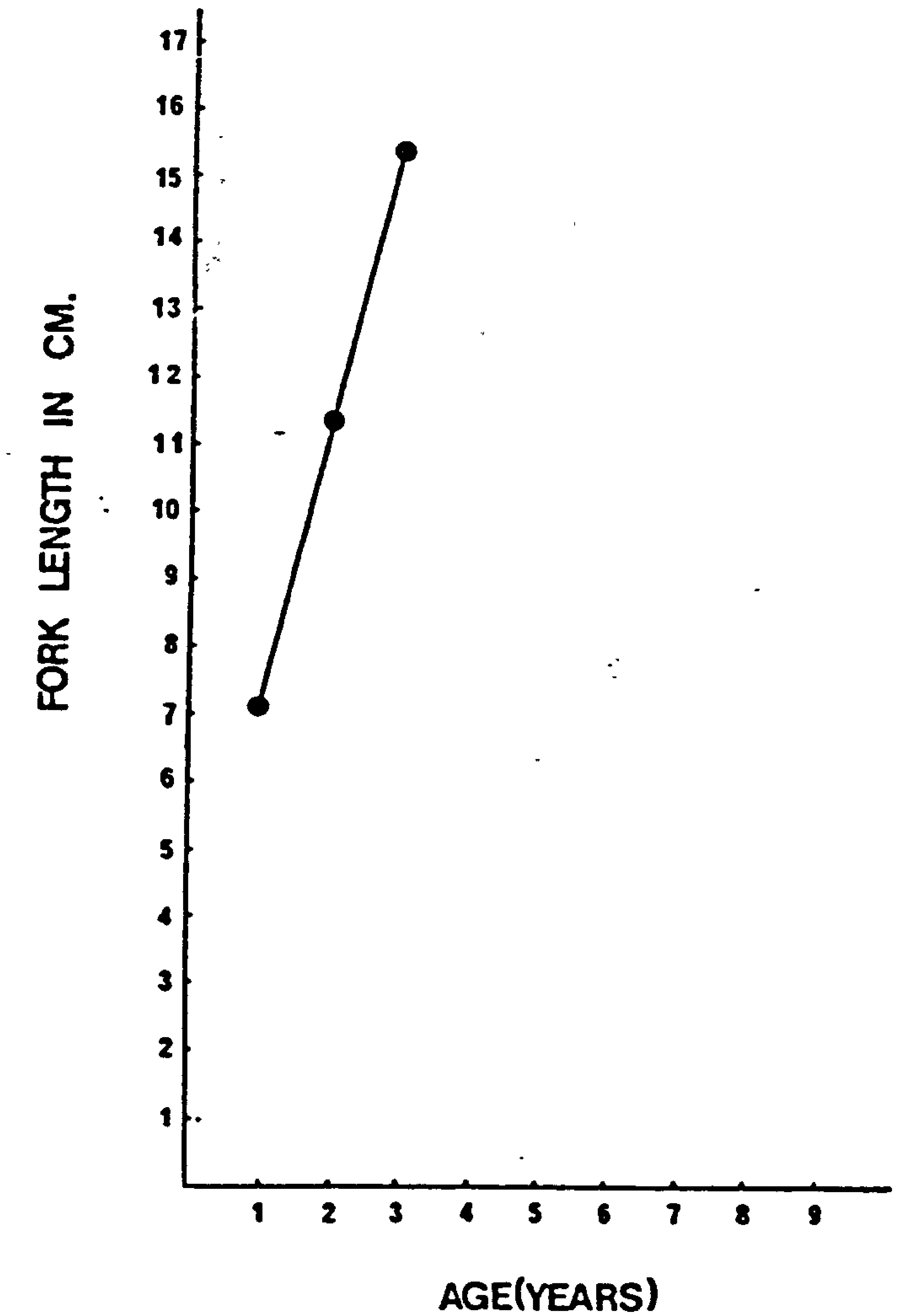
(a) Separate Year-classes

(b) Composite Year-classes

Fig. 30 Back-calculated Growth of Perch in Twyford 32



(a) Separate Year-classes



(b) Composite Year-classes

Fig. 31 Back-calculated Growth of Perch in Twyford 33

(g) Tench

The scales of tench were impossible to read though Weatherley (1959) claims to have had no difficulty. It was not possible to remove many tench so the number of opercula taken was small. Those opercula obtained were found to be extremely difficult to read, bones often having a large number of indistinct opaque and translucent zones. The majority of tench caught during the survey were 30-35 cm in length so that their opercula were very thick, and checks obscure.

During investigations not directly concerned with this survey a large sample of tench was obtained from a small gravel pit at Farnborough (18(b)) which had at one time been part of lake 18(a). The opercula of some of these fishes are shown in Plate 2. Four or five 'checks', similar in appearance to those on perch and pike opercula, are clearly visible. Lengths-at-age were back-calculated assuming these marks to be annual checks (Appendix 1; fig. 32). The implied rapid growth at the beginning of life suggests that there may be one or more checks hidden by the thickened bone near the origin of the operculum. Assuming that tench grow according to the von Bertalanffy growth equation (Bertalanffy, 1938) a Walford plot (Walford, 1946) was constructed (fig. 33). This suggests that 12.3 cm is excessive for a single year's growth and is more likely to correspond to the second true check. The Walford plot indicates the possibility of one additional check corresponding to a length of 7 cm.

The results shown in fig. 32 for Farnborough 18(b) are at variance with those of Weatherley (1959) in which Tasmanian tench are reported to take 4-5 years to reach 12 cm, lengths at first check formation being 2.6-3.2 cm. Occasionally very small tench (2-6 cm) were seen in the gravel-pit lakes but no individuals in the range 6-15 cm were taken. Whether or not this is a result of rapid growth is not known. Weatherley (1959) does show that rapid growth is possible in Tasmanian tench in experimental dams after a period of slow initial growth, fish reaching 15-20 cm in 3 years.

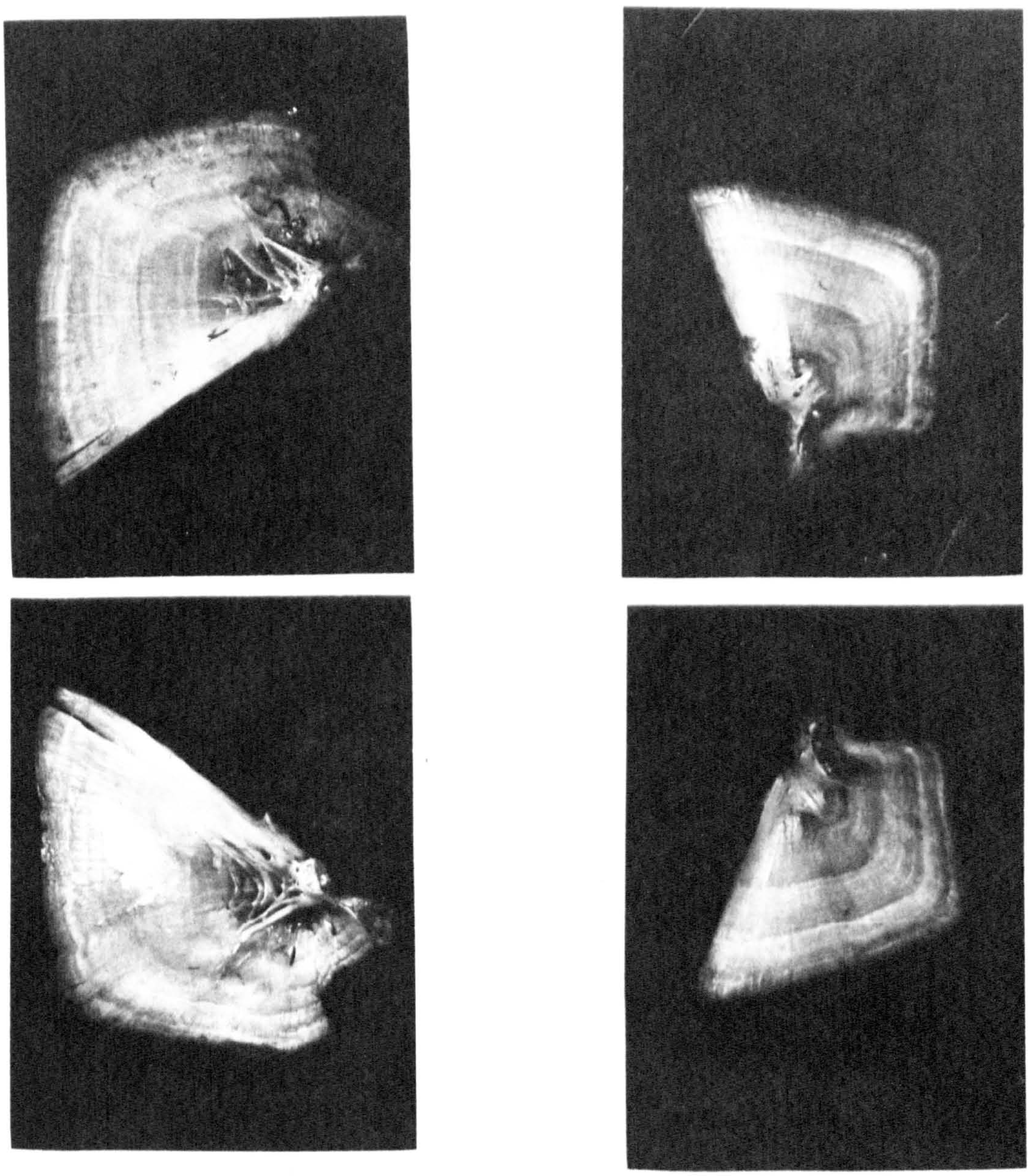


Plate 2 Opercula from Farnborough 18(b) Tench

(a) (right) 4+

(b) (left) 5+

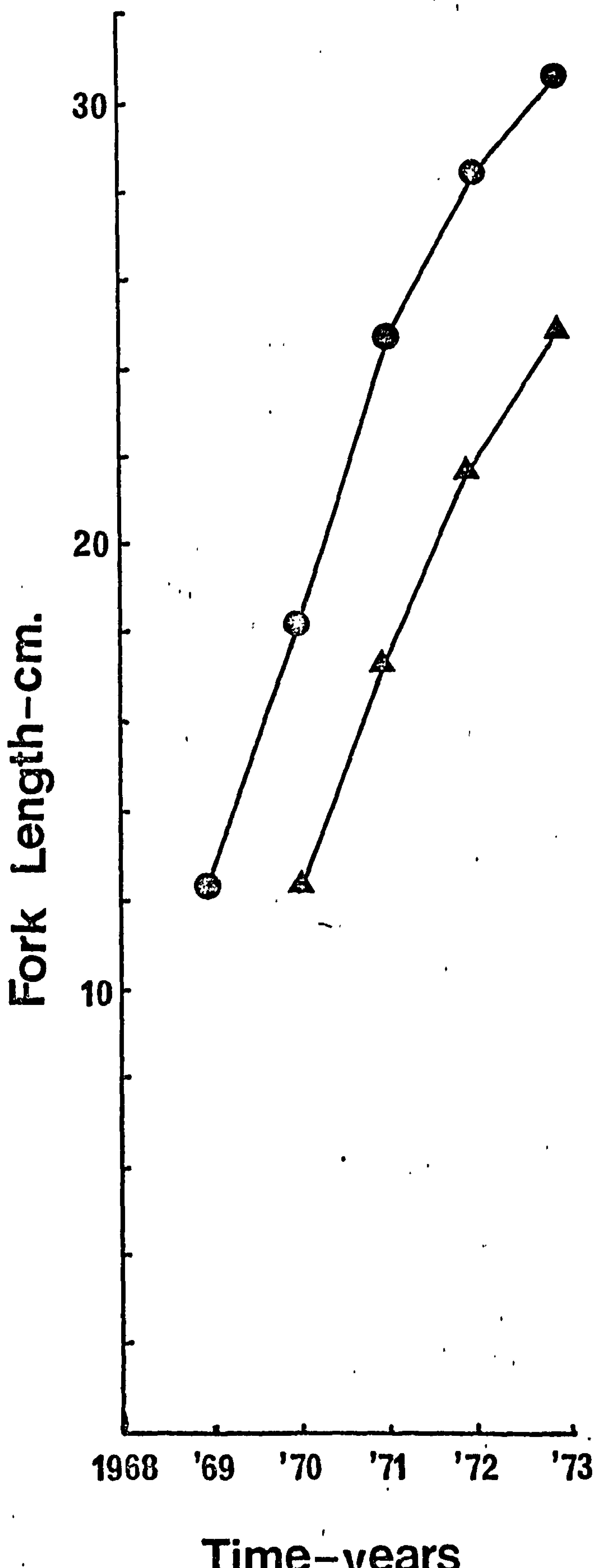


Fig. 32 Back-calculated Growth of Tench in Farnborough 18(b)

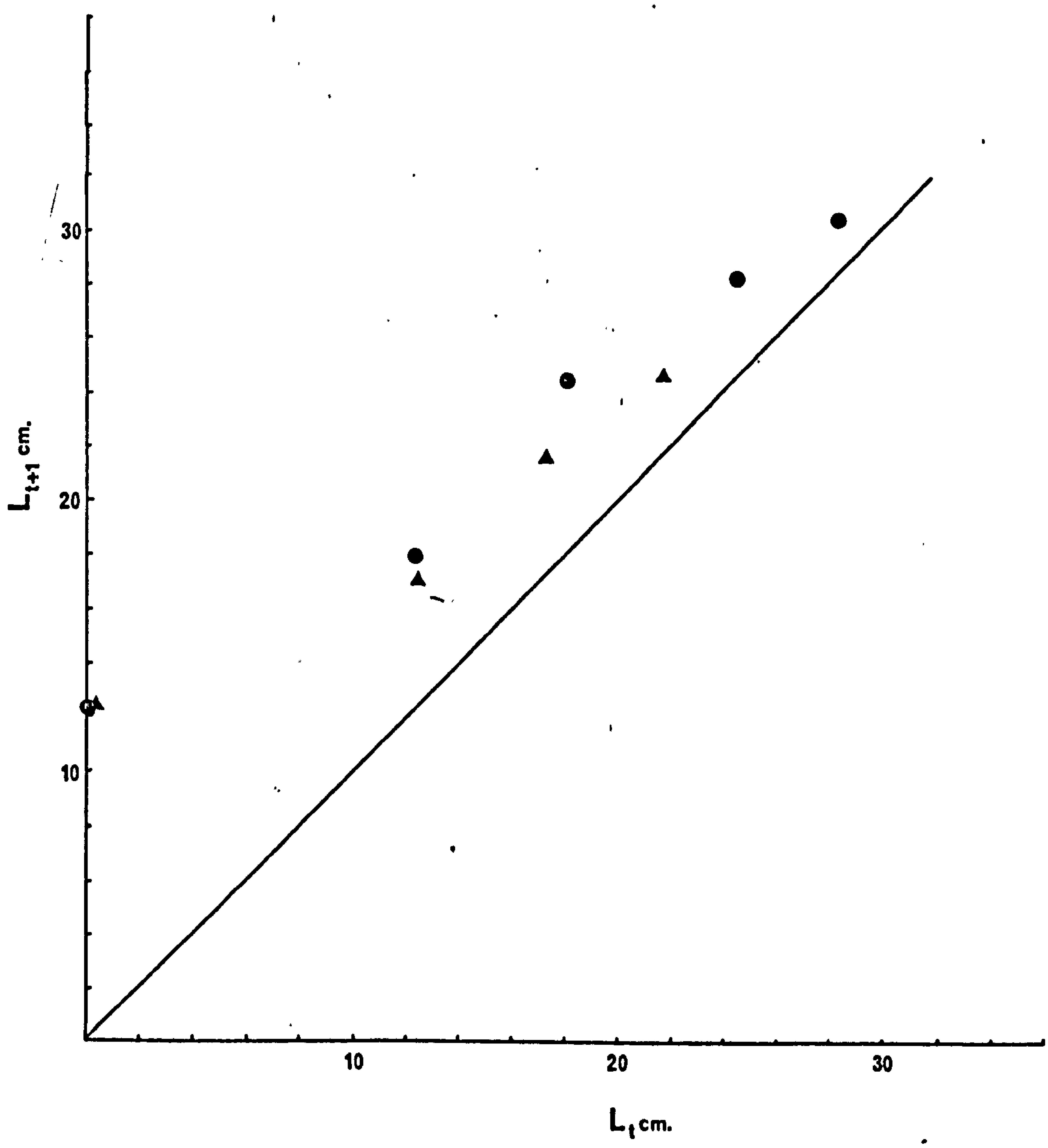


Fig. 33 Walford-plot of Back-calculated Lengths-at-age of Farnborough 18(b) Tench

3.3 Population Studies on Selected Lakes

3.3.1 Introduction

The survey shows the wide range of lake character, fish species composition and fish growth in these gravel pits. Comparison of growth curves derived from back-calculation shows that, in all species, variation occurred from lake to lake and from year to year, no lake having a consistently higher or lower growth rate during the life history of its oldest fish. More detailed investigation of selected lakes was undertaken to elucidate the reasons for growth-rate differences. Selection was based on the following criteria.

Two main kinds of fish community are identifiable from the survey: (1) those consisting of a mixture of cyprinids, usually roach and bream and (2) those in which cyprinids are rare or absent and the fish community is composed of perch and pike. The majority of the lakes fall into the first category with Twyford 32 and 33 in the second.

Many of the lakes provided such small samples that no adequate assessment could be made of their fish stocks. Lakes at Broxbourne (43, 44, 45) and Papercourt (24,25,26) were of this kind.

The Wraysbury (16,17), Woolwich Green (27, 28, 29) and Burghfield (30, 31) lakes were too large for adequate sampling

The Sutton-at-Hone site was very interesting in having several lakes (34, 35, 36) in close proximity but with different species composition. The roach of lakes 35 and 36 had a greater age range than most pits (up to 9 years). However, it was not possible to sample these by seine-netting because of the large amount of refuse present.

Of the lakes where fish were relatively easily caught, those in which the dominant gravel-pit fish, the roach, showed the widest range of growth rates were considered the most suitable for population studies.

Predation is a factor likely to affect population size and possibly growth rate. The main predator in these lakes is the pike, but this species is not present in all lakes. Their absence from survey samples (see Table 6) was not considered proof of their absence from a community. However, the more experienced and reliable anglers were adamant that pike were absent from all the Farnborough lakes. (No evidence to the contrary was ever obtained).

Parasitism, particularly by Ligula intestinalis, is another factor which might affect the growth rate of fish either directly or through its role in predation (see page 164). Ligula was absent from a few lakes, e.g. Farnborough 18(a).

Six lakes were chosen, taking into account the above criteria, and had the following pertinent characteristics:

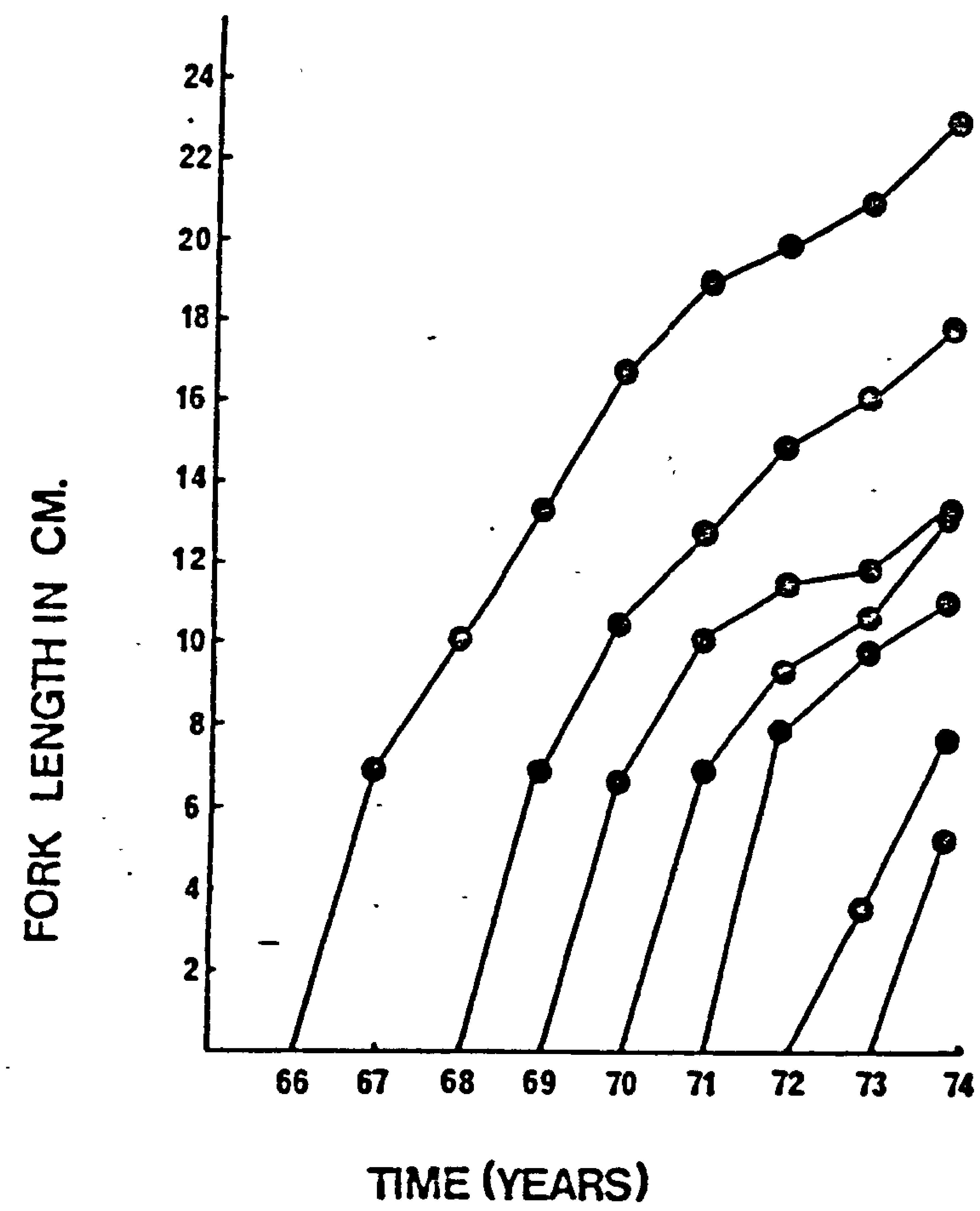
1. Farnborough 18(a) - a roach-dominated lake free of Ligula intestinalis and pike (by heresay).
2. Twyford 32
3. Twyford 33 both lakes dominated by perch and pike, and relatively free of cyprinids.
4. Daventh 39 - essentially a roach-bream lake with high incidence of Ligula intestinalis in the roach.
5. Darenth 40 - chosen mainly for its mixed species community and ease of netting.
6. Larkfield 41 - chosen for its slow-growing roach and bream, and its large size compared with those above.

3.3.2 Growth Rates

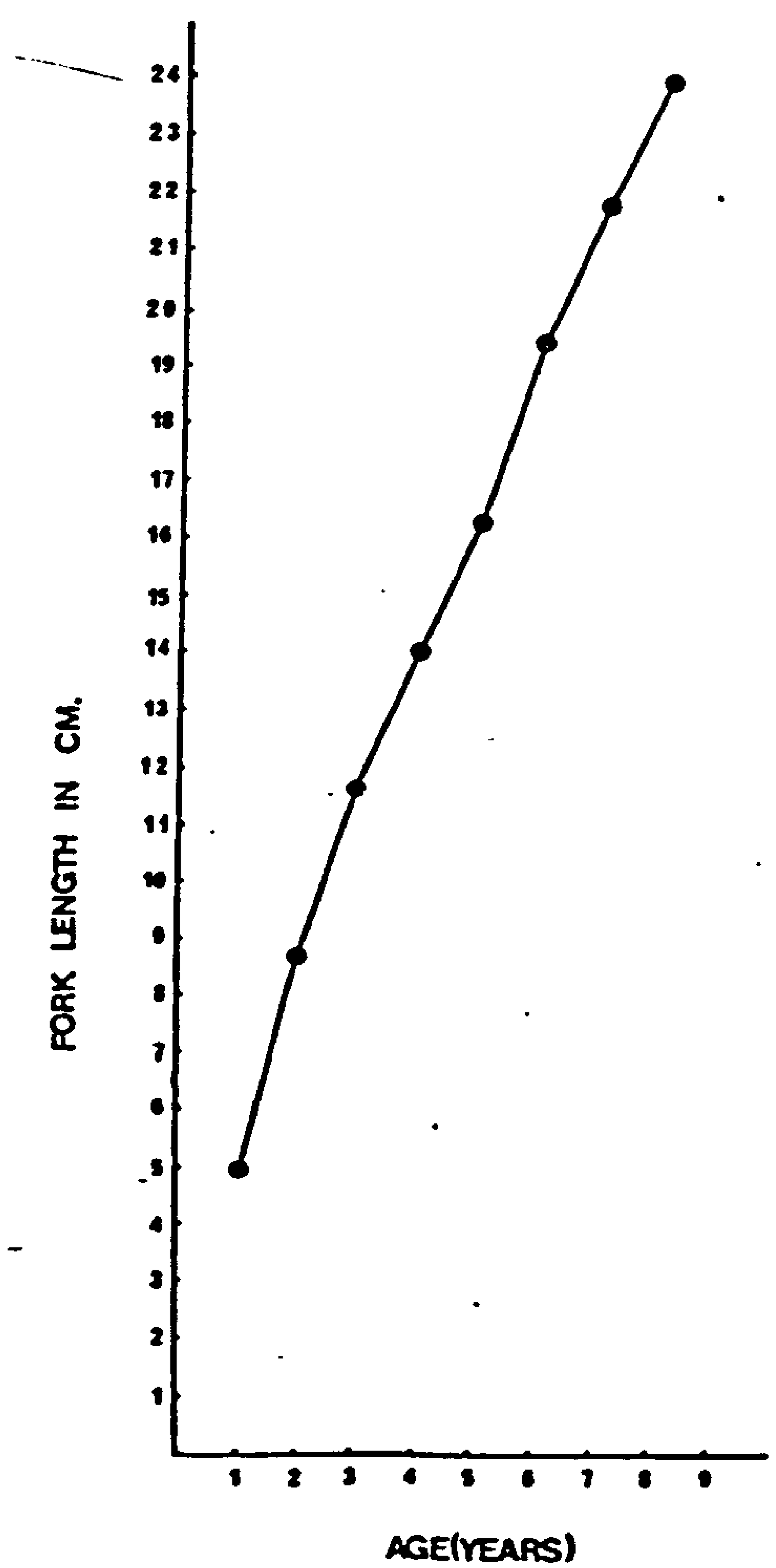
(a) between lakes

(b) between years

Roach of several age groups were present in all but one of the lakes (Twyford 33). Bream, though present in Darenth 39 and 40, were abundant and represented by many age groups only in Larkfield 41. Where samples were large enough growth rates were back-calculated and growth curves constructed as in the survey (see figs. 34-39 and Appendix 1). Growth rates of the same year-class of roach in different lakes are compared

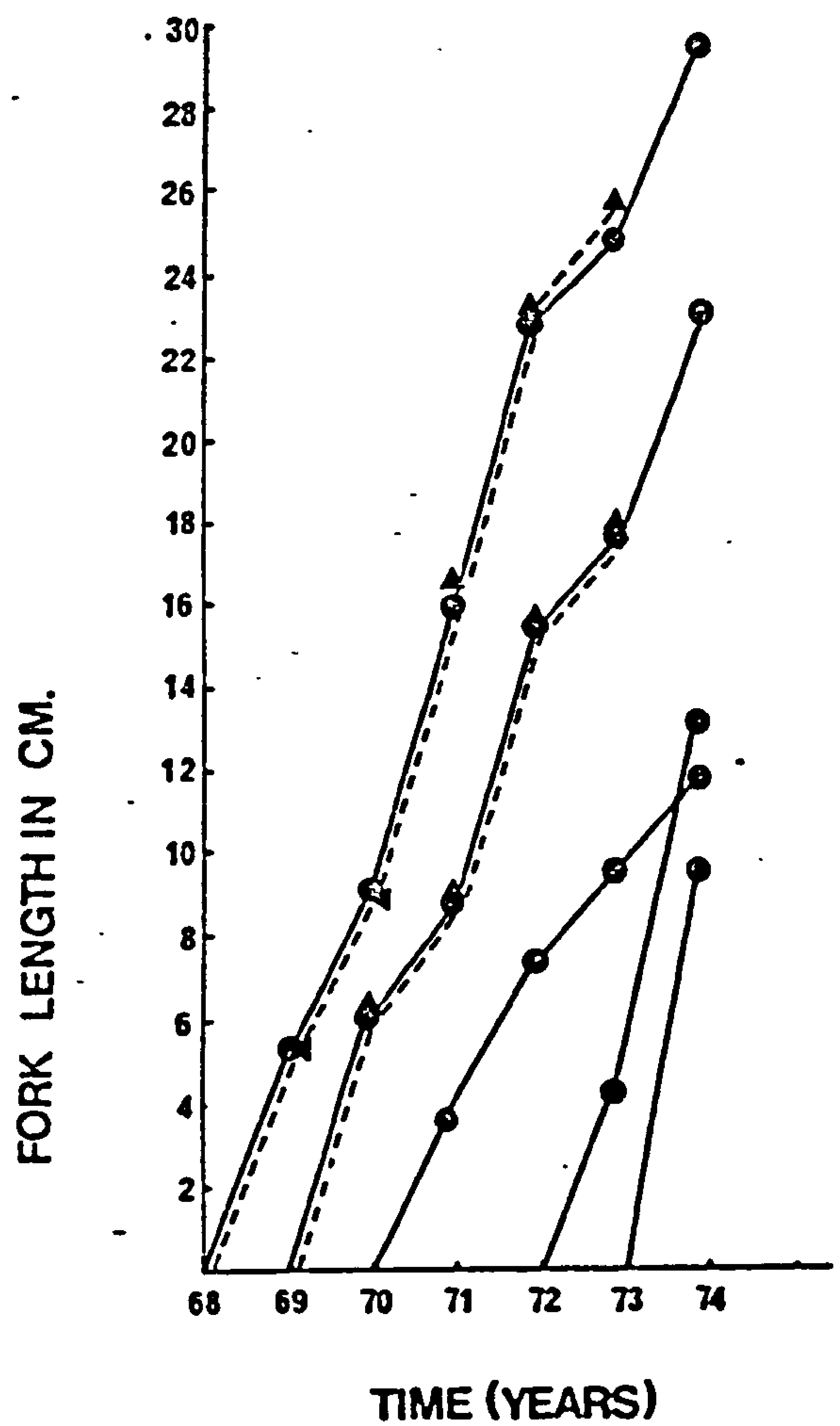


(a) Separate Year-classes

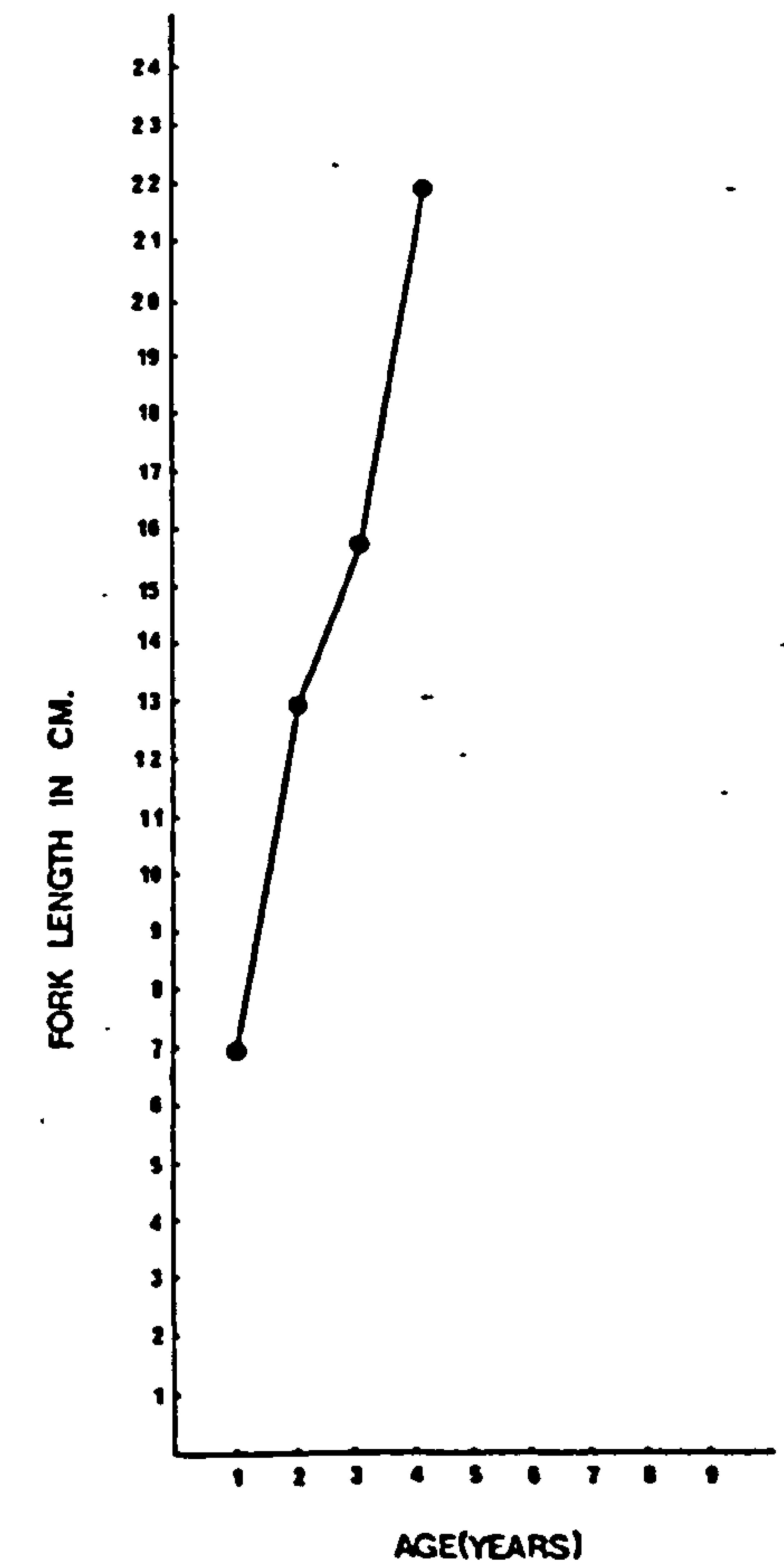


(b) Composite Year-classes

Fig. 34 Back-calculated Growth from Series 2 of Farnborough 18(a) Roach

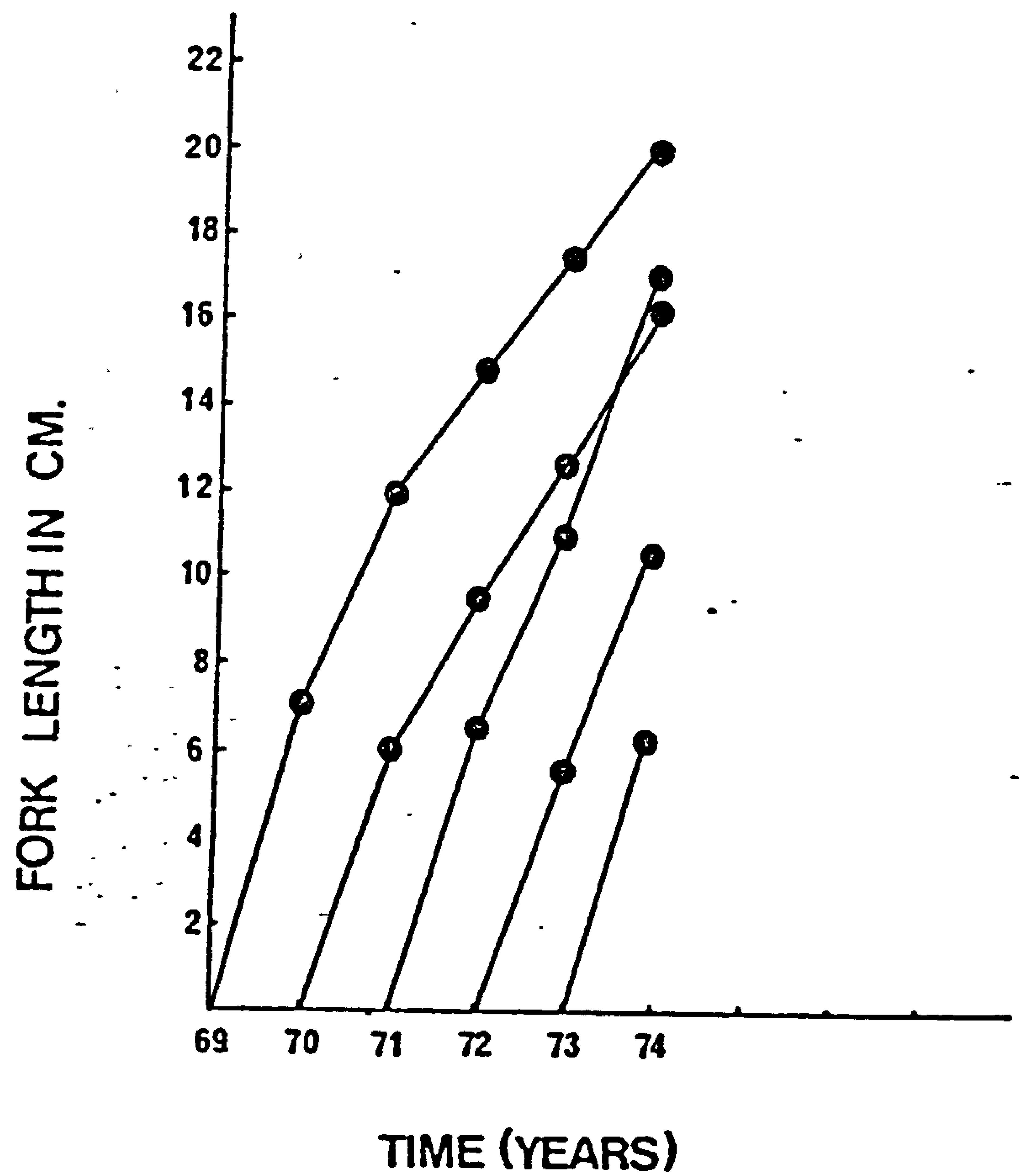


(a) Separate Year-classes

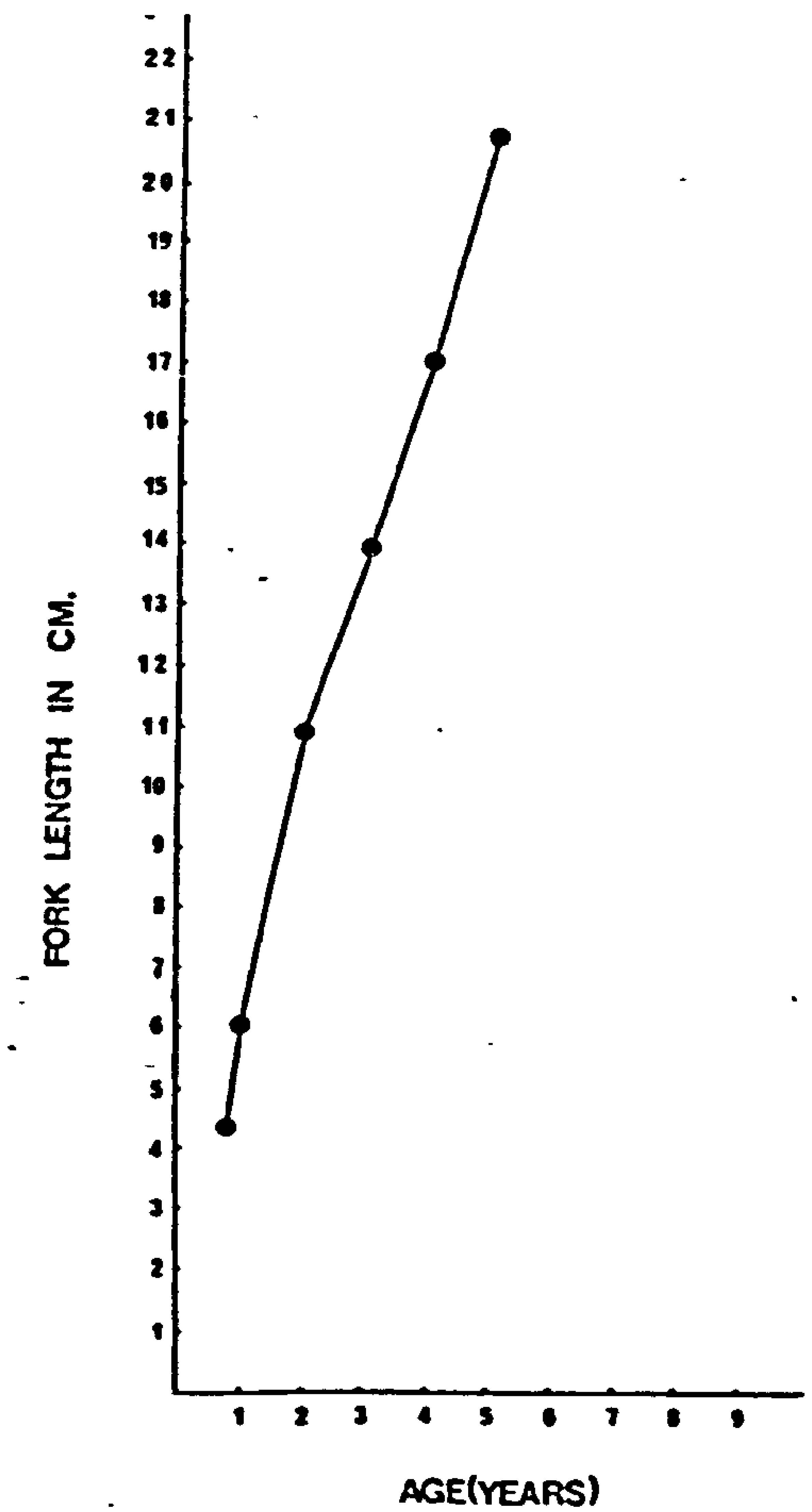


(b) Composite Year-classes

Fig. 35 Back-calculated Growth from Series 1 and 2 of Twyford 32 Roach

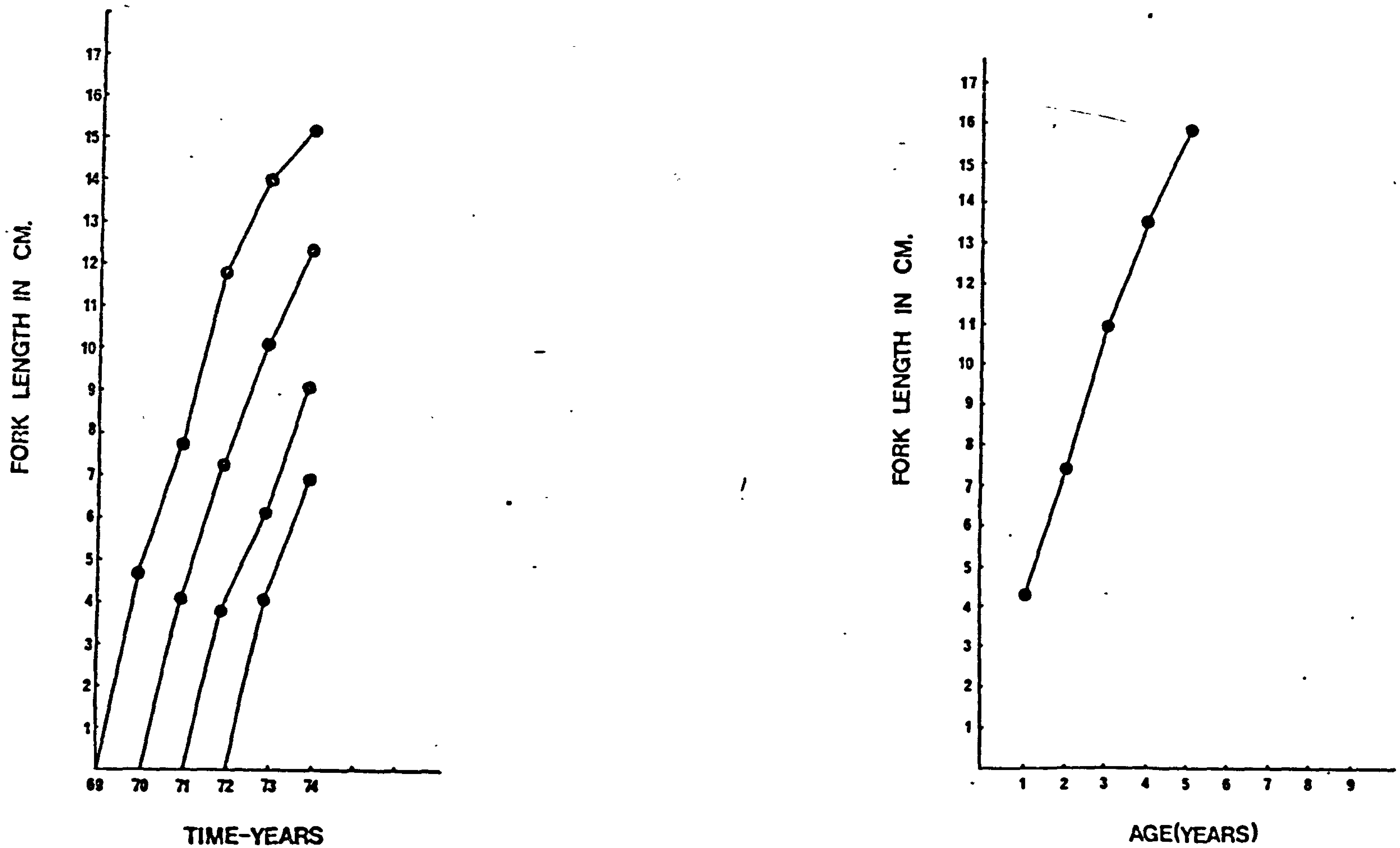


(a) Separate Year-classes



(b) Composite Year-classes

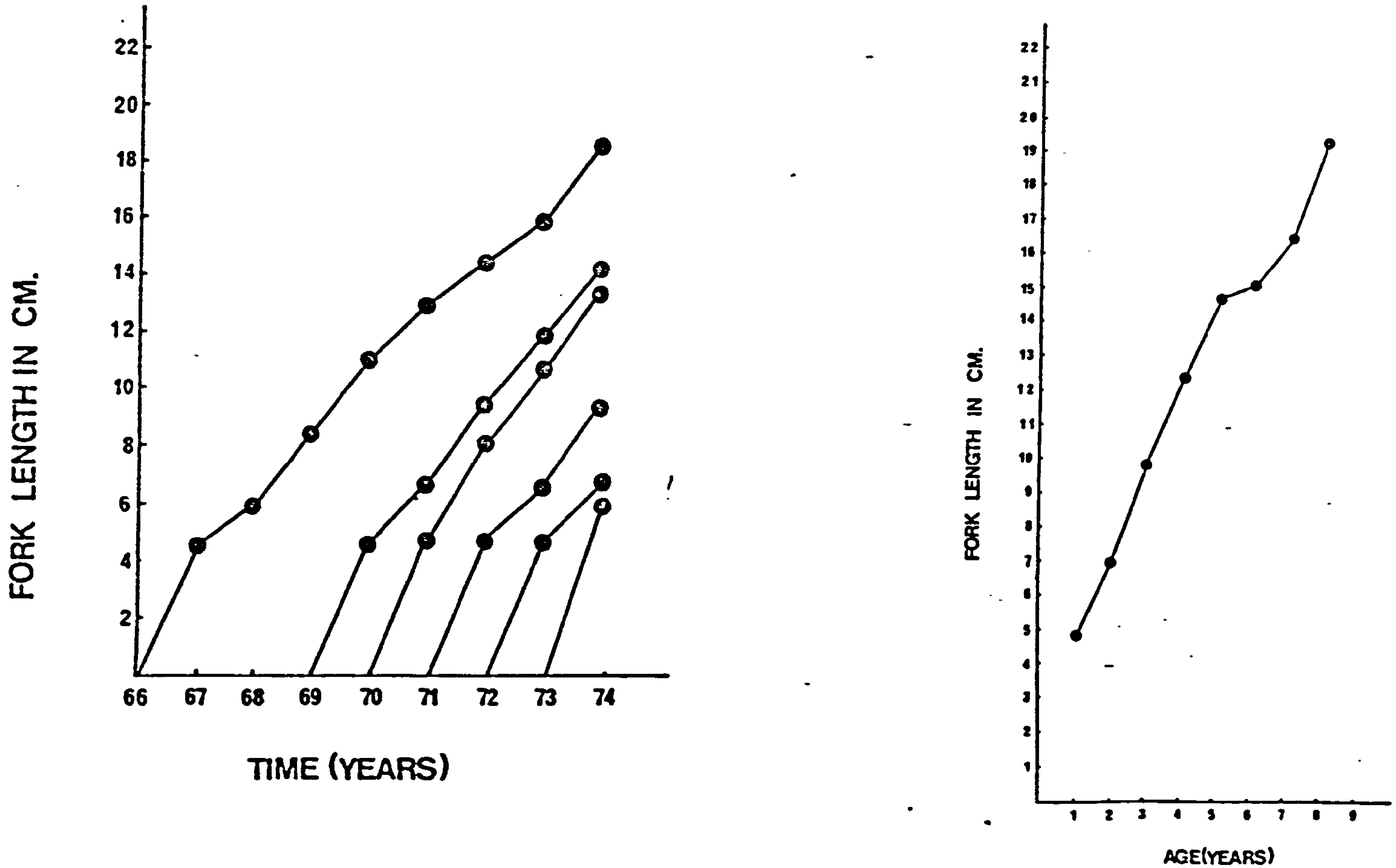
Fig. 36 Back-calculated Growth from Series 2 of Darenth 39 Roach



(a) Separate Year-Classes

(b) Composite Year-classes

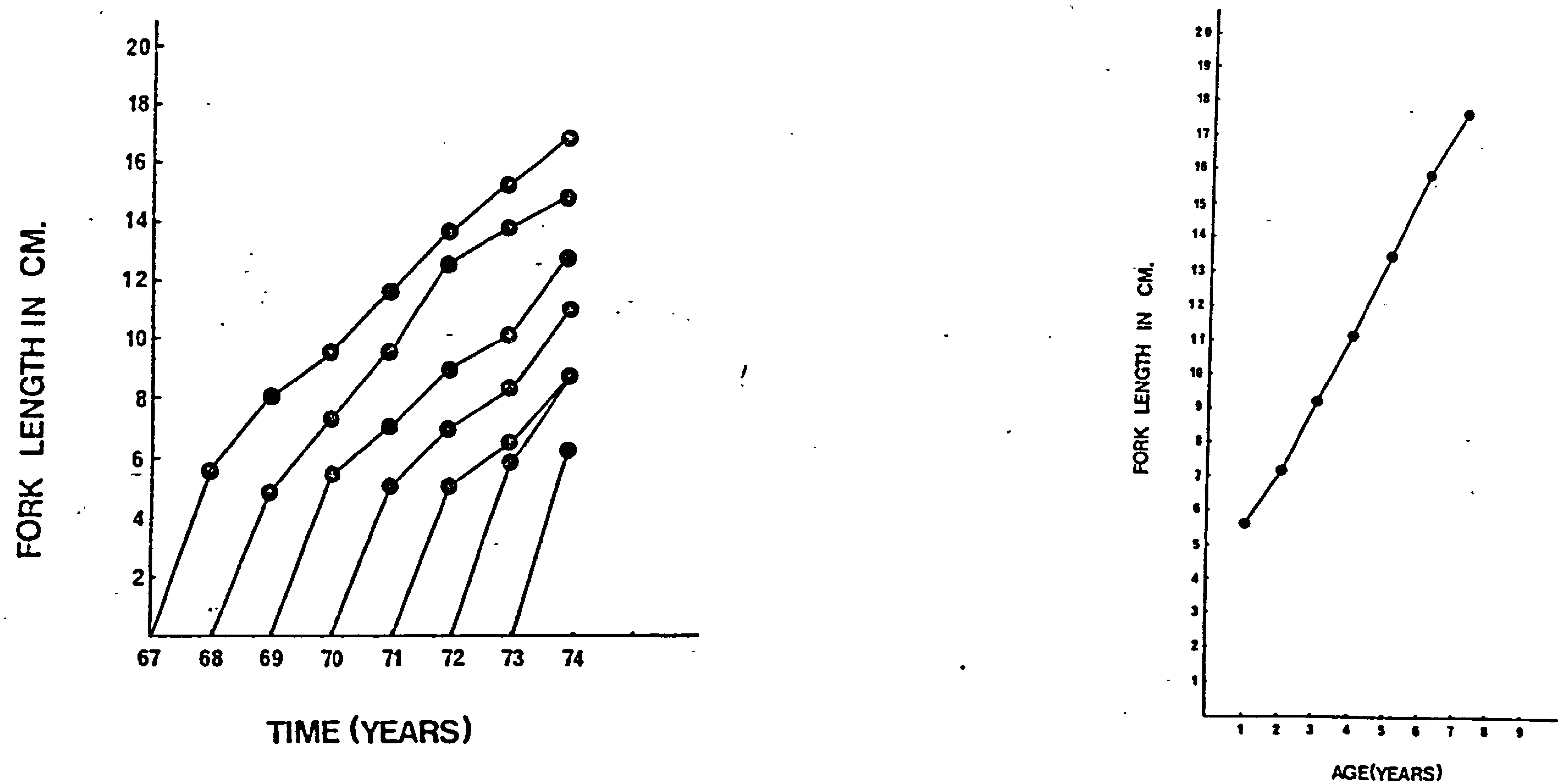
Fig. 37 Back-calculated Growth from Series 2 of Darenth 40 Roach



(a) Separate Year-classes

(b) Composite Year-classes

Fig. 38 Back-calculated Growth from Series 2 of Larkfield 41 Roach



(a) Separate Year-classes

(b) Composite Year-classes

Fig. 39 Back-calculated Growth from Series 2 of Larkfield 41 Bream below followed (in 3.3.2(b)) by a comparison of growth in different years in the same lake.

(a) Comparison of Growth between Lakes

Mean lengths for 1+ roach of the 1972 year-class in different lakes were compared using the t-test described in Section 2.5(a) and the t-values are given in Table 12. All differences between the five lakes are significant ($P < 0.01$). The sixth lake, Twyford 33, contained no 1+ roach. These lengths-at-age are equivalent to the growth achieved in their first year, and though the degrees of freedom differ between pairs of lakes, they are all large and the relative magnitude of the t-values (and therefore of the mean lengths themselves) indicates a league of lakes (A) in descending order of first-year growth shown in Table 13. A similar comparison of growth during the second year of these same fishes gave the t-values shown in Table 14. The corresponding league (B) is given in Table 13. The t-values are all highly significant ($P < 0.01$) and indicate relative growth rates completely different from that achieved in the first year of life of these roach. Similar comparisons of back-calculated lengths of 2+ and 3+ roach (1971 and 1970 year classes respectively) were not significant at the 5% level, but there were fewer fishes of these age groups in the samples.

This evidence strongly suggests that within any one year-class there is no correlation between the growth achieved in adjacent years (see Section 3.2(a)).

One 'unusual year's growth' can bias the relative growth performance of roach in the five lakes. To avoid such bias the increments achieved in the second growing season were compared using composite year-class data and t-tests applied as before. The results are given in Table 15. All values are highly significant ($P < 0.01$) and it can be seen that the two leagues B and C of Table 13 are very similar. There is only one difference, namely the relative positions of Darenth 39 and Twyford 32. The latter, as described in Section 3.3.3(b) is unusual in many ways. Therefore, the growth of the 1972 year-class in 1973 is of the order expected for all lakes except in lake Twyford 32.

TABLE 12 Student's t-values and Degrees of Freedom for 1972 year-class Roach 0-1 year increments (for explanation see text)

	39	41	32	18(a)
40	-18.78 (114)	-5.38 (73)	-3.75 (78)	6.82 (85)
39		11.81 (95)	15.58 (100)	27.47 (107)
41			2.94 (59)	14.37 (66)
32				13.56 (71)

TABLE 13 League of Lakes in Descending Order from Left to Right of the Growth Achieved

(a) by the 1972 year-class of roach

(b) all year-classes combined

	GROWTH PERIOD	LAKES (CODE NUMBERS ONLY)					LEAGUE
(a)	1972 - 1973	39	41	32	40	18(a)	A
	1973 - 1974	32	39	18(a)	40	41	B
(b)	Second growing season	39	32	18(a)	40	41	C

TABLE 14 Student's t-values and Degrees of Freedom for 1972 year-class roach 1-2 year Increments (for explanation see text).

	39	41	32	18(a)
40	-10.91 (114)	3.33 (73)	-27.77 (78)	-8.36 (85)
39		12.36 (95)	-16.07 (100)	4.61 (107)
41			-30.97 (59)	-15.53 (66)
32				27.25 (71)

(b) Comparison of Growth Between Years

Though all possible combinations of lengths-at-age and annual increments were compared the most interesting results were obtained from the younger, faster growing fishes. The situation of relative growth of roach in each lake for which detailed population estimates were undertaken will now be described separately.

(i) Farnborough 18(a)

The back-calculated growth data for the 1969, 1970, 1971 and 1972 year-classes of roach show significant differences ($P < 0.05$) between the first year growth in each of these years apart from the 1969-1970 growing season. Growth increments of all these year-classes in 1970, 1971, 1972 and 1973, when the fish were age 1+, were all significantly different from one another ($P < 0.05$).

(ii) Twyford 32

The back-calculated growth for the 1968, 1969 and 1972 year-classes during their first year of life gave the following results. 1968 and 1969 were not significantly different from each other ($P = 0.8$) but 1972

TABLE 15 Student's t-values and Degrees of Freedom for 1-2 year Increments using Composite year-class data (for explanation see text)

	39	18(a)	41	32
40	-9.38 (183)	-2.59 (147)	5.73 (145)	-7.84 (136)
39		3.96 (160)	14.00 (158)	-3.24 (149)
18(a)			5.79 (123)	-4.63 (114)
41				-9.26 (112)

was very significantly smaller than both 1968 and 1969. Growth during the second growing season of the same fish was again not significantly different between the 1968 and 1969 year classes but growth in 1973 (ie 2nd growing season of the 1972 year-class) was this time significantly greater than in 1969 and 1970 (P = 0.001 in both cases).

(iii) Darenth 39

Like Twyford 32 the growth of roach fry in 1972 was significantly less than in both 1969 and 1970 (P = 0.001 in both cases). Whereas growth of fish in their second year of life (1+) was significantly smaller in 1970 than in 1972 (P = 0.001). Other comparisons showed no significant differences between other years.

(iv) Darenth 40

With one exception the growth rates of fry in 1969, 1970, 1971 and 1972 were all significantly different (P < 0.05). The growth rates of fry in 1970 and 1972 were not significantly different from one another, neither was there a significant difference between the growth of 1+ roach in the years 1970, 1971, 1972 and 1973.

(v) Larkfield 41

The growth of roach fry (0+ fish) was significantly different in each of the years 1969, 1971 and 1972 as was the growth of 1+ fish in 1970, 1972 and 1973 and of 2+ fish in 1971 and 1973 ($P < 0.05$).

Using the above comparisons a league of growing seasons was constructed in order of the growth achieved. For roach the following league was obtained (Table 16).

TABLE 16 The Growth of Roach in Different Years Expressed as a League of Growing Seasons

Age	Lake (Code No.)	Years in Descending Order from the Left			
0+	18(a)	1971	1970	1969	1972
	40	1969	1970	1972	1971
	39	1969	1970	1972	
	41	1969		1972	1971
	32	1968		1972	
1+	18(a)	1973	1970	1971	1972
	40	1971	1970	1972	1973
	39	1973	1970	1971	
	41	1973	1970	1972	
	32	1973	1969	1970	

There is remarkable uniformity of order here, with the exception of 0+ fish in Farnborough 18(a) and 1+ fish in Darenth 40; the latter lake suffered a large reduction in water volume (∿50%) during 1973 and the water temperature rose to >24°C. Population studies show that population size and structure are variable from one year to the next suggesting the action of an external, possibly climatic factor. Unfortunately an attempt to install automatic temperature recorders in 1972 failed because of vandalism.

3.3.3 Abundance and Mortality

Sampling returns did not permit abundance estimates to be made for all species. Table 17 shows an example of the capture-recapture data divided into species groups and, where possible, age groups. The corresponding estimates of abundance and standard error are given in Table 18. Full details of these data for all lakes are given in Appendix 2; the 'best' estimates for most species are given in Table 19.

Comparing the estimates derived from the different models it is clear that no model gives consistently higher or lower estimates than any other. Where the numbers of recaptures are high there is a closer agreement between the estimates.

In the majority of cases there is no means of evaluating the estimate of any of the models. If such means were available they would be most useful where the proportion of the population marked and recaptured was smallest. Unfortunately such a check on the estimates is possible in only one lake, Darenth 40, where the numbers of roach and carp obtained in successive seines were analysed by the catch-depletion method of de Lury (1947) (Table 18). Since these estimates are based on criteria other than those involved in capture-recapture models they are good standards with which to compare the estimates of the 6 models. The simple Lincoln Index gives good estimates in each case, though those of the multiple Lincoln Index are consistently low. The Triple Catch model also gives a low estimate for roach and carp. Allowances for mortality in the marked members results in consistently good estimates, but neither the Leslie nor Jolly model give good estimates in comparison with the catch-depletion estimates.

Where possible, estimates were made of instantaneous mortality rate between the times of Series 1 and Series 2 samples. Generally, such estimates were possible only for those groups of fishes for which estimates of abundance were available in both series. Values of Z are given in Table 20 together with estimates of biomass (B).

TABLE 17 Capture-recapture Statistics for Darenth 40 in Series 2 Sampling (31.10.73 - 4.12.73)

Species	Size	DAY 1	DAY 2			DAY 3			
	Group (cm)	S1	C2	S2	M1	C3	M1	M1+2	M2
Roach	>9.0	294	230	13	217	199	29	160	10
Bream	>9.2	27	17	1	16	15	0	15	0
Rudd	all sizes	46	36	5	31	43	2	33	3
Perch	>6.0	5	5	0	5	4	1	3	0
Chubb	all sizes	15	20	6	14	12	2	8	2
Tench	"	5	1	1	0	2	2	0	0
Carp	"	33	19	2	17	19	13	5	1

S1/2/3 = Numbers of fish newly marked and released on day 1/2/3
C2/3 = " " " examined for marks on day 2/3
M1/2 = Recaptures from day 1/2
M1+2 = Recaptures from day 1 and 2

TABLE 18 Estimates of Abundance (and Standard Error) for Darenth 40 in Series 2 Sampling

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (Marked Deaths only)	Leslie Method B	Jolly Stochastic Model	Catch Depletion	'Best' Estimate
		N1	N2	N2	N1	N1	N1		
Roach	> 9.0	311 (5)	232 (2)	234 (15)	307 (9)	270	272 (7)	318	310
Bream	> 9.2	28 (2)	17 (0)	15 (4)	27	16 (1)	18 (2)	-	25
Rudd	all sizes	53 (3)	40 (2)	50 (7)	52	37 (3)	38 (3)	48	50
Chubb	"	21 (3)	22 (1)	28 (5)	23	23 (5)	25 (2)	-	25
Tench	"	10 -	-	4 -	7 -	-	3 (1)	-	5
Carp	"	36 (3)	19 (0)	20 (4)	35	58 (20	65 (17)	35	35

TABLE 19 'Best' Abundance Estimates for Certain Species in the Selected Lakes

Lakes / Species	18(a)		32		33		39		40		41	
	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
Roach	12000 >6cm	300 6-10cm 600 >10cm	12	300 <11cm 1000 11-16cm	4*	2*	1047*	480 7-10cm 1000 10-14cm	700	310	4000 <9cm 400 >9cm	7000 <8cm 890 >8cm
Bream	0	0	0	0	0	0	392*	1500 8-22cm 50 >22cm	513	25	60,000 <8 cm 7000 >8 cm	87,000 7-10cm 2000 >10cm
Tench ♂ ♀	400 450	400 350	0	12 40	0	0	2*	1*	8	5	14*	6*
Carp	0	9*	0	0	0	0	9*	5*	7*	35	7*	2*
Rudd	0	0	0	0	0	0	6*	3*	180	50	54*	0
Perch		1000 <9.5cm 16 >9.5cm	700 <8.5cm 220 >8.5cm	500	400 <8.5cm 300 >8.5cm	24 >23cm	0	0	50	14	118*	4000 >7.5cm
Pike	0	0	3500 <30cm 70 >30cm	20	24	20	0	4*	0	0	0	48*

S1 = Series 1; S2 = Series 2
Estimates refer to all sizes of fish caught unless otherwise stated

* = Total number of fish caught, but no recaptures obtained
0 = No fish caught

3.3.4 Population Structure

Length-frequency histograms were drawn for each species population during Series 1 and Series 2 using all the length frequency data collected during the estimation of abundance. Data for all unmarked fish were totalled and the resultant histograms are shown in Figs. 40 to 60. Though fry are numerically poorly represented in many of the catches these diagrams are thought to give a fairly accurate picture of the size-structure of the populations concerned. The relative abundance of the different year-classes can be deduced from the results of the population estimates (Table 19).

(a) Farnborough 18(a)

Roach

The roach is the commonest fish species in this lake. The numbers of 0+ roach are not known accurately but were estimated at about 40,000 in October 1973 (see Section 2.4(b)). The Series 1 length-frequency distribution (Fig. 40) does not include 0+ fish which, by back-calculation from 1+ fish in Series 2, would have been about 3.6 cm long. Such fish would have passed through the meshes of the seine net. In fact, large numbers of fish of approximately this size were seen swimming out of the net as the seine was drawn to the bank during Series 1 sampling. Fig. 40 does, however, show a large number of adult roach in the population. The estimated abundance of about 12,000 is large for such a small lake ($\sim 1/m^2$). The two main peaks in the length frequency distribution consist of the 1971, 1970 and 1969 year-classes. Poor growth in 1972 resulted in the 1969 year-class having nearly the same mean length in October 1973 as the 1970 year-class (Fig. 34). The growth pattern, as back-calculated from the sample taken in October 1973 (Fig. 34) agrees well with that of the survey sample in March 1972 (Fig. 9). Unfortunately, the latter sample was taken prior to the period of very slow growth during the summer of 1972. That 1972 was a poor growth year is emphasized by the exceptionally small size (3.6 cm) of the 1972 year-class at the time of formation of their first

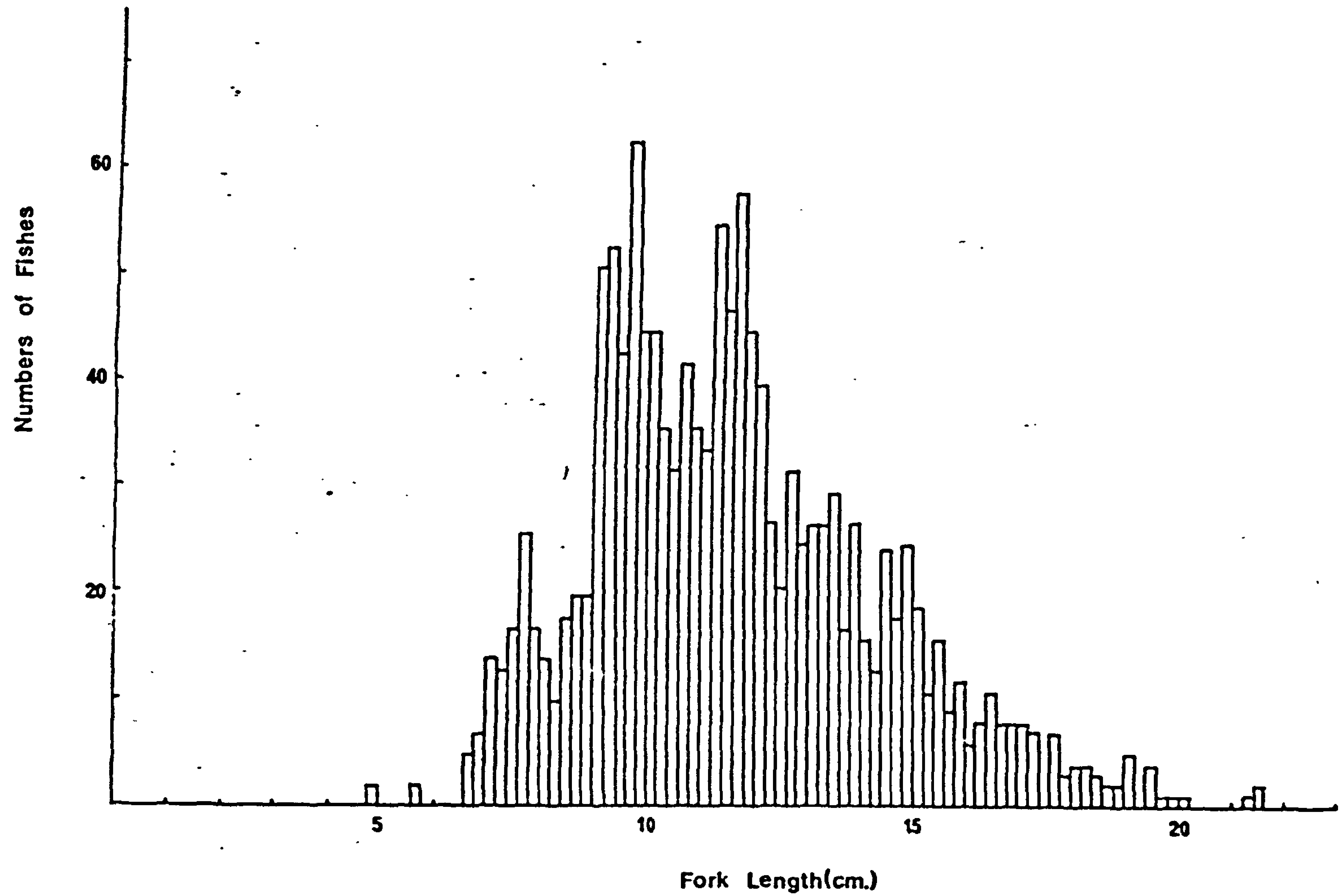


Fig. 40 Size Frequency Histogram for Farnborough 18(a) Roach During Series 1

annulus. In contrast, 1973 was a far better growing season, 0+ fish reaching 4.8 cm by October. The growth rates of all year-classes increased in relation to previous years, though, for reasons unknown, the growth of the 1969 year-class was not as much as for other year-classes.

The length-frequency histogram (Fig. 41) for the roach population at the end of 1973 differs considerably from that prior to the 1973 growing season (Fig. 40). The three distinct modes of the latter would suggest three age-groups, o+, 1+ and 2+. Scale readings, back-calculation and comparison with the corresponding diagram for Series 1, however, show that this is not the case. The peak at 5 cm corresponds to the 0+ group and that at 7-8 cm represents the 1+ group, ie those fish of about 3.5 cm during Series 1 which escaped through the net meshes. A different interpretation may be appropriate for the peak at 14 cm, which corresponds to the whole of the histogram in Fig. 40. The year-classes 1966-1971 are all represented here, the contribution of the 1971 year-class being very small. The first population estimate (Series 1) for this group was 12,000 and the second (Series 2) only 600 implying a high mortality corresponding to an annual rate of $Z = 2.9$.

These results indicate a dramatic change in the roach population of Farnborough 18(a) over a period of less than 8 months. This population was investigated further after the survey because pike and <u>Ligula intestinalis</u> were absent. It is particularly surprising, therefore, that such heavy mortality of roach should occur. No explanation can be suggested at present.

<u>Tench</u>

The 800 tench present in the lake (Table 19) represent a considerable biomass (∿230kg). Such numbers would be expected to have a significant effect on the ecology of the lake and of the benthos in particular. Large fish such as carp are known to increase the turbidity and reduce the vegetation of small lakes (Cahn, 1929). No growth curves have been drawn for these tench because of difficulties in obtaining sufficient opercula (see Section 3.2(g)).

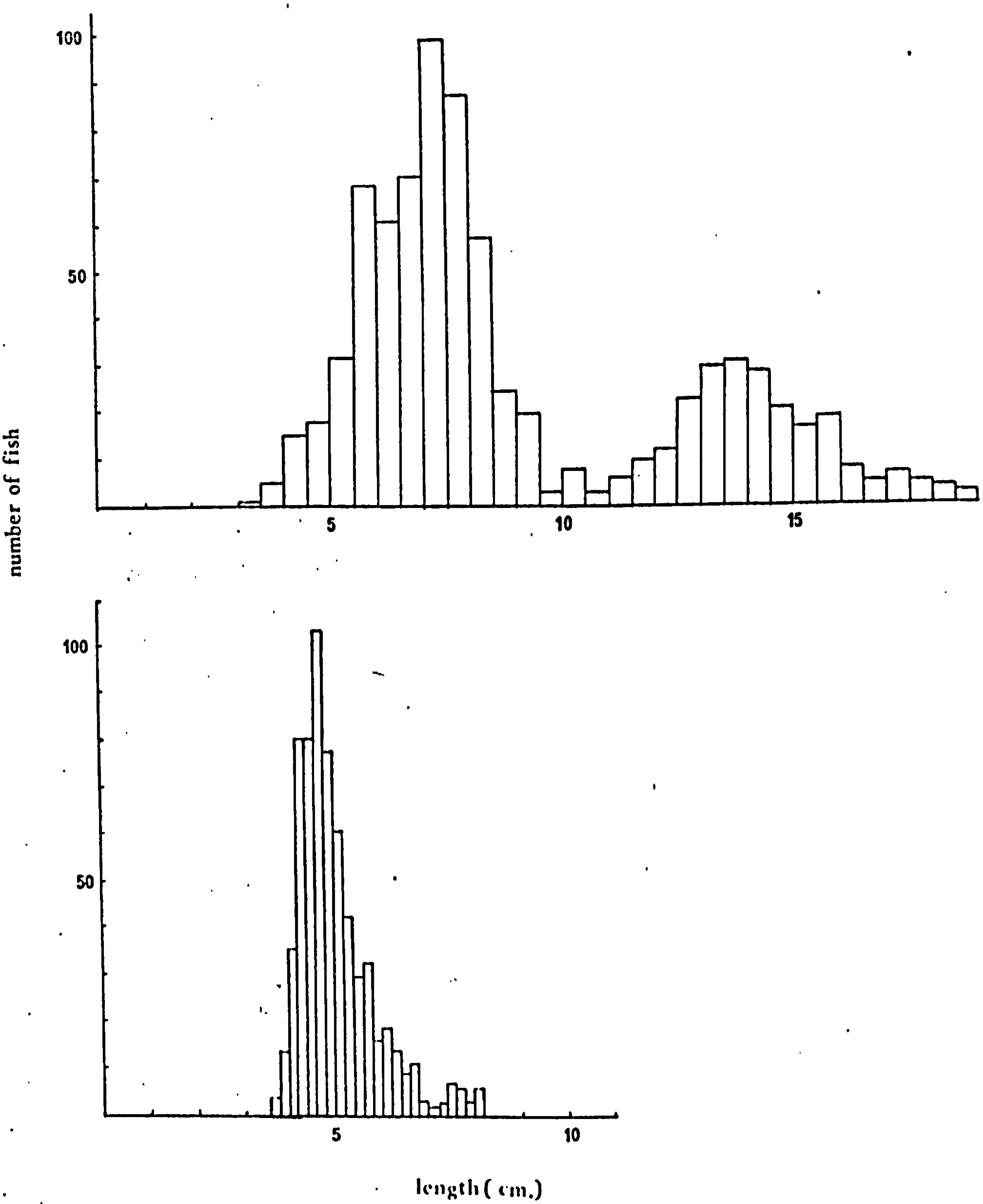


Fig. 41 Size Frequency Histogram for Farnborough 18(a) Roach During Series 2

The Series 1 length-frequency histograms (Fig. 42) suggest two peaks or age groups for both males and females. Series 2 histograms (Fig. 43) are more unimodal. This change in size structure may be due to a difference in growth rate between smaller and larger tench.

The most puzzling phenomenon is the decrease in the estimate of the abundance of female tench (Table 19). Estimates for the males remain constant, but those for the females suggest a loss of about 100 fish from the population (approximately 25% of the female population). If this is a real and common situation it could have serious consequences for small lake fisheries. Tench do not seem to spawn successfully every year; in all the gravel pits surveyed samples were lacking in small tench, when present the tench are in the length range 15-50 cm.

<u>Perch</u>

Farnborough 18(a) contained several large perch in 1972. Very few fish were caught in March 1973 (see Appendix 2), and by October of that year the estimate for perch larger than 9.5 cm is only 16 (Table 19). There were, however, an estimated 1,000 0+ perch present at this time (Table 19). Comparing the situation with that in other lakes, and in particular with Twyford 32 and 33 it is interesting to speculate that the population consists of a large number of fry, probably declining rapidly through the summer, autumn and yinter and are replaced by a large number of new fry each spring, the whole being maintained by very few mature adults.

<u>Other Species</u>

Approximately 400 gudgeon were present in October 1973 (Table 19), very few rudd and roach-rudd hybrids. Four common carp were caught.

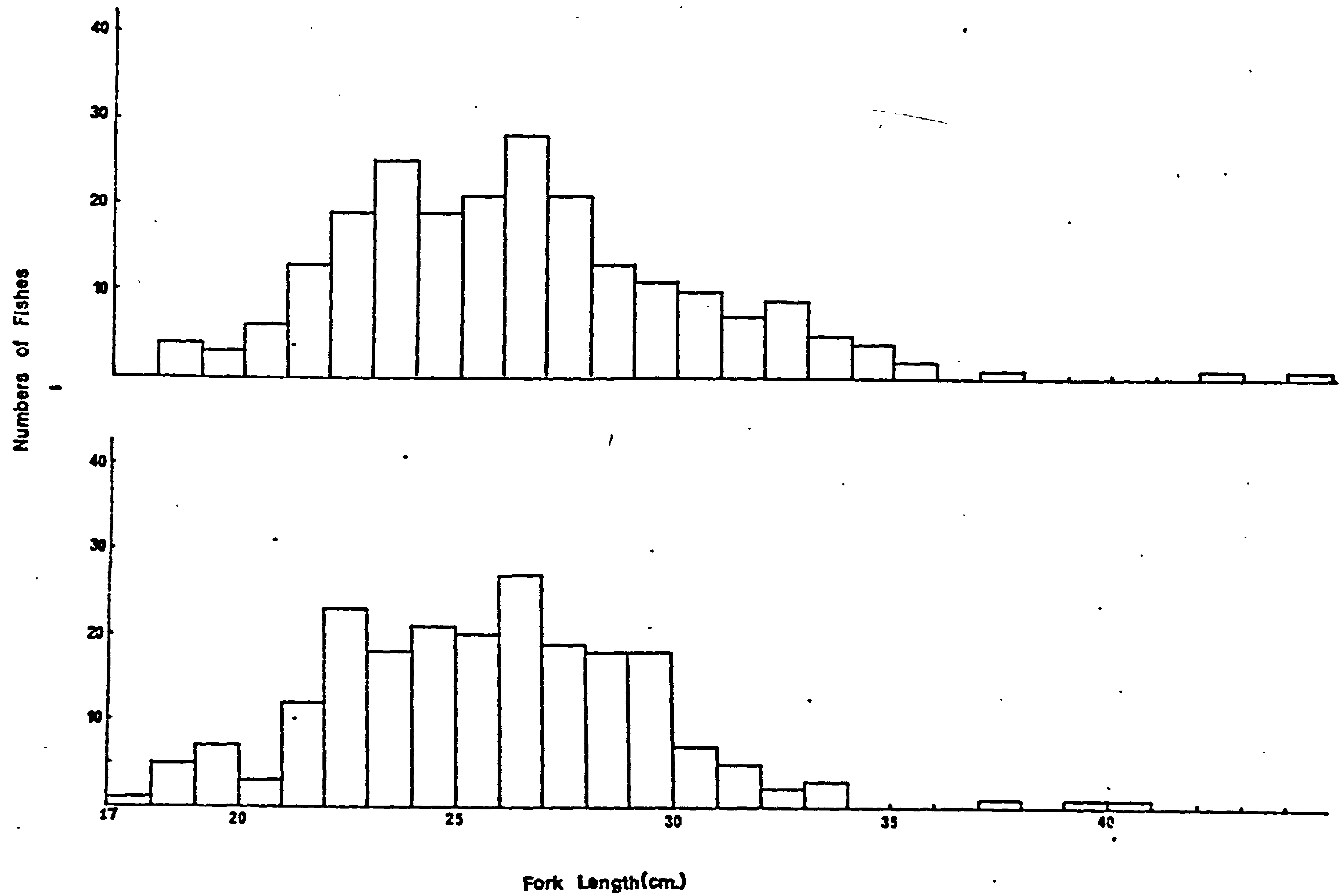


Fig. 42 Length-frequency histogram for Tench in Farnborough 18(a) in Series 1
Top - males; bottom - females

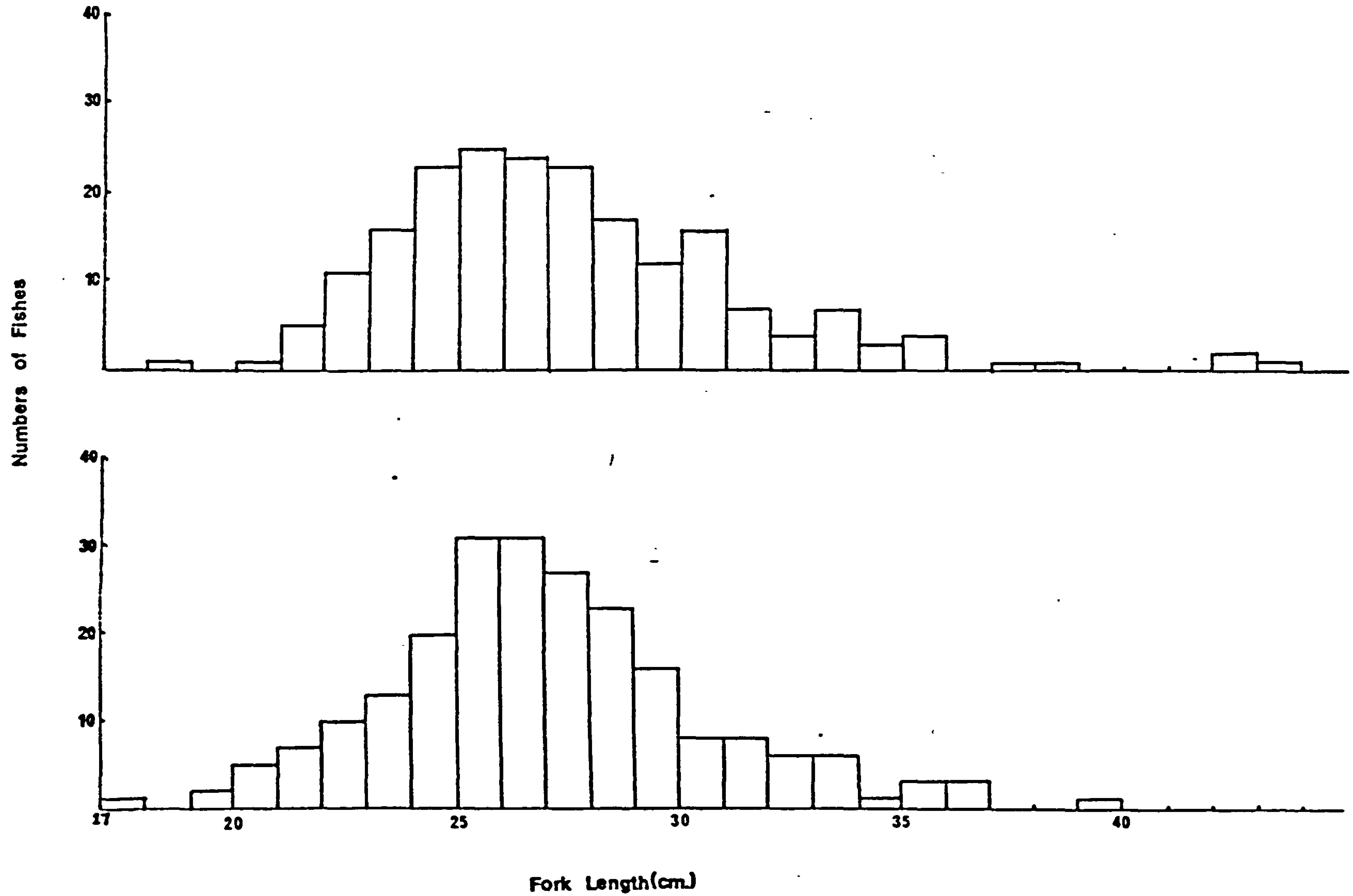


Fig. 43 Length-frequency histogram for Tench in Farnborough 18(a) in Series 2.
Top - males; bottom - females

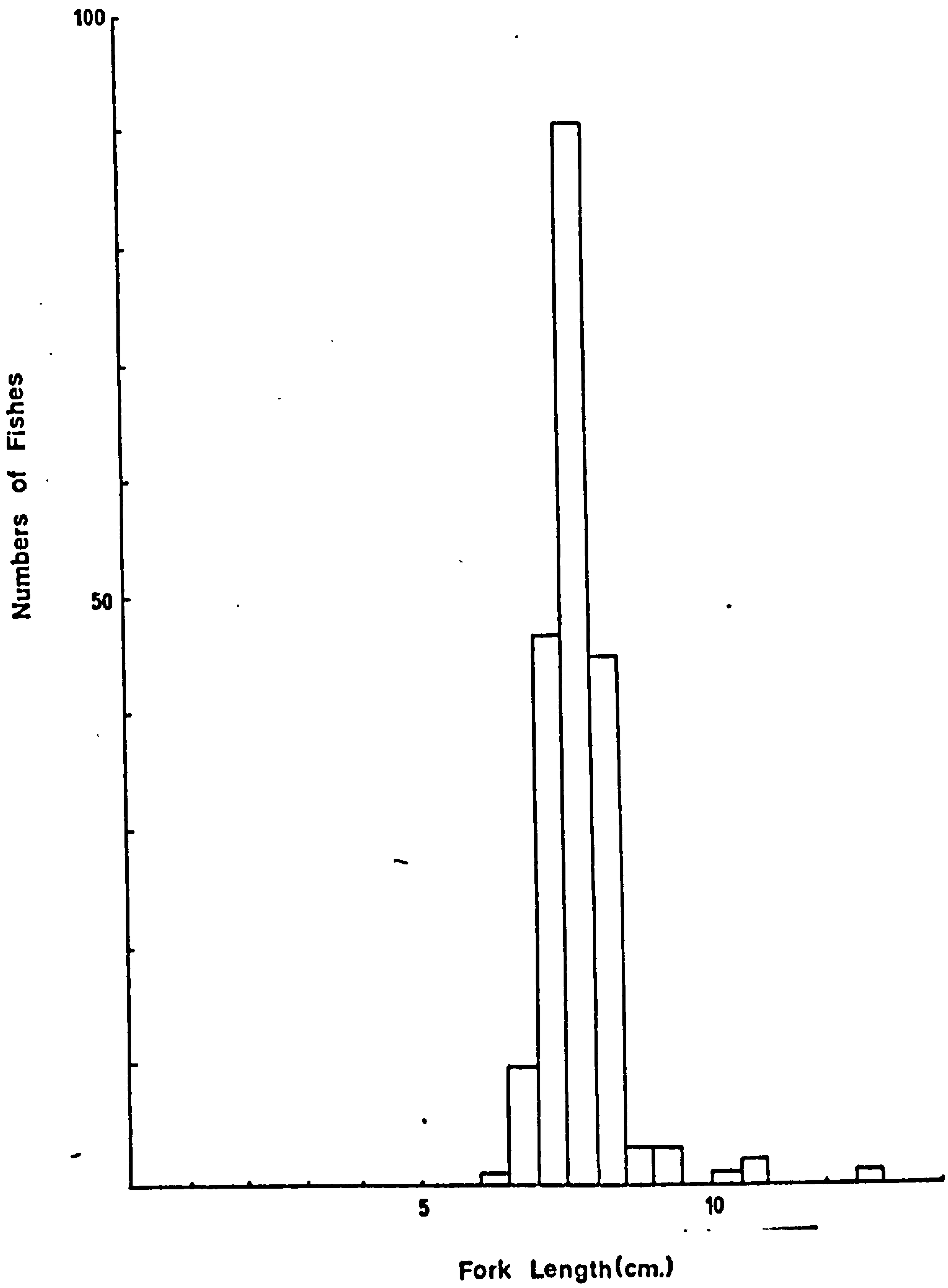


Fig. 44 Size Frequency Histogram for Farnborough 18(a) Perch During Series 2

(b) Twyford 32

Roach

During the survey, in January 1972, Twyford 32 was classified as a perch-pike lake (see p. 101). No roach were caught during intensive seine netting. It was a surprise, therefore, when in January 1973 large numbers of roach fry were seen, although very few were caught because of their small size relative to the mesh of the net. At this time 12 large (10-27 cm) roach were caught, presumably the parents of these fry. This change in community structure was small compared with that which became apparent in October 1973. Large numbers of roach were caught which fitted distinct biomodal length-frequency distribution as shown in Fig. 45. The fish of mean length 9.6 cm were 0+ (1973 year-class) and those of 13 cm were 1+ (1972 year-class). The latter, on back-calculation (Fig. 35) were found to have been 4.2 cm long at the time of check formation, the same length as the mean of the sample of fry taken in January 1973. The growth rate of these roach is exceptionally high, surpassed only by roach in cultivated carp ponds in the Netherlands (Hofstede, 1963). The 1972 year-class grew to only 4.2 cm in their first year compared with 9.6 cm for the 1973 year-class, giving further evidence that 1973 was a good growth year. In addition, though only growing to 4.2 cm in their first year, the 1972 year-class grew an additional 8.9 cm in their second year. This again illustrates the labile nature of roach growth.

Mark-capture data and summation of the total number of different individuals encountered during all the netting work at this lake indicate a population of approximately 12 adult roach (Table 19). It is notable that under favourable conditions so few adults can produce sufficient viable offspring to alter the species composition of the lake in less than 2 years. This is comparable with the perch situation in Farnborough 18(a) (p.122).

The scales of 3 large roach caught in February 1973 were used to back-calculate growth, serving as a check on similar calculations carried out one growing season later. These two sets of calculations were carried

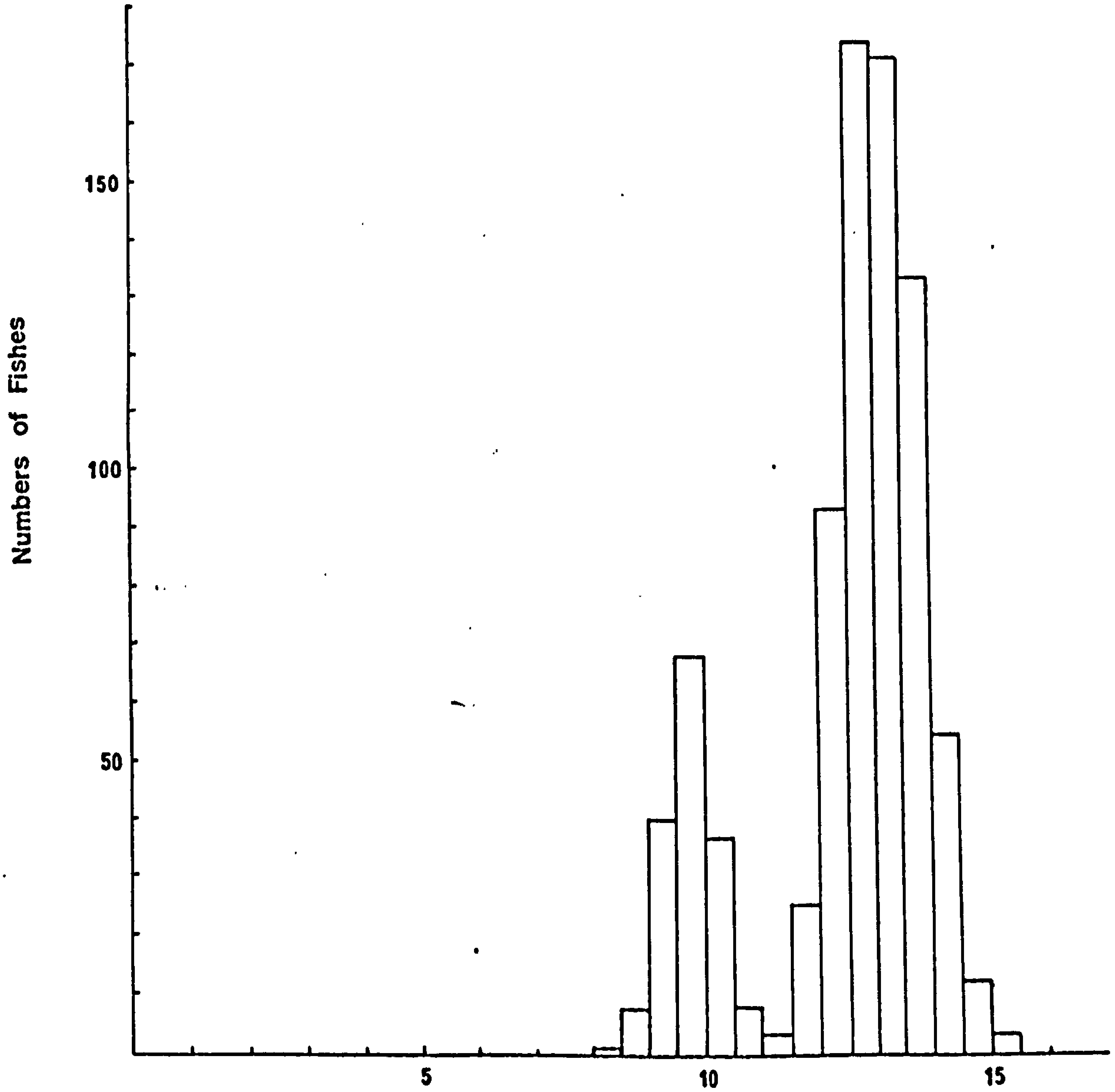


Fig. 45 Size Frequency Histogram for Twyford 32 Roach During Series 2

Fork Length(cm.)

out without reference to one another and it is reassuring to find that the derived growth curves are in close agreement (Fig. 35). Only one fish of the 1969 year-class was caught in February 1973 and was recaptured in the following October.

Perch

The Series 1 histogram (Fig. 46) showing the length-frequency distribution of perch caught has 4 quite distinct modes. These correspond to 0+, 1+, 2+ and 3+ fish. The different capture-recapture models give very variable estimates of abundance (see Appendix 2), but there were approximately 500-600 0+ fish and approximately 220 older perch present at this time (Table 19). By October, only 8 months later, the population structure changed to an almost unimodal state (Fig. 47). The majority of the population consists of 1+ fish, the survivors of the 0+ fish of Series 1. The remaining year-classes have practically disappeared.

The growth rates indicated by the Series 1 histogram (Fig. 46) are approximately the same as calculated for previous years during the survey (Fig. 30). The growth of the 1972 year-class in their second year is also within the range previously experienced. Furthermore, the mean lengths of the 1971 and 1972 year-classes at 2 years of age are almost identical. Therefore, despite the great changes in population structure the growth rate of the perch does not seem to have changed.

Pike

Described as a perch-like lake during the initial survey and chosen as such for further investigation, Twyford 32 changed considerably during the study period. In February 1973 large numbers of pike were caught giving estimates of 3,500 about 20 cm long and 40-70 over 30 cm (Table 19). The former were 0+ being the 1972 year-class. Compared with other species in other lakes, these pike seem to have grown and survived very well during 1972. The summer of 1973, as previously mentioned, was very warm and dry resulting in a drop in water level in this lake of about 0.5 m which

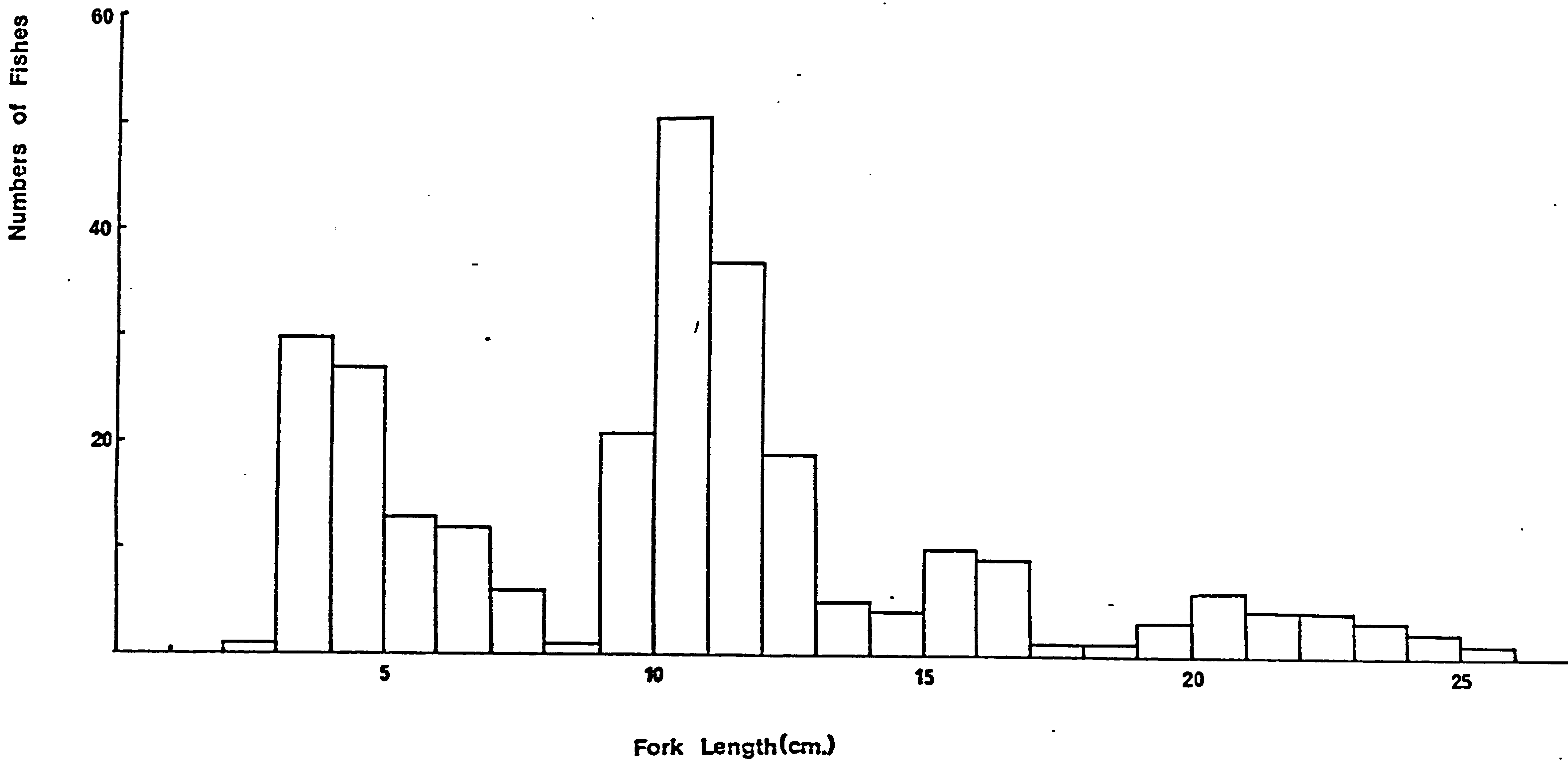


Fig. 46 Size Frequency Histogram for Twyford 32 Perch Series 1

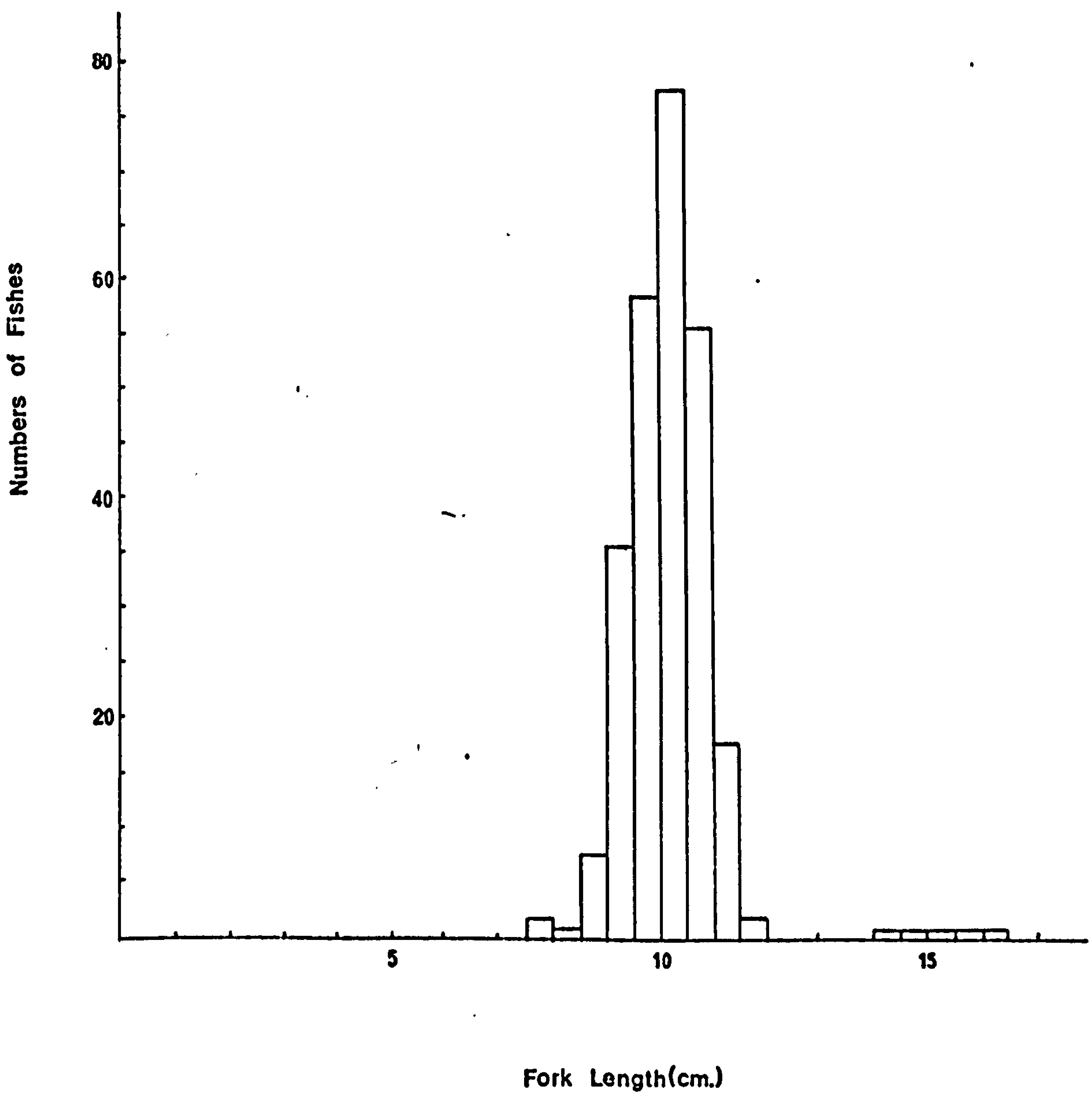


Fig. 47 Size Frequency Histogram for Twyford 32 Perch During Series 2

exposed a large proportion of previously submerged sand banks, and reduced the average depth to less than 0.5 m. The water temperature rose to 24°C during mid-summer. As pike are essentially a cold-water species the high temperatures of 1973 could explain the apparent high mortality of pike during this period. The total estimate of numbers in October (Series 2) was only 20 (Table 19) based on 13 fish caught. Several large pike were seen dead in the water in August-September 1973 though decomposition was too advanced to determine the cause of death. It is likely that a minimal survival of the 1972 year-class occurred. The work of Franklin et al (1963) suggests that the lack of recruitment could be due to desiccation of the eggs and early fry in the littoral spawning areas in early summer 1973.

Bleak

Up to 1973 Twyford 32 was a lake favoured by pike anglers who used bleak from nearby streams as live-bait. It is likely therefore that the large numbers of bleak caught in February 1973 were introduced by such anglers as no bleak were found during the survey 12 months previously. A high mortality rate of this species was observed during the 3 weeks of sampling in February 1973 (Appendix 2), possibly the combined result of marking and predation by the large pike population. (This phenomenon is illustrated by the discrepancies in the estimates for day 1 and day 2 in Appendix 2). Very few bleak were caught in October, the estimate of population size having been reduced from 200 to 40 (Table 19).

Tench, Chub and Dace

Very little is known about these species in this lake but numbers are thought to be low. The chub and dace were probably introduced by anglers in the same way as bleak.

(c) Twyford 33

Roach

During the survey Twyford 33, like 32, was classified as a perch-pike lake, but unlike lake 32, it has remained essentially free of other species.

During Series 1 sampling in December 1972, only 4 roach were caught. Similarly in Series 2 in January 1974, 2 roach about 8.5 cm long were caught.

Perch

The survey sample was taken three months prior to the first population estimate and so the growth rates calculated from these are in effect, the growth rates of the Series 1 fish. Only three year-classes of perch were present in the survey sample, and comparison between Fig. 31 and the length-frequency distribution (Fig. 48) shows that in the latter the first mode represents the 0+ (1972 year class) perch, the second mode the 1+ and the indistinct grouping around 15-16 cm the 2+ fish. During Series 1 sampling a total of 13 larger perch were marked but no fish were killed for their opercula. These fish of about 20 cm would be expected to be 3+ whilst those about 24 cm would be 4+. The survey sampling in September 1972 yielded large numbers of 0+ perch, one seine sweep providing a sample of about 500 fish (most of which were returned to the water). Yet, in December 1972 effort statistics suggested far fewer 0+ perch were present, which is confirmed by the capture-recapture estimate of only 400 (Table 19) in total. Mortality of perch fry would appear to have been very high.

The remainder of the population is represented, in terms of structure and relative abundance of size groups, by the length-frequency histogram of Fig. 48. The estimate of 300 perch over 8.5 cm (Table 19) means that there were very few adult perch present.

In January 1974 few perch were caught, 80 seine sweeps in 4 days spread over 3 weeks yielded only 23 perch (Appendix 2). Eighteen of these fish were over 20 cm in length. Six perch traps were laid for 3 weeks and inspected several times but no fish were caught, and gill nets of a range of mesh sizes were laid for 24 hours which caught one perch and one pike.

Sampling of the lake had been attempted in September 1973. This was much hampered by a very dense growth of Elodea canadensis similar in extent to that in Twyford 32. However, approximately 100

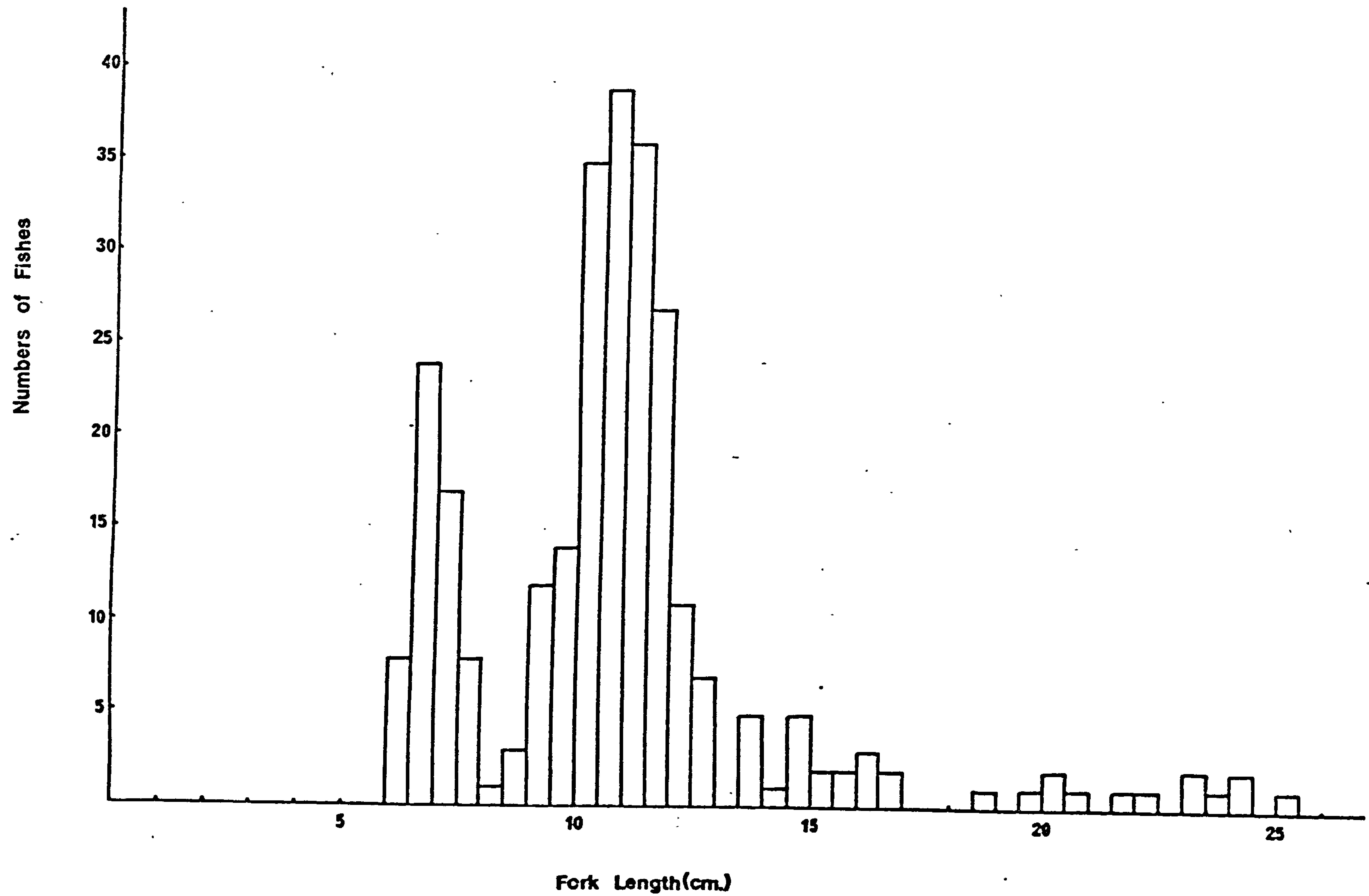


Fig. 48   Size Frequency Histogram for Twyford 33 Perch During Series 1

perch fry were caught in one seine sweep, indicating high mortality between September 1973 and January 1974. The experience of the previous winter suggests that heavy mortality of 0+ perch occurs leaving virtually no survivors. In 1972 almost 300 perch survived to the end of December but it appears that the majority of these died during 1973. Reasons for this decline will be discussed in Section 4.

Pike

Only 6 0+ pike were caught in Series 1, the majority of the catch of 22 pike being 28-81 cm (mean 50 cm). The estimate of 24 represents a large predatory force for a lake with so few prey. Many workers have shown the pike's preference for perch as prey and have commented on the large amount of food consumed by pike in a year (Toner and Lawler, 1969; Johnson, 1960). Johnson (1960) concluded that Windermere pike eat about twice their own body weight of fish in one year. The numbers of perch in Twyford 33 are insufficient to support the estimated pike population. Although pike have low preference for their own young they are taken under certain circumstances (Mauck and Coble, 1971). It is suggested that in Twyford 33 the very small number of pike <20 cm present in the population is due to predation by the larger pike. It is also suggested that the apparent heavy mortality of perch is due, at least in part, to pike predation.

During Series 2 sampling pike were caught in numbers similar to those of Series 1. These fish were, however, very thin indeed.

Other Species

The only other species present was the 3-spined stickleback. These were numerous in weed dragged up in the net but none exceeded 3 cm in length.

(d) Darenth 39

Roach

Roach were caught and marked in Series 1 sampling in June 1973 but only 4 recaptures were obtained over 4 weeks of netting (Appendix 2). No estimate of population size was possible, but the catch statistics indicate that the population was large. Seine netting in lakes as large and deep as Darenth 39 is difficult, the lead-line of the seine being frequently off the bottom allowing fish to escape.

By June the roach (and other species too) had made some plus growth after check formation on the scales so that the back-calculated lengths (Fig. 36) do not correspond with the modes of the length-frequency distribution for Series 1 (Fig. 49). The 1972 year-class increased in length about 1.5 cm between the last check and June 1973. The 1971 year-class is represented by very few individuals, the majority of fish other than yearlings (1+) consisting of the 1969 and 1970 year-classes.

In November 1973 (Series 2) the population structure had changed completely (Fig. 50). 1973 roach, too small to be caught during Series 1 now formed a distinct mode at 6.2 cm. The following two modes are difficult to interpret. Scale readings show that the 1972 year-class had a mean length of 10.5 cm in November 1973 which is a length intermediate between these two modes. It would appear, from scale readings therefore, that all the fish between about 8 and 13 cm are 1+. 88.6% of these roach were infected with Ligula intestinalis though infected fish had lengths which were equally distributed between both modes. No significant difference between the Ligula intestinalis infection, i.e. the percentage of individuals infected, of these two peaks could be found. The roach between 14 and 18 cm were 3+ corresponding to the second major mode of the Series 1 histogram (Fig. 49).

Bream

Few bream were caught until the fourth day in Series 1. The length-frequency distribution (Fig. 51) shows one distinct mode at ∿8.5 cm, confirmed by scale readings to be the 1972 year-class. These fish had just formed a check on the scales and had a few circuli of plus growth. No larger bream were caught.

The histogram (Fig. 52) for the Series 2 sample shows that the 1972

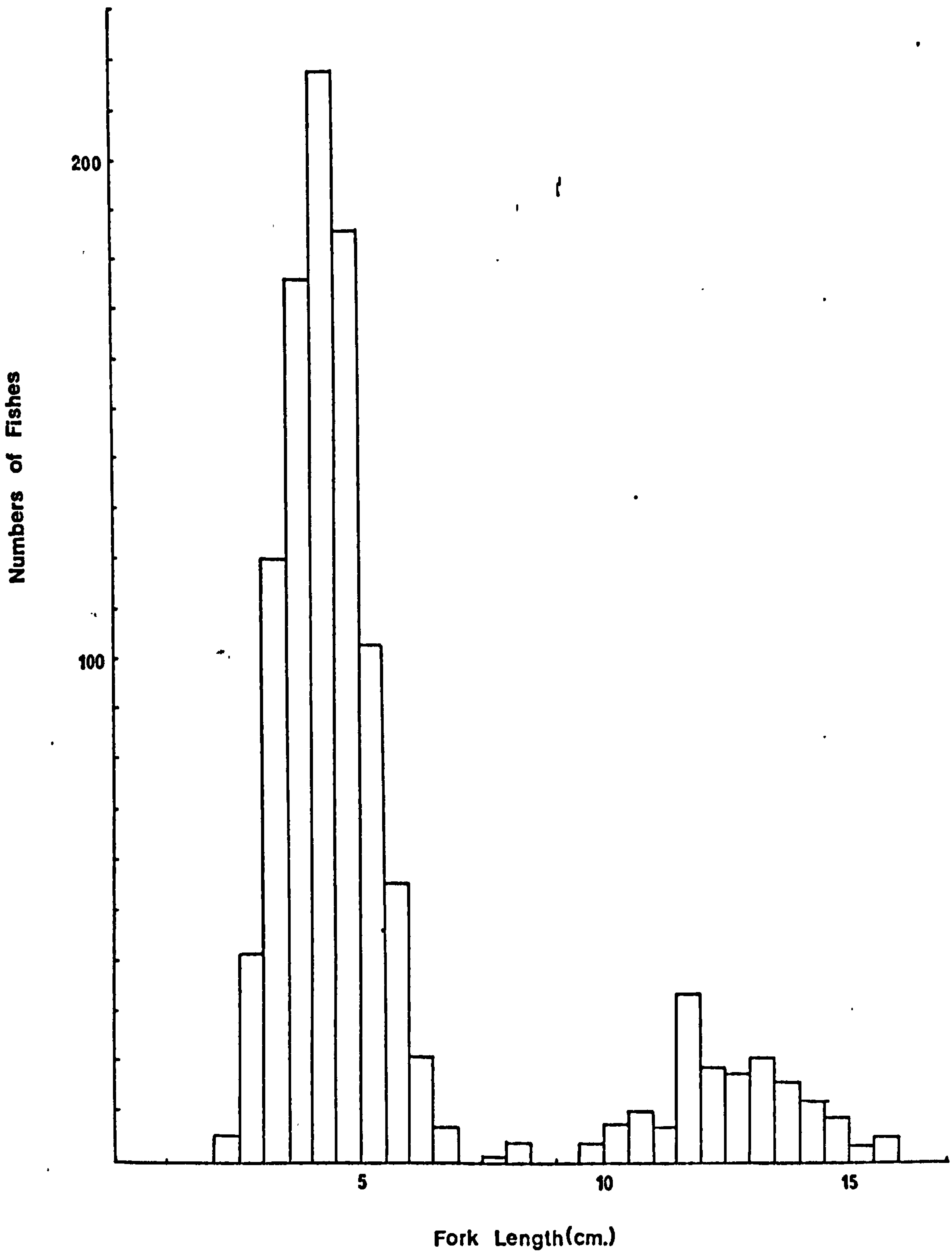


Fig. 49 Size Frequency Histogram for Darenth 39 Roach During Series 1

Fig. 50   Size Frequency Histogram for Dareth 39 Roach
During Series 2

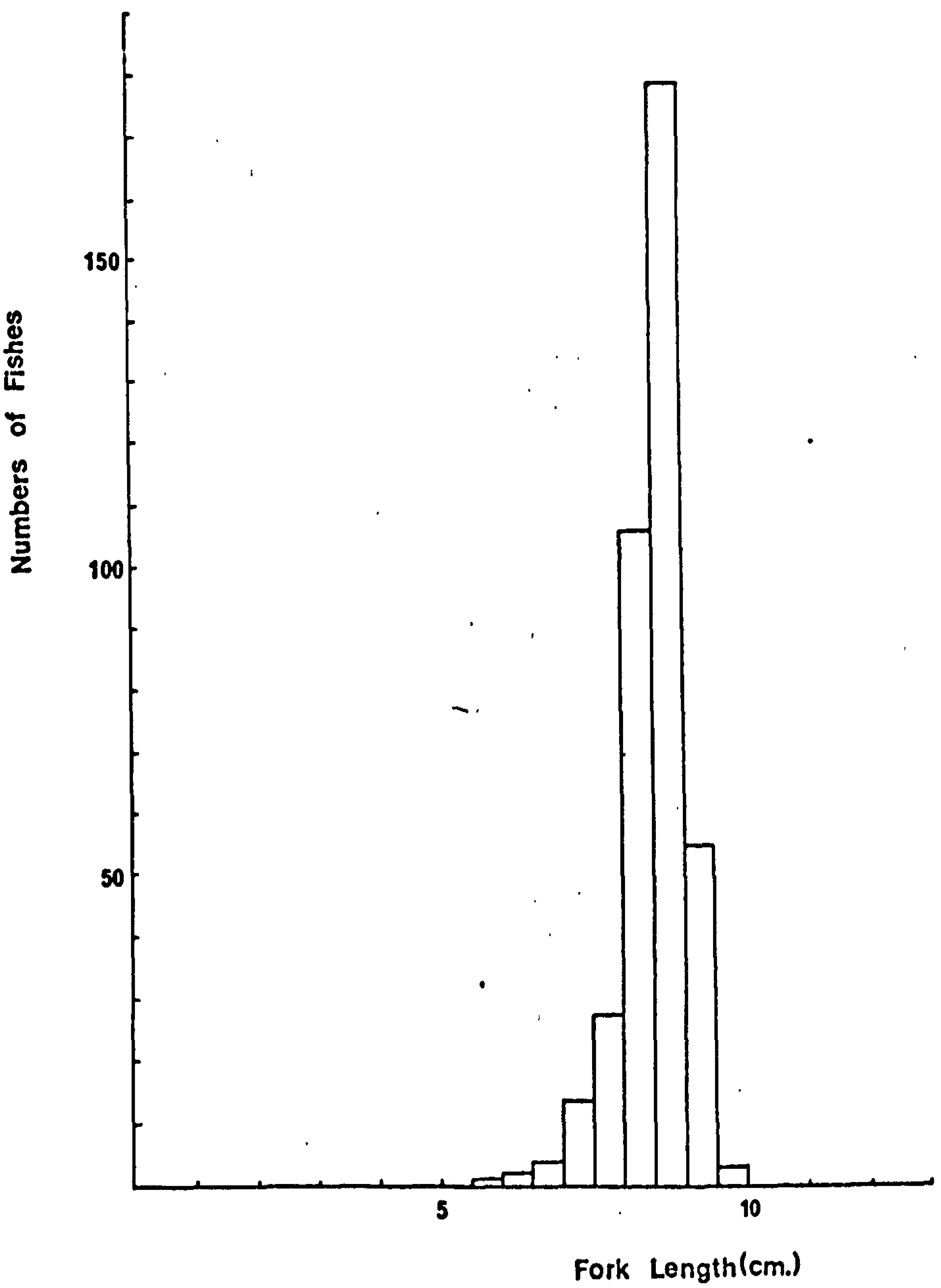


Fig. 51 Size Frequency Histogram for Darenth 39 Bream During Series 1

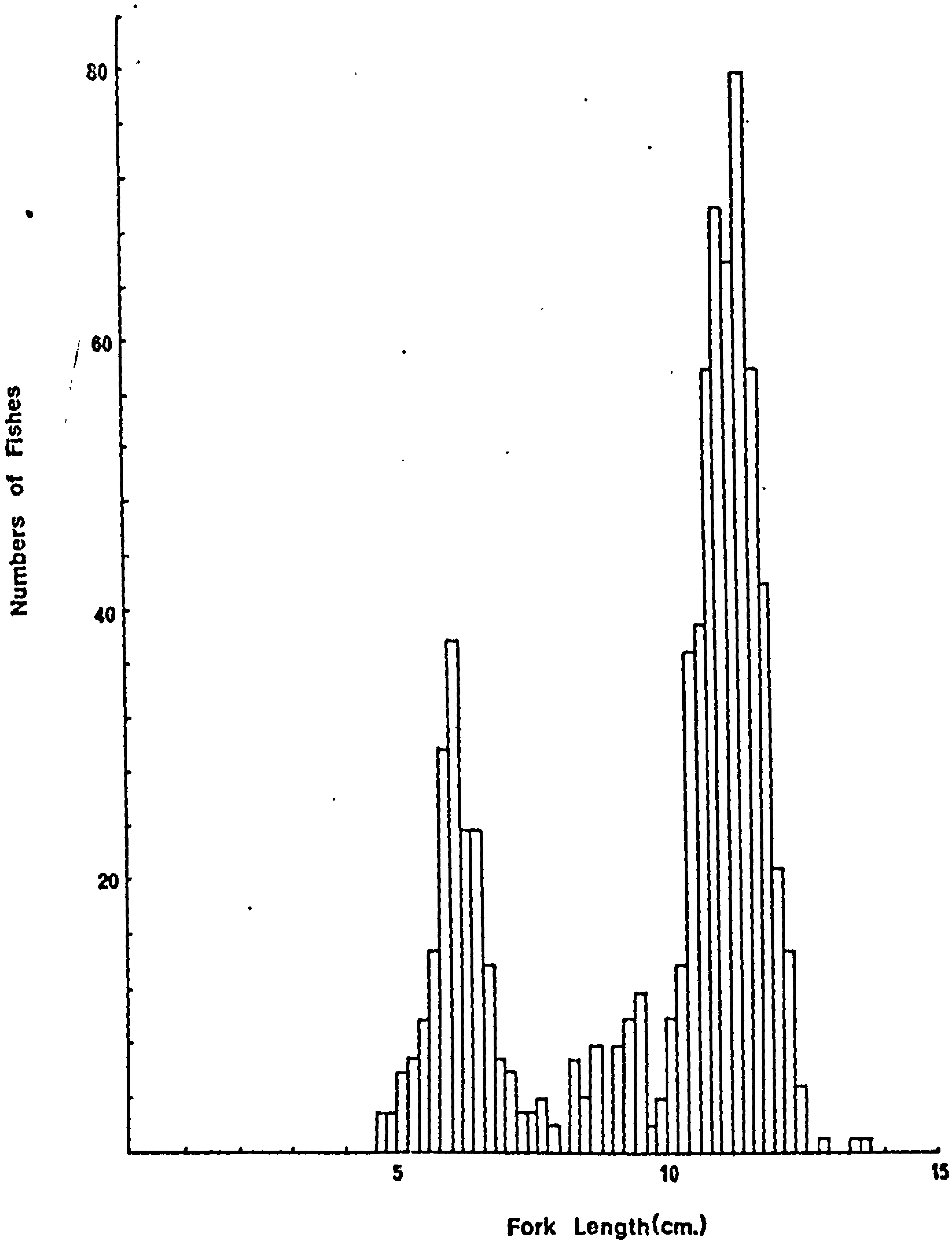


Fig. 52   Size Frequency Histogram for Darenth 39 Bream During Series 2

year-class had grown about 3 cm. The first mode represents the fry or 1973 year-class. Many larger bream were caught, including 60 bream ranging in length from 22 to 40 cm, a subsample of which were aged at 3+. On day 1 three larger bream (>50 cm) were marked but were not recaptured. These bream were tentatively aged at about 10+.

Rudd

During both Series 1 and 2 sampling large rudd were encountered (Appendix 2). These fish, between 25 and 31 cm in length, are rarely found in gravel pits and unfortunately no recaptures were obtained to permit estimation of their abundance. No scales were taken so that their age could not be determined.

Carp

Darenth 39 is a lake favoured by carp anglers in South-East England. Several carp were caught during netting but no recaptures were obtained in either Series 1 or Series 2.

Pike

The capture of only 5 pike in over 100 seines indicate a very small population of pike in this lake.

Gudgeon

The estimate of approximately 30 gudgeon (Table 19) seems low for a lake of this size. The gudgeon's demersal habit could result in bias in the seine net catches.

(e) Darenth 40

Roach

In Series 1 sampling (April 1973) roach and bream were both numerous in Darenth 40, by Series 2 sampling (October 1973) there were far fewer bream than roach, as shown in Table 19. Dry weather in 1973 caused the feeder stream to this small lake to dry up resulting in a drop in water level of 2-3 m, and a reduction in area of 75%. It appears that in these conditions roach were incapable of producing viable fry and the youngest roach in October 1973 were 1+ (1972 year-class). Back-calculation shows that these fish were about 4 cm long at the time of formation of their first check (Fig. 37). The scales of all the roach examined gave ages consistent with length-frequency data. Very few 2+ fish scales were found, agreeing with the small representation of this size group (∿10 cm) in the length-frequency histogram (Fig. 53). The relative size structure of the 3+, 4+ and older roach remained unchanged during 1973, as shown by the length-frequency distributions for Series 1 and Series 2 samples (Figs. 53 and 54). The 1972 year-class (estimated length 4 cm) passed through the seine net in April 1973. The whole of the Series 1 sample is therefore represented in Series 2 by the 8.5-18 cm length group. The mortality rate of the latter group is quite small ($Z = 0.82$) compared with that for bream ($Z = 3.22$).

Bream

In April 1973, prior to the reduction in size of the lake, there was a large population (>500, see Table 19) of bream in Darenth 40, consisting mostly of 0+, 1+ and 2+ fish (Fig. 55). Compared with bream from other waters, these would be described as stunted (see Section 3.2(b)). Difficulties in the capture and marking of such small, delicate fish prevented an estimate of the 1972 year-class being made during Series 1. By October 1973 the population consisted almost entirely of one year-class (1972). The relevant length-frequency distribution is shown in Fig. 56. The 1970 and 1971 year-classes had practically disappeared, implying a mortality equivalent to $Z = 3.22$.

Carp

In April 1973 the water depth was sufficient for carp to escape the net and no estimate of population size was made. However, after the 2-3 m drop in water level an estimate of 35 carp, 30-50 cm in length, was obtained from the October netting.

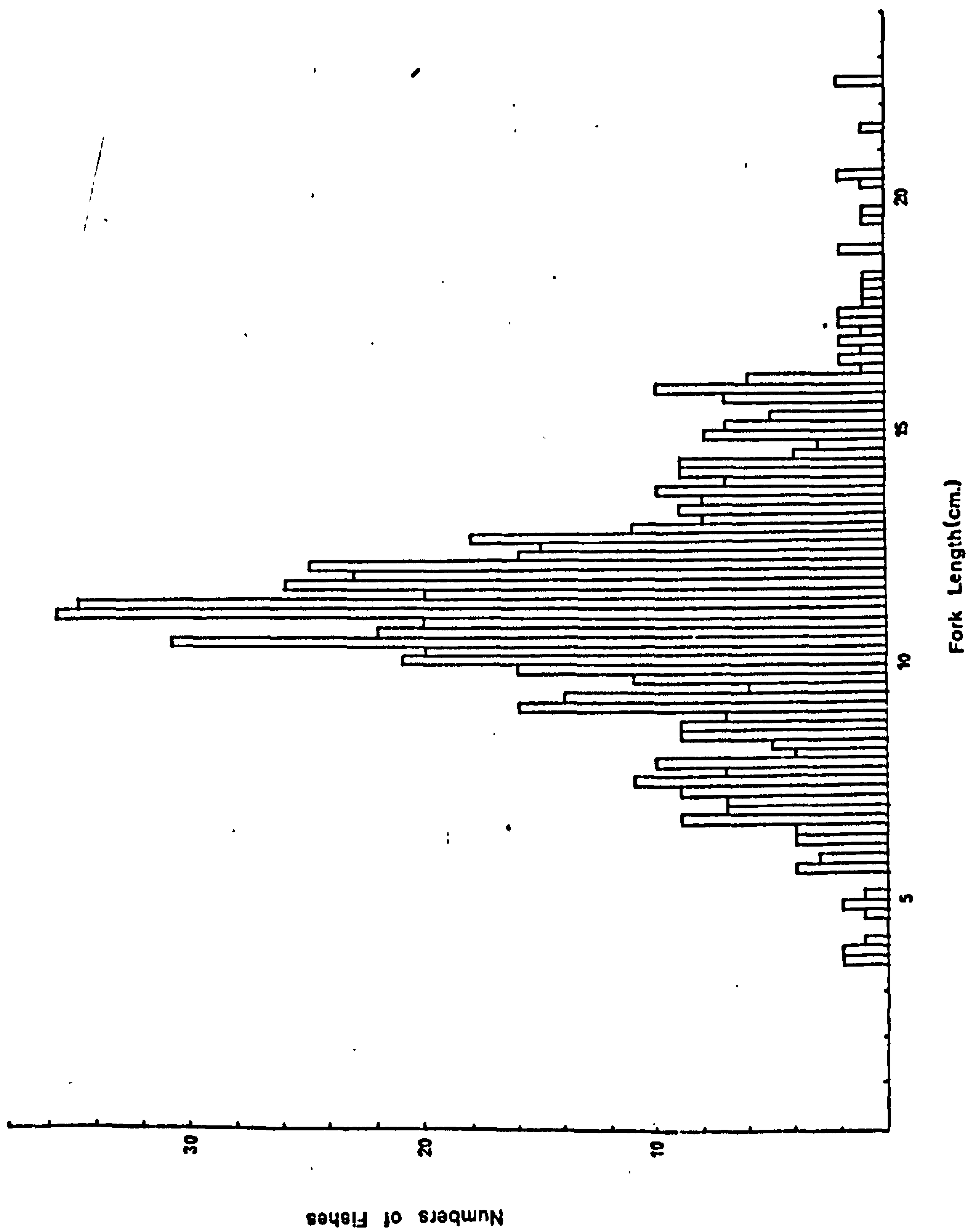


Fig. 53 Size Frequency Histogram for Darenth 40 Roach During Series 1

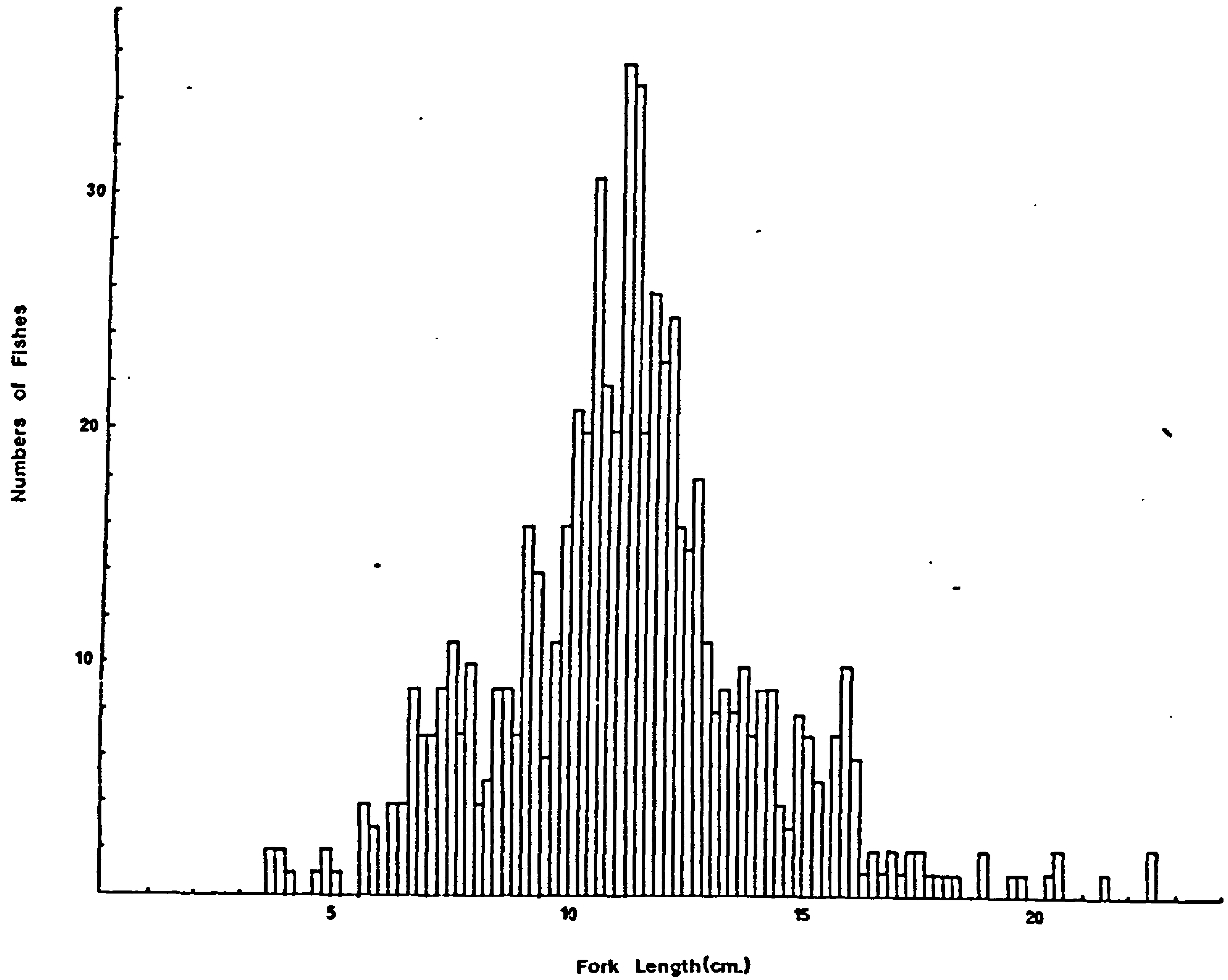


Fig. 53 Size Frequency Histogram for Darenth 40 Roach During Series 1

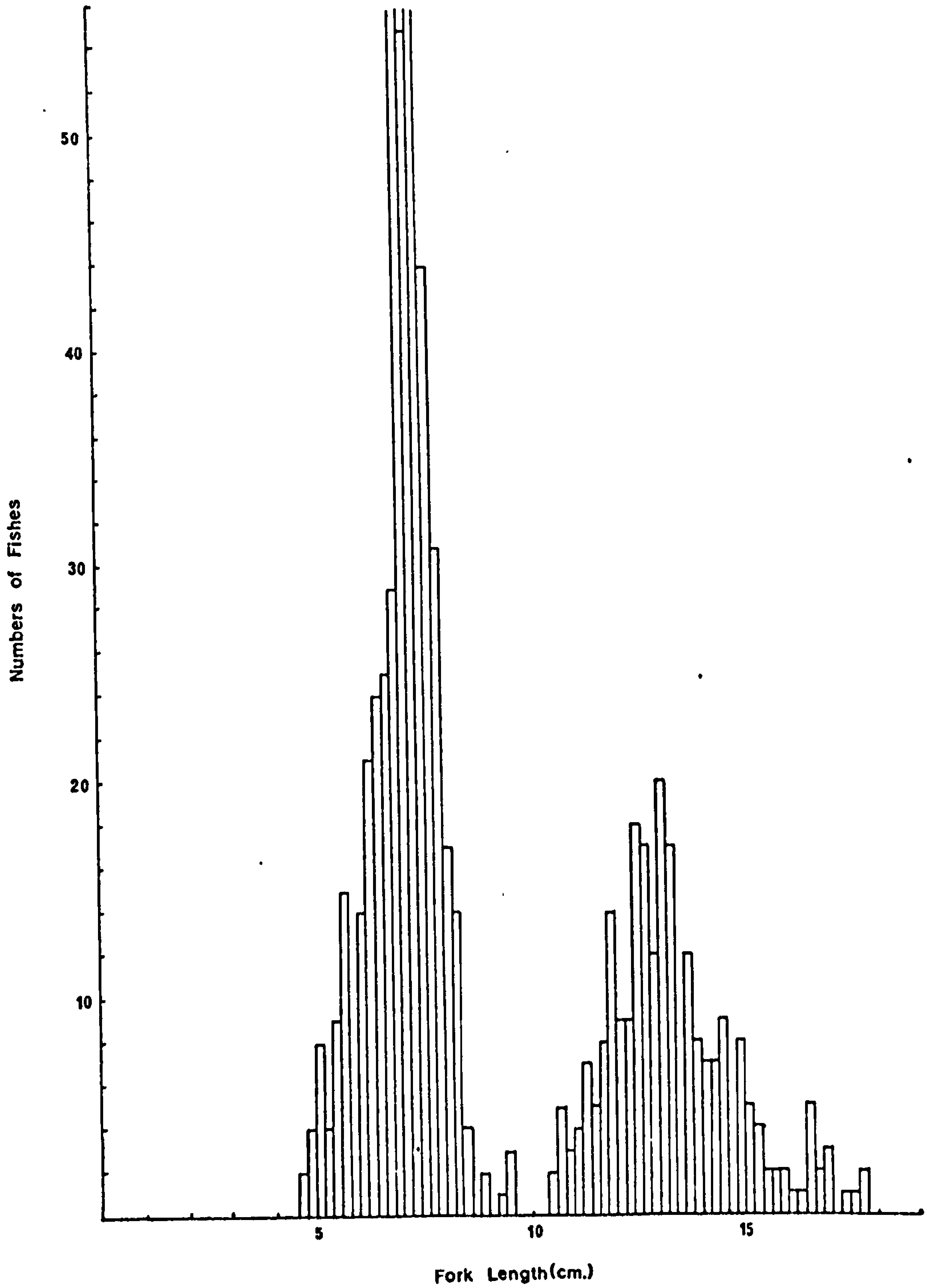


Fig. 54 Size Frequency Histogram for Darenth 40 Roach During Series 2

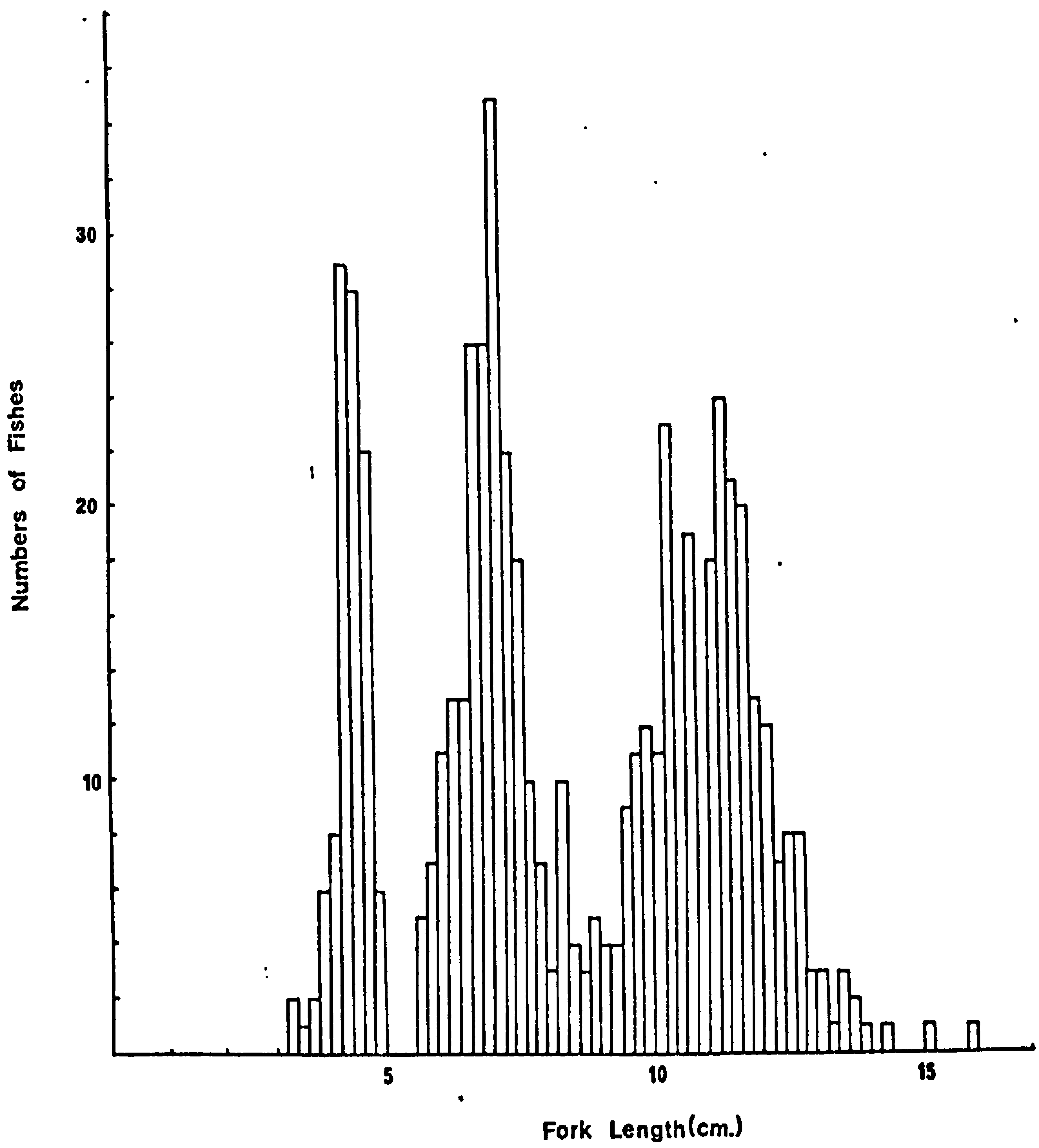


Fig. 55 Size Frequency Histogram for Darenth 40 Bream During Series 1

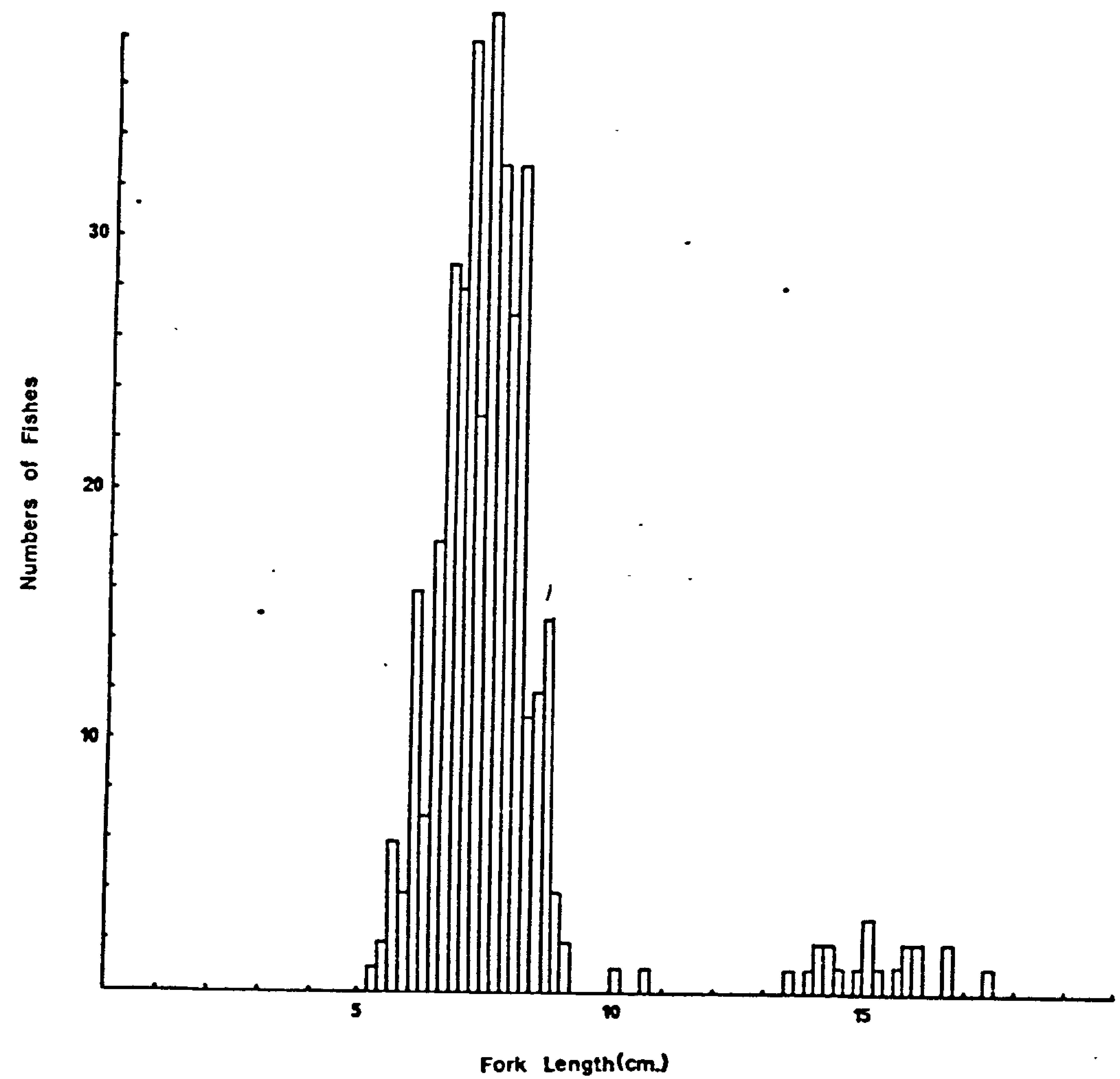


Fig. 56 Size Frequency Histogram for Darenth 40 Bream During Series 2

(f) Larkfield 41

Roach

The back-calculated growth (Fig. 38) from the sample taken in Series 2 (December 1973) indicate that lengths attained at age I are constant over a period of about 6 years with the exception of the 1973 year-class which had a faster growth rate. In contrast, the lengths attained by age II are extremely variable (5.9 - 8.2 cm). The change in the size of the lake that occurred during 1972 appears to have had little effect on the growth of fry or older fish. The increased growth rate in the 1973 growing season is common to the other gravel pit lakes also (see league of lakes in Table 16) and is likely to be a function of the higher temperatures in 1973 compared with 1972. The length-frequency distributions of the samples taken in Series 1 (May 1973) and Series 2 (December 1973) are very similar as shown in Figs. 57 and 58. The population structure changed little during the growing season. Comparison with the growth data (Fig. 38) indicates that the majority of the population in May and December consisted of 0+ and 1+ fish. In May these were the 1972 and 1971 year-classes whilst in December they were the 1973 and 1972 year-classes. The difference in mean length between the 0+ and 1+ fish in May was greater than in December due to the comparatively greater growth of fry in 1973. More 2+ roach are represented in the December sample than in May due to either a real increase in survival or that the Series 2 sample (taken in December) did not show the entire winter mortality which might be biased towards older fish.

The roach population appears to be in a steady state, mortality of one age group being compensated by the following generation. Like most gravel pit roach populations, Larkfield 41 is dominated by the 0+ age group.

Bream

Bream is the dominant species in Larkfield 41(see Table 19). During the survey in 1971 bream were caught in greater abundance than were roach. The slow growth of this population makes the interpretation of the length-

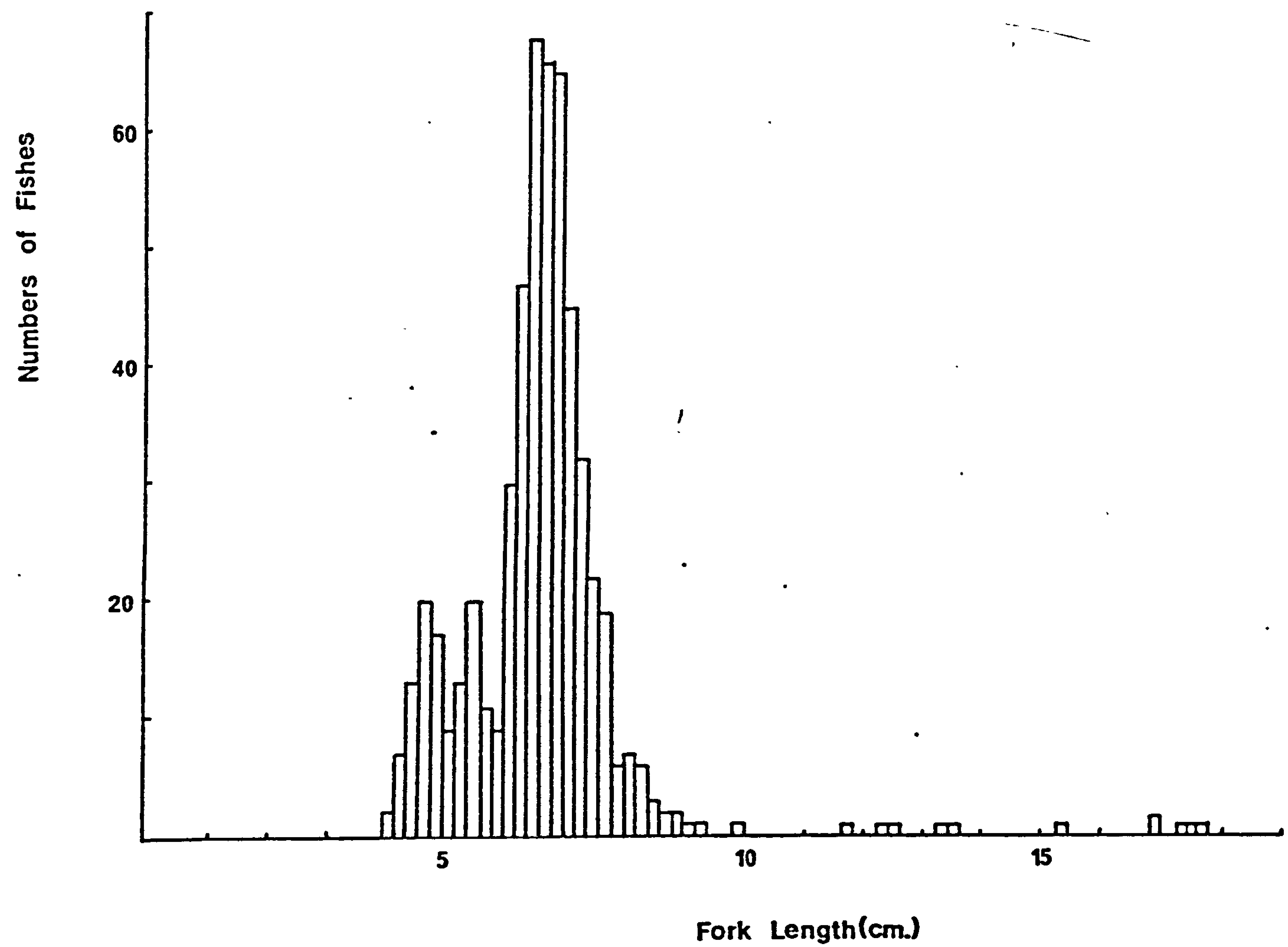


Fig. 57 Size Frequency Histogram for Larkfield 41 Roach during Series 1

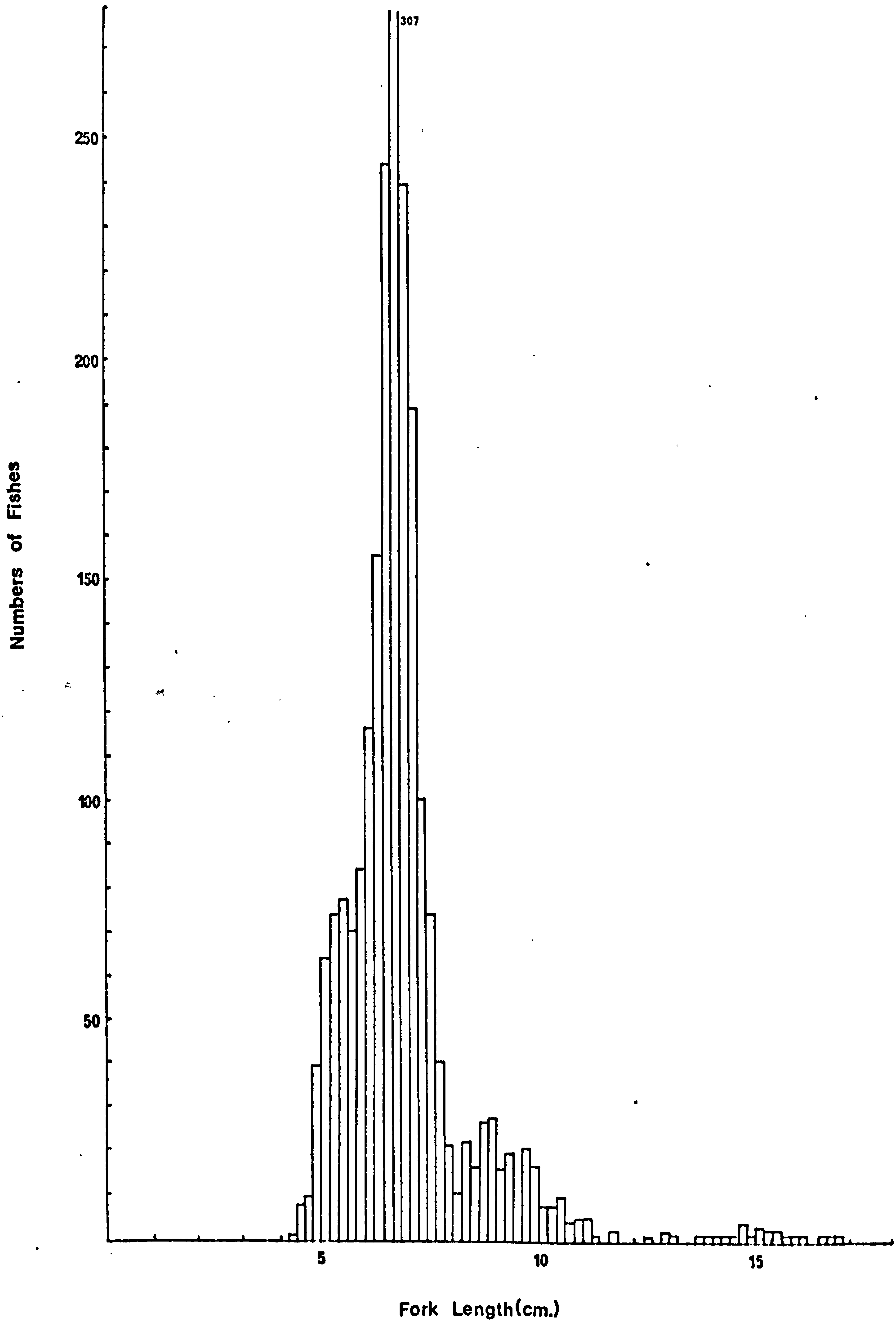


Fig. 58 Size Frequency Histogram for Larkfield 41 Roach During Series 2

frequency distributions (Fig. 59 and 60) very difficult. The first major peak in Fig. 59 (by back-calculation (Fig. 39)) consists of 0+ and 1+ bream (1972 and 1971 year-classes). In Fig. 60 the 0+ (1973 year-class) bream are easily distinguished, due partly to the rapid growth of the 1972 year-class. Bream between 7.0 and 10.4 cm in length belong to the 1971 and 1972 year-classes (2+ and 1+ respectively). The separate age groups of older fish are not distinguishable as seen in the length-frequency histogram (Fig. 60).

Unlike roach, bream are represented by a wide range of age and size groups. They are slow growing but have a lower mortality rate ($Z = 1.2$ over 3 years old).

Perch

During May 1973 very few perch were caught but in December 1973 large number of fry were taken (Appendix 2). The estimates for the total perch population and for fry only are similar. If the population structure at the end of 1973 is typical for this lake in the winter then very high fry and yearling mortality is likely.

Other Species

Very few fish other than those of the three species mentioned above were caught during the sampling program. Thirteen carp of the 'leather' and 'mirror' variety were marked but none were recaptured. Possibly as many as 50 carp of 15-25 lb live in the lake if the local anglers' estimates are to be believed. Fewer pike were caught in December than in May 1973 (see Appendix 2), the number in the population being at least 30. Insufficient recaptures were obtained for estimation of abundance. A few small rudd were caught in May but none were seen in December.

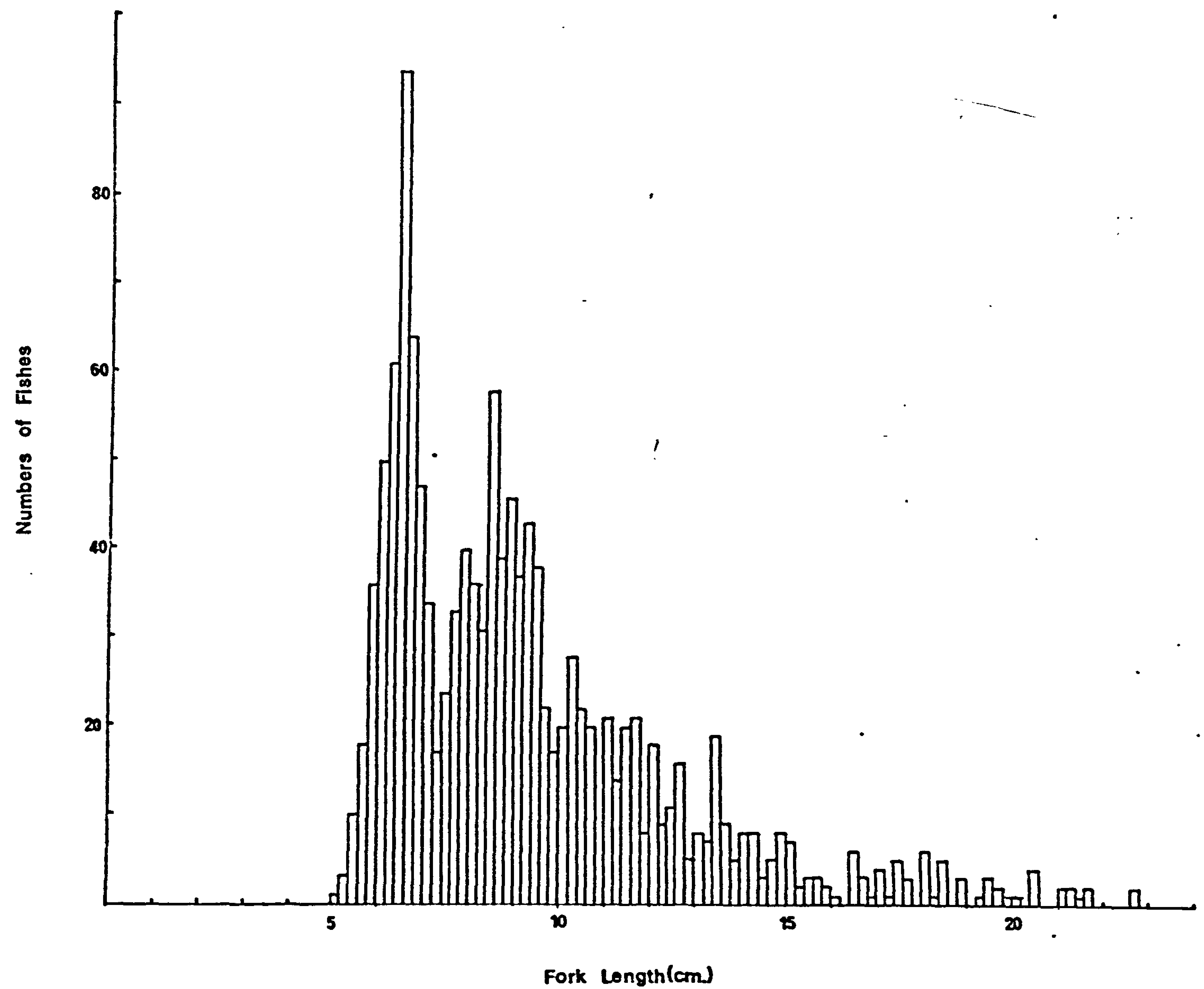


Fig. 59 Size Frequency Histogram for Larkfield 41 Bream During Series 1

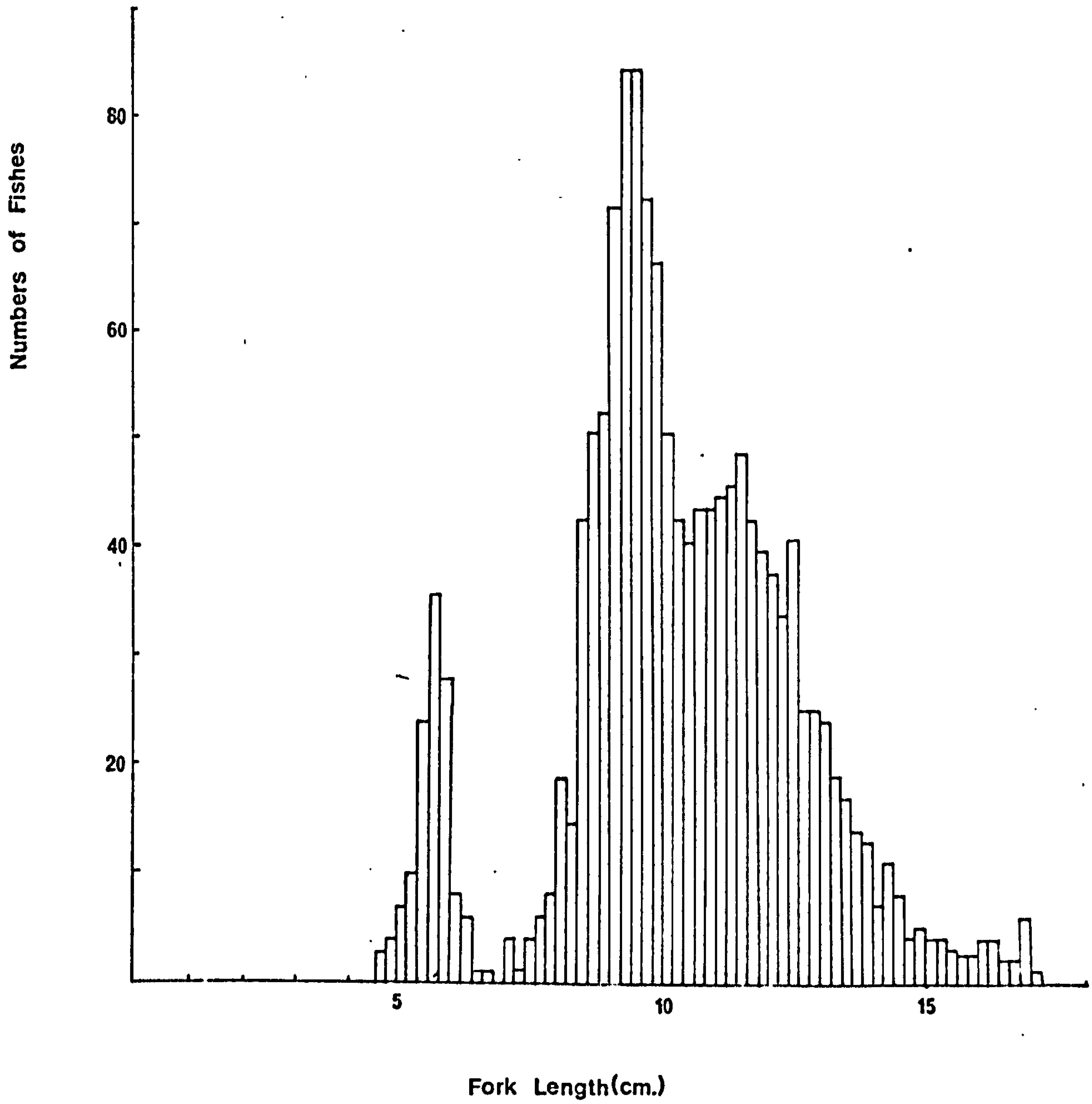


Fig. 60 Size Frequency Histogram for Larkfield 41 Bream During Series 2

3.3.5 Biomass and Production

Biomass and production estimates are given in Table 20; these are approximate in the case of 0+ fish as there was no initial estimate of biomass. A value for the instantaneous growth rate (a) of 0+ fish was obtained assuming an 'initial length' of 0.8 cm based on the mean length of samples of fry of several species after the absorption of the yolk sac. Mean biomass, $\bar{B}$, was calculated assuming an initial biomass value of zero.

TABLE 20 Population Parameters for 5 Lakes

Lake	Area m^2	Species + Age Groups	Density m^{-2}	G	Z	B2 $g.m^{-2}$	P $g.m^{-2}.yr^{-1}$	$P/\bar{B}$	Total P $g.m^{-2}.yr^{-1}$	Total $P/\bar{B}$
18(a)	11,740	Roach 0+	3.40	5.29	-	4,90	12.9	5.3	51.4	1.4
		1+	0.026	2.30	4.2	0.26	5.94	1.2		
		>2+	0.051	2.3-2.8	3.0	1.96	28.4	2.3		
		Perch 0+	0.09	7.59	-	0.52	1.95	7.6		
		Tench	0.034	0.15	0.0	9.8	1.44	0.15		
			0.030	0.08	0.25	9.3	0.78	0.08		
32	68,300	Roach 0+	0.044	8.13	-	0.06	0.46	4.1	1.96	2.8
		1+	0.15	3.57	-	0.51	0.91	1.8		
		Perch 1+	} 0.074	2.35	0.34	0.015	0.27	4.7		
		2+		1.37	2.76	0.009	0.31	2.8		
39	49,500	Roach 0+	-	6.69	-	-	-	-	7.54	1.9
		1+	0.03	2.11	3.15	0.49	4.93	2.11		
		2+	} 0.004	1.25	} 1.39	0.34	1.04	1.5		
		3+		1.71						
		Bream 1+	0.03	2.24	-	0.67	1.50	2.2		
		3+	0.001	0.30	-	0.26	0.07	0.3		

TABLE 20 Continued

Lake	Area m^2	Species + Age Groups	Density m^{-2}	G	Z	B2 $g.m^{-2}$	P $g.m^{-2}.yr^{-1}$	$P/\bar{B}$	Total P $g.m^{-2}.yr^{-1}$	Total $P/\bar{B}$
40	1,623	Roach 1+	1.42	1.75	-	6.59	11.55	1.8	49.8	1.3
		≥2+	0.19	0.26-1.32	0.82	4.92	5.96	0.75		
		Bream 1+	0.82	1.65	-	4.08	3.76	0.92		
		≥2+	0.015	1.51	3.22	0.84	28.8	1.5		
41	27,400	Roach 0+	} 0.26	6.76	} -	0.92	3.73	4.1	35.7	1.3
		1+		1.36						
		2+	0.031	1.21	1.55	0.38	0.55	1.2		
		≥3+	0.0015	0.77	2.30	0.085	0.38	0.76		
		Bream 0+	-	7.19	-	-	-	-		
		1+	} 3.18	1.35	-	35.2	26.5	1.2		
		2+								
		≥3+	0.066	0.27-1.22	1.20	1.98	4.49	1.0		

G = instantaneous rate of growth in weight

Z = " " " mortality

B2 = biomass during Series 2 sampling

P = annual production

$\bar{B}$ = mean annual biomass (between Series 1 and Series 2)

SECTION 4: DISCUSSION

4.1 Growth Rates of Fish in 39 Gravel-pit Lakes

The survey of the growth of coarse fish in 39 gravel-pit lakes has shown that growth between lakes is variable and allows comparison with that found by other workers in different waters.

In the case of the roach, survey catches in some lakes contained only 0+ fish, so that comparison is restricted to the length attained by the time of formation of the first check. Hartley (1974) examined roach from a variety of still and flowing waters in England. He commented on the large range of growth-rates in the species. The majority of Hartley's fish are 6-7 cm fork length at the time of formation of the first check, though fish from a pond of area 1 acre had a mean fork length of 8.9 cm. During the survey described in this thesis the highest value recorded was 9.5 cm in Darenth 38 and the smallest 3.5 cm in Larkfield 41. The majority of age I lengths are in the range 5.5 - 7.5 cm. Hartley (1947) quotes a German roach population with an age I length of only 3.35 cm. Hartley suggested that the high growth rate of his small-pond fish was due to 'the youth of the fish comprising the sample'. In the present investigation a similar hypothesis is possible for the extremely rapid growth of roach colonising a lake (Twyford 32) previously dominated by pike and perch (see Section 3.3.2.a(ii).

Frank (1962) reports the labile growth pattern of roach from ponds in the Elbe region of Czechoslovakia. The growth rate rapidly increased at the beginning of their third year of life following a considerable reduction in population number. Average age I lengths (probably standard lengths) were in the range 4.2 - 6.5 cm. All Frank's roach were less than 8 years old.

Kempe (1962) also observed variable growth rates of roach in large Swedish lakes. Characteristically, a reduction in population density resulted in faster growth of individual fish compared with former conditions, at least for a few years. Kempe suggested a length of 4.0 cm at the end of the first year was 'common in lakes of "natural" type'. It is interesting that Kempe could find no connection between age I lengths and the relative abundance of the year classes. He describes many of his roach populations as stunted.

River Thames roach during the 1960s are often described as particularly slow growing. Williams' (1965) data show that the first year lengths were small (∿4.2 cm) and roach reached only 18 cm in 10 years. In contrast, Darenth 38 roach reach 17 cm in 5 years, Darenth 40 roach 22 cm in 7 years and Yateley 3a + b roach 26 cm in 6 years. The oldest roach for which growth curves were drawn in the present investigation were 9 years old and 28.0 cm long (Sutton-at-Hone 35).

Holcik (1967a + b) studied roach-dominated reservoirs in North-West Slovakia. First year lengths (standard lengths) were similar in both reservoirs and, at 4 cm, considerably smaller than in gravel pit lakes. The two reservoirs described had dramatically different growth rates in different years, however. One had roach up to 8 years of age, at 23-27 cm, whilst the other contained 18 year old roach only 26 cm long. Holcik ascribes the rapid growth rate to the low density of fish and high productivity of food organisms in the newly built reservoir. In a foot-note to his paper (1967a) he reports a decrease of the growth trend, suggesting that the roach population might have 'outrun the development of food supply' with intra-specific competition increasing as the food supply decreased.

Observed lengths-at-age of roach in Willow Brook, Northamptonshire (Cragg-Hine and Jones, 1969) indicate an average or slightly less than average growth rate for the species compared with other waters, and a much slower rate than most gravel pit lakes. Competition for food is suggested as the likely cause of the slow growth rate in Willow Brook. No estimate of population density or of available food was made for the gravel pits during the survey period.

The slowest growth rates recorded for British roach are those by Mills (1969) in several Scottish waters. First year fork lengths are typically about 3 cm, Hunbie Reservoir fishes attaining only 16.3 cm (males) and 18.2 cm (females) in 9 years.

Banks (1970) states that the growth of the roach in Rostherne Mere is 'faster than any British population yet described'. Rostherne Mere is dominated by perch, and pike are quite common. The Rostherne roach have little competition for food from other species, as the lake does not contain any other cyprinids. The two Twyford lakes 32 and 33 are similar in this respect, though at the beginning of this study roach numbers were also low. Rostherne Mere roach growth rates are similar to those of most gravel pit lakes surveyed.

Wilson (1971) gives the highest recorded growth rate for roach in Britain. First year lengths of up to 15 cm are shown in a graphical plot of length-at-age, though the accompanying tables give a range of 7-15 cm for fish aged 1+ in October. This suggests that a length of 15 cm is not attained in one season. 0+ roach in October lie in the size class 0-7 cm suggesting up to 7 cm fork length attained by age 1 year. Wilson's roach were heavily parasitised by *Ligula intestinalis* plerocercoids as are many gravel pit roach. Assuming the lower lengths-at-age described above, Wilson's roach are still fast growing, and are comparable with the faster growing roach of gravel pit lakes.

Hellawell's (1972) growth estimation for River Lugg roach is difficult to evaluate because no tables are provided, and the graphs are based on fish of 3 years of age and older. Lengths for the first 2 years are obtained by extrapolation. His approach of combining all year-classes in monthly samples for the purposes of calculating a mean length-at-age obscures any differences there may have been between year-classes, and consequently makes comparison with other waters less meaningful.

The most recent published data on the growth of roach in Britain are those of Mann (1973) for two chalk streams in southern England. Though there are differences between the growth rates of the sexes, the difference between rivers is considerably greater, particularly in the case of older fish. In fact the growth rates during the first 3 years in both these rivers are similar, being slower than in most of the gravel pit lakes.

The bream is a very common freshwater fish in Britain (Maitland, 1972) but very little has been written about its growth rate. Kennedy and Fitzmaurice (1968) describe in detail the biology of the bream in Irish waters, and the very extensive foreign literature on the species is summarised by Backiel and Zawisza (1968). Gravel-pit bream compare favourably in growth rate with Irish fish. Kennedy and Fitzmaurice quote 22 cm as slow growing and 33 cm as fast growing for 7 year old fish. Their fast growing fish took 14 years to reach 50 cm which compares well with those few 'specimens' aged in the present work. Backiel and Zawisza (1968) quote the range of growth rates found over the species range, namely 13.9 cm to 40.5 cm in 7 years. A 'medium' growth rate, in their estimation, would result in a fish of 31.8 cm at this age. Gravel-pit bream, compared with fish from other waters, can therefore be described as having medium growth rate. Bream (maximum age 5 years) described by Hartley (1947) from the Norfolk Broads appear to have a 'medium' growth rate being similar to some gravel pit populations particularly those of Sutton-at-Hone 35 (Fig 10).

There are few published data on rudd growth. Hartley (1947) gives no information on growth during the first two years of life. The range of growth rates he describes is wide, fish reaching up to 14 cm in 4 years or as little as 9 cm in the same period. Typically, the gravel-pit rudd reach 15 cm in this period, though the 1968 year-class in Yateley 9 reached 18.2 cm in 4 years (Fig 22). Wide variations in growth rate occur between different year-classes and different years even within one lake. Frank (1962) quotes remarkably uniform growth rates between different year-classes of rudd in Czechoslovakia all of which are slow growing. He mentions that the growth of rudd in rivers is commonly slow compared with that in ponds. The growth rate of rudd in small experimental ponds in the Netherlands is far faster than found in any gravel pit surveyed, fish averaging over 21 cm in 4 years (Steinmetz, 1974). The gravel-pit rudd examined can therefore be described as having medium growth rate compared with rudd from other waters.

The best documented perch population is that of Lake Windermere (e.g. LeCren, 1958). This work describes the variability of perch growth from year to year and the dependence of growth rate on temperature and population density. Dramatic changes in growth rate took place in Farnborough 18(a) perch between 1964 and the years subsequent to 1968, (Fig. 29). In contrast, perch from both Twyford lakes have very uniform growth rates. Wide fluctuations in abundance and accompanying growth rates are common in perch (Alm, 1952; LeCren, 1955) and yellow perch, <u>Perca flavescens</u>, (Forney, 1971). The Farnborough 18(a) 1968-1972 year classes are slow-growing compared with Twyford 32 and 33 perch, being similar to those of the River Thames (Williams, 1967). Both Twyford lakes show growth rates similar to those described for three Irish lakes by Healy (1954) and for 1949 male perch in Windermere by LeCren (1958). Compared with most recorded growth rates these are very fast. These two groups are also comparable with Dubh Lochan and Loch Lomond perch respectively (Shafi, 1969).

The difficulty of obtaining large samples of ageable pike is probably responsible for the scarcity of growth rate information available on British pike.

Banks (1970) had difficulty in ageing pike from Rostherne Mere, the opercula being impossible to read and the scales unreliable. However, the large samples Banks obtained permitted the construction of growth curves based on direct measurement of lengths of the fish when caught. Even so, the large variance of lengths-at-age of each year class provided only approximate values for each mean. Rostherne pike are slower growing than is common in Windermere and slower than in most gravel-pit lakes. Banks (1970) attributes this slow growth to the inhibition of successful prey capture by limited visibility resulting from turbidity.

The scarcity of information on other species of coarse fish in the literature prevents any useful comparison with that in this thesis.

4.2 The Capture-recapture Method for Estimating the Populations of Fish in Gravel-pit Lakes.

As outlined in Section 3.3.3 it is difficult to evaluate the relative performance of the models used to analyse the 3-4 day capture-recapture data. The similarity between the estimates obtained by the de Lury (1947) catch-depletion method and the modified Triple-catch model which allows for marking 'mortality' does suggest that the latter model has some advantage under the circumstances encountered in this present work. Other data also support the case for using the modified Triple-catch model, e.g. the Series 1 results for tench at Farnborough 18(a), (Section 3.3.3). The proportion of the population marked is quite high (40%) and the panjet marking is unlikely to cause mortality in fish of this size. Neither is there likely to have been any immigration. Yet, the differences in the estimates, particularly the Lincoln Indices and the two Triple Catch methods, suggest non-random recapture. The estimates for males and females separately are smaller in the Triple Catch method which assumes some mortality indicating that there has been either mortality or a decrease in catchability of marked members. Comparison of the simple Lincoln Index and Triple Catch results, however, indicate the reverse. There is no obvious trend for an increase or decrease in Leslie estimates in comparison with the other methods, though Jolly estimates for these tench are consistently higher.

If marked fish either die after release or are subsequently more difficult to catch the estimate allowing for marking mortality should give a larger estimate of abundance than the standard Triple Catch model. The majority of estimates in Tables 18 (and in Appendix 2) do in fact show this phenomenon.

Should marked fish suffer mortality after release or become less catchable by the sampling gear the Leslie and Jolly estimates are likely to decrease. For example, though the death of marked individuals will reduce m_i in the Jolly model thus lowering the value of a_i, the effect is likely to be greater on the estimate M_i, thus resulting in a lower estimate

N_i. There are few instances where such comparisons are possible, four sample periods being the minimum requirement. Series 2 Darenth 39 day 3 estimates are, except for gudgeon, lower than those of day 2 indicating some loss of marked members. In all these cases the calculated probability of survival was less than unity for the interval between the second and third day samples. As we would expect, the Lincoln Index estimates for these groups of fishes are also smaller on day 2 compared with day 1. Similarly, allowance for death of marked fish results in higher estimates using the Triple Catch model. Leslie estimates are in all cases higher on day i + 1 compared with day i. Provided marking mortality is not excessive, however, the increase in the proportion of marked members in the population with increase in the number of sampling periods should give more precise estimates of abundance. As there is no independent evidence available to check the behaviour of marked fish it is considered more prudent to rely on the clues provided in the comparison of the two Triple Catch methods.

4.3 Parasitism and Predation

Some accidental deaths do occur as a result of angling in spite of coarse fish being returned to the water after capture. There is some evidence during warm weather of increased mortality; dead fish of catchable size were often seen floating around lake margins after weekends of heavy fishing. Unlike game fisheries there is no record available of fishing mortality.

Natural mortality results from many causes such as senescence, predation, parasitism and disease. The majority of gravel pit fish are young (see page 147) and it is unlikely that senescence contributes significantly to mortality. During this investigation there was no evidence of any disease likely to cause high mortality. In gravel pit lakes more important factors are parasitism and predation. During this study examination of the parasite fauna of these fishes has implicated the cestode *Ligula intestinalis* in fish mortality. The plerocercoid larvae of this parasite, though occasionally found in other species, only survive and develop in cyprinid fish. During the survey plerocercoids were found in many gravel pit fish (Table 8). Both roach and bream in Darenth 39 were found to be heavily ligulosed. A sample of fish taken in November 1973 was found to have the following degree of ligulosis:

Species	Age	% Ligulosed	No. of Fish Examined
Roach	0+	30	30
"	1+	89	68
"	3+	36	11
Bream	0+)	90	50
	1+)		44

Individual roach normally contained about three *Ligula* though one fish, 19.3 cm long, contained 20 Ligula contributing 19% of its total weight of 134 gm. The pathological effects of *Ligula* are severe (Arme and Owen, 1968) and it can castrate its host (Brylinski, 1972). Wilson (1971) reports a marked decline over a 3 year period of roach which he attributes to the high incidence of *Ligula*. Brylinski (1970) found up to 72.3% of a large bream population to be infected by *Ligula*, with up to 50% mortality in those heavily infected. The mortality due to the parasite was found to be higher in the younger age groups. Harris and Wheeler (1974) suggest that heavily ligulosed bleak in the Thames die during autumn and winter following their infestation. The deleterious effects of *Ligula* on its host can also be indirect. The pathological effects and the gross distortion of body shape and breakdown of camouflage (Sweeting, 1971) probably affect the fish's ability to avoid predators. The decrease in the percentage of ligulosed roach in Yateley 4, as discussed in Section 3.1, indicates higher mortality of infected fishes. The decrease in the size of the roach between November 5th and December 6th (Fig. 2, p. 50) is likely to be due to the selective predation of larger fish. The pike population is large compared with the probable roach population.

Unfortunately, experiments conducted to test the hypothesis of increased predation on ligulosed roach by pike failed for a number of technical and climatic reasons.

Twyford 33 is an example where the recruitment of perch is affected by a large pike population. This is complicated by the presence of a large eye fluke Tylodelphys podicipina in the perch. The parasite's unusually large size together with its high density per eye could affect the perch's vision and possibly its efficiency in seeing and avoiding predators (R.A. Sweeting, personal communication).

Pike and perch are voracious predators, occurring in many gravel pit lakes, though, with the exception of Twyford 33, very few of the perch are more than 10 cm in fork length.

Piscivorous birds can contribute to the mortality rate of gravel pit fishes. Such birds are often very numerous, especially gulls. Resident pairs of Great Crested Grebe, Podiceps cristatus, are common on gravel pit lakes, and were often observed eating roach and bream.

All six lakes studied in detail show high mortality rates (Table 20). It is unfortunate, however, that in most cases, accurate estimation of mortality was not possible because of the difficulties involved with abundance estimation. The population structure of each lake in Series 1 and 2, discussed in Section 3.3.4 indicate high mortality rates, particularly in the younger age groups. Pike predation is a likely factor operative in Twyford 32 and 33. The very few pike in Darenth 39 and Larkfield 41 are unlikely to cause such a high level of mortality on their own; the contribution of large numbers of Ligula was probably important. Ligula probably contributed to mortality in Darenth 40 but a more significant factor in 1973 was the large drop in water level. Farnborough 18(a) is unusual in having neither pike nor Ligula. The population certainly contains a higher proportion of older fish than in other waters, yet the annual mortality rate is high at 3.0.

There is no obvious relationship between density and mortality rate in these six lakes. No exact measure of mortality can be obtained because most lakes were dominated by 0+ and 1+ fish. There is a wide range of stock densities but it is not known if this is due to differences in egg production or survival. It seems unlikely, under the conditions experienced during the present study, that density affects mortality. The wide range of growth rates emphasises this point.

4.4 Biomass and Production

The population studies carried out on the six selected lakes have confirmed many observations made during the survey of the whole series. But, not only are gravel pit lakes variable in their composition and growth rate of species, major differences can occur with time within any one lake. Lakes have species compositions ranging from a pike+perch to a roach+bream dominated fauna. They are also variable in area and population density. It is of particular interest that one of the largest lakes (Twyford 33) should have not only the lowest fish density but also the smallest total population. The decline of the Twyford population was so great as to prohibit any estimation of production. Comparisons of growth or production rates of individual species between different lakes are not very meaningful because of the degree of variability of the populations studied. For instance, roach growth is extremely variable between lakes but in some waters roach is the dominant species whereas in others bream or tench are more numerous. The contribution of different year-classes and species to the overall production is also variable (Table 20). However, given the many shortcomings of the estimates of the basic population parameters, the total fish community production (P g $/m^2$/year) is logarithmically related not to numerical density but to biomass density ($\bar{B}$ g $/m^2$). Those few species not included in the production totals are present in such small numbers that their contribution to either production or biomass is probably insignificant. For the 1973 growing season the relationship is shown in

Fig. 61 to be $P = 2.4\ \bar{B}^{0.82}$. Since production is calculated by Ricker's formula (Ricker, 1946) as $P = G\bar{B}$, the concept of an average community growth rate, $\bar{G}$, allows us to write (Fig. 62) $\bar{G} = 2.4\ \bar{B}^{-0.18}$.

Thus, the 'average growth rate' $\bar{G}$ is inversely density-dependent. The concept of an 'average growth rate' also implies some degree of interaction between individuals of the same and different species. It is surprising that fish as different in size as roach fry and tench adults should have this interaction. It will be noted, however, that though different in species composition, the populations of all the lakes studied are similar in comprising mostly small, immature fish, predominantly cyprinids. If growth is a resultant of such community interaction as proposed above, it follows that growth rate of individual species in such contrasting community types should be so different.

The P : $\bar{B}$ curve in Fig. 61 is probably applicable to the time of sampling only. A similar relationship might be expected under other conditions but with numerically different coefficients. Temperature in particular would affect the intercept of the curve.

The effects of density on fish production have been the concern of fish culturists for many years. Walter (1934) showed how increases in stocking density (numbers of fish per unit area) decreased the growth in weight of individual carp. Transformation of the data showed an inverse relationship between the average individual growth in weight of these carp and the logarithm of the original stocking density. Beckman (1941) was able to demonstrate an increase in the growth rate of previously stunted rock bass, (Ambloplites rupestris) Rafinesque following a reduction in population density through poisoning with rotenone. A reduction in the population of perch in Windermere to less than 10% of the former level resulted in no appreciable increase in average growth rate (LeCren, 1958), but LeCren suggests that initially in such cases food supply is not a limiting factor for production or growth. Comparison of LeCren's work with Fig. 62 shows that in the gravel pit lakes in 1973 a reduction in mean biomass from 40

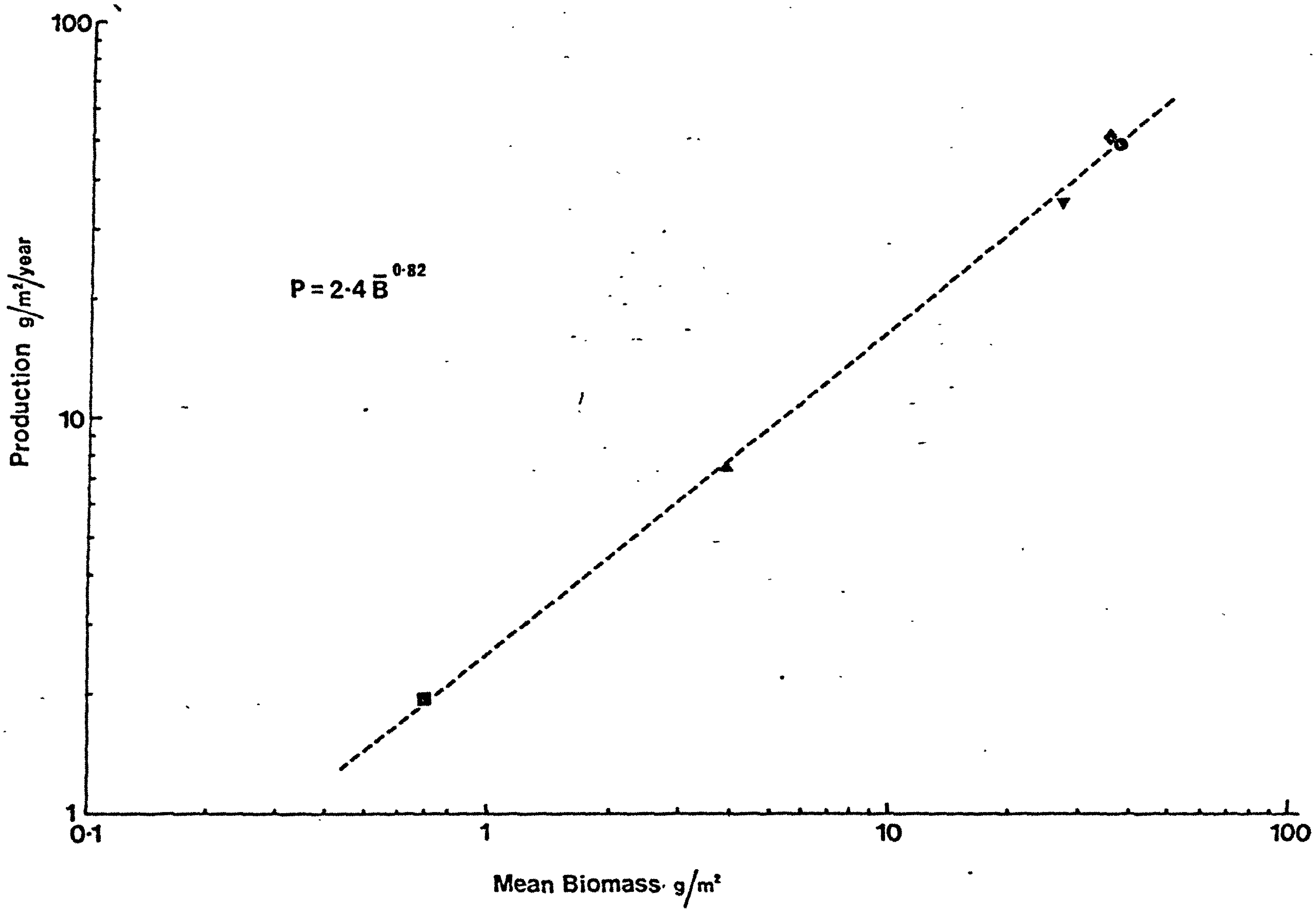


Fig. 61 Logarithmic Plot of Total Fish Community Production v. Mean Biomass

■ Twyford 32 ▼ Larkfield 41 ◆ Farnborough 18(a)
▲ Darenth 39 ● Darenth 40

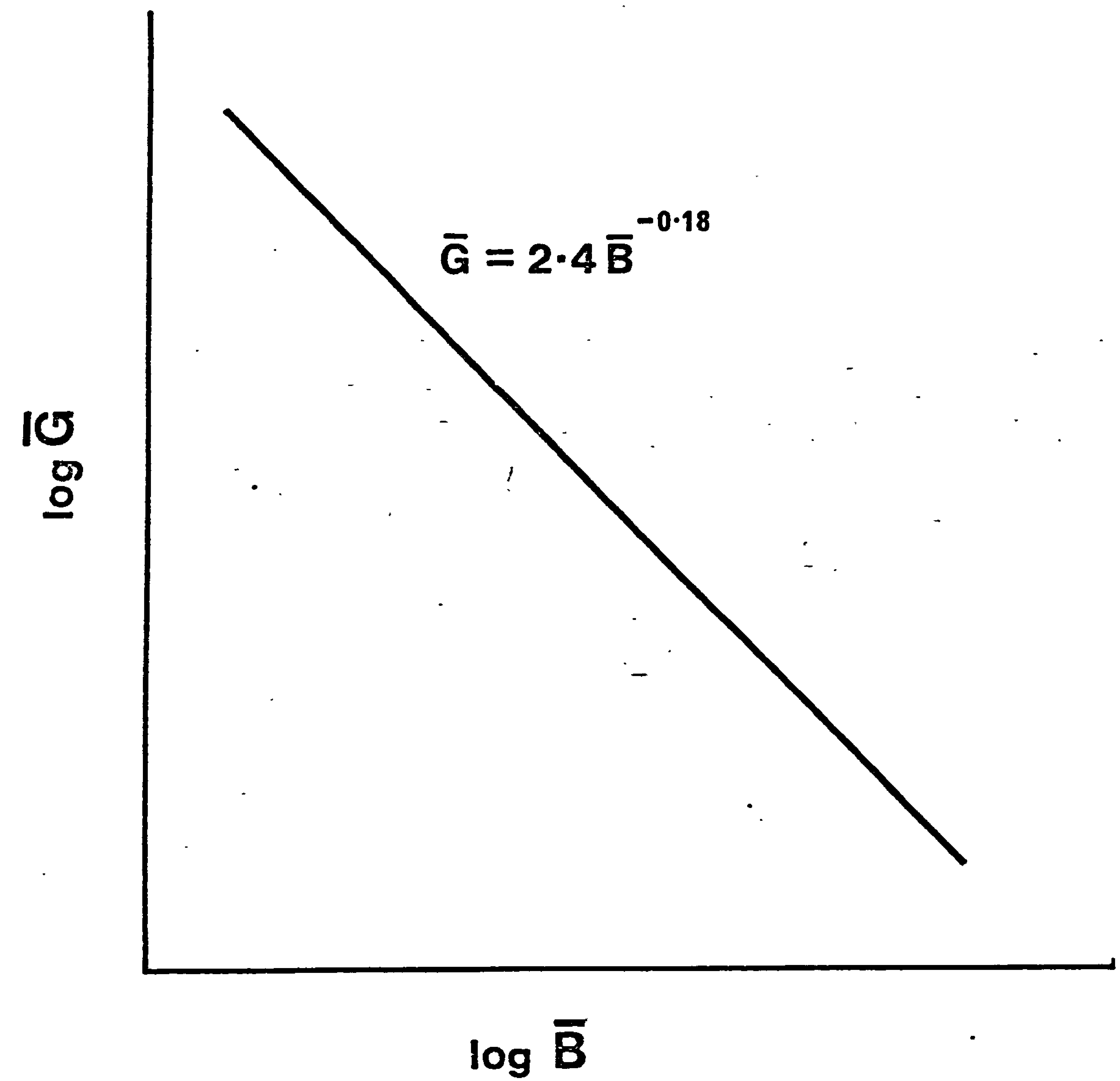


Fig. 62 Theoretical Plot of Mean Instantaneous Growth Rate of the Total Fish Community v. Mean Biomass

to 20 gm/m^2 would also have had little effect on increasing the growth rate. Therefore, as LeCren showed, though changes in growth rate are not always density related, controlled experiments suggest that growth rate is inversely related to density. Backiel and LeCren (1967) summarize their review of the subject by stating that '... in the less complex communities at least, major changes in population density are nearly always accompanied by inverse changes in growth rate' (my italics). Unfortunately, the majority of published studies have been concerned with single species systems or with one species in a mixed community. The gravel pit lakes studied in this work, though often containing several fish species, are usually dominated by one species. Even where two or three species are abundant they are mainly represented by small or immature fish, such as roach, bream and perch in Larkfield 41, and roach and bream in Darenth 39. In this way these gravel pit lake communities can be considered 'less complex' in the sense used by Backiel and LeCren and so an inverse relation between growth rate and density is to be expected. Larger fish such as carp and pike in Darenth 39 and Larkfield 41 and tench in Twyford 33 make little contribution in terms of either production or density to the fish community.

The extrapolation from growth rate to production is logical; yet firm evidence of density-dependent relationships is scarce. Single species communities have been shown by Walter (1934) and LeCren(1965) to increase production with increase in stocking density; in carp ponds production falls off above a certain threshold density but this does not occur in trout streams (possibly because the density never reaches a high enough value). Ricker and Foerster (1948) found that production of young sockeye salmon (*Onchorhynchus nerka* Walbaum) in Cultus Lake increased with higher population density but there was a limit of population size above which production did not increase. Likewise, Davis and Warren (1965) found that production of cottids (*Cottus perplexus* Richardson) increased with increase in biomass but decreased above a certain biomass level. In contrast, Allen (1946) found no correlation between growth rate and density, and LeCren (1949) discussing this work, implied that the food supply was not a limiting factor for growth or production at that population level. The territoriality of salmonids in streams can suppress density to a level below that at which the food supply would be limiting. Comparison of the gravel pit situation is therefore more meaningful when applied to other pond or lake communities than with those in flowing water. One of the few published accounts of a multi-species system (Mann, 1971) emphasizes this difference. Mann showed that trout production in chalk streams may not be affected by the abundance of other species but that the production of coexisting bullheads is dependent upon the density of 0 group trout. Mann postulates that for the trout fry and bullheads an optimum initial biomass exists beyond which production will not be increased. It is also interesting that the total fish community production in the Dorset Stour was as high as 59.6 $gm/m^2/year$, comparable with Farnborough 18(a) and Darenth 40.

Backiel and LeCren (1967) also describe a number of instances where evidence of density-dependence is conflicting. They postulate that some species, such as stream-living salmonids, suffer high density-dependent mortality through intense territoriality early in life so that population density is regulated below the level at which density would adversely affect growth and production. Pond- and lake-dwelling fishes would not be expected to behave in this way. The present study has shown that cyprinids, for instance, can experience great changes in population density from year to year and are able to survive under a wide range of stock densities.

Production : Biomass ratios (P/B) have interested workers for many years since they invariably fall within a very narrow range. Chapman (1967) quotes numerous ratios from coho salmon (Onchorhynchus keta) to bluegills (Lepomis macrochirus Rafinesque) with P/B in the range 1.0 - 2.5. Mathews (1971) found a wider range for separate age classes of roach and bleak in the River Thames, but found 0+ fish to have consistently higher ratios (∿2.3) and older fish to have lower values (∿0.2 - 1.0). The mean of all values is given by Mathews as 1.77. Table 20 shows P/$\bar{B}$ ratios for gravel-pit fish to be of the same order. The total fish community ratios are all in the range 1.3 - 2.8. Hunt (1966) found P/B decreased as B increased, and as Chapman (1967) points out, this implies that G was inversely correlated with B.

Odum (1959) states that '...interspecific competition is any interaction between two or more species populations which adversely affects their growth and survival'. Milne's (1961) definition is rather different: 'Competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)'. Thus, competition implies a shortage of some resource and it is the identification of such a resource that is often difficult (Larkin, 1956).

It appears from Figs. 61 and 62 that density (biomass/m^2) does affect both production and growth rate, suggesting competition of some kind between all members of the fish community in a gravel pit lake. The degree of competition between year classes or species is proportional to the relative biomass of these groups.

The density-dependent relationship discussed above suggests that, whatever the limiting resource in the gravel pit lakes, competition at the intra- and inter-specific level is operative.

It is known that coarse fish can reduce the production of more desirable game fishes (Lagler, 1944; Bennett, 1944) particularly in lakes and ponds, and that the production of one species is 'curtailed by the presence of one or more competitor species' (Larkin, 1956). This competition is usually for food but space and the associated increase in stress can be a factor even in non-territorial species (Williams, 1967; Chapman, 1966). Carp can alter the physical nature of a lake as well as destroy the aquatic vegation (Cahn, 1929). Specialization does of course occur, different species effectively separating themselves spacially and so avoiding competition (Larkin, 1956). The 'fundamental niches' (Miller, 1967) though theoretically suggesting competition, are sometimes restricted when two or more species are in close proximity (Cadwallader, 1975). However, Larkin (1956) concludes that such separation and avoidance of competition is unusual in freshwater fish communities. He suggests that freshwater environments offer little opportunity for specialization. The catholic diet of most fishes necessarily bring them into contact with each other with some form of competition inevitably occurring. The present study indicates that inter- and intra-specific competition is common in those gravel pit lakes investigated. The vast majority of the gravel pit lake fish are small and have very similar food requirements. Large piscivorous fish such as pike and large perch are rare and contribute very little to the total community biomass and production. Williams (1967) showed that fish such as large roach and perch can have much faster growth rates than the majority of the stunted overcrowded community. He maintained that such large fishes were either competitively superior or had a specialized diet which buffered them from the severe effects of overcrowding.

Since higher mean biomass can support higher production, gravel pit lakes are more suitable for dense than sparse populations. However, such species as roach, bream and perch often have population structures biased considerably towards immature, small individuals in gravel pit lakes. A high population biomass density of these species will therefore be composed of large numbers of small, slow-growing fish. This problem is common in the United States of America where man-made lakes and ponds are used extensively as sport fisheries (Bennett, 1944; Moyle, 1949). When population density is low then the growth of roach and bream is fast, e.g. in new gravel pit lakes (due to low initial stocking, lack of cover for fry or limited spawning substrate for adults). Given suitable conditions roach and bream in particular tend to produce large numbers of fry so that these low density conditions do not last long. The majority of gravel pit lakes studied are thus dominated by large numbers of small fish. This development in a gravel pit may be offset by the presence of predators such as pike and perch. Population control of this nature is ecologically inefficient and evidence from this work suggests that the balance between predator and prey is delicate and difficult to maintain. For example, Yateley 4 has a high pike population (see Section 3.1) which appears to have drastically reduced the roach (see p. 50).

4.5 Management Implications

The lakes under examination form part of an angling scheme. Several management techniques become apparent.

1. Reducing Species Diversity in Some or All Lakes

Coexisting species in gravel pit lakes apparently compete with each other such that the 'total available production' is shared between all species. This would seem to be true of at least cyprinids and small perch. Therefore, as far as the fishery is concerned, the production of those species of no interest to the angler is wasted. This problem is common in American waters (Bennett, 1944, 1971; Moyle, 1949) where 'rough fish', i.e. those fish not angled for, are removed by netting or by poisoning with rotenone. In the latter method it is, of course, necessary to restock the lake with the desired species. Netting is laborious and expensive and may aggravate the 'rough fish' situation unless carried out on a sufficiently large scale. Rotenone treatment is similarly expensive, unselective and may only alleviate the problem for a short period of time; the 'rough fish' may recover their former position in a few years.

2. Selecting Different Species for Different Lakes

This approach would maximise the production of those species most desirable in the fishery whilst at the same time allowing freedom of choice in terms of the species sought. Various waters in the scheme, could, for instance, be devoted to bream and roach, to tench, to carp or to pike and perch. As these species are taken at different times of the year it would also enable maximum use to be made of the lakes throughout the fishing season. However, the practical difficulties of maintaining the desired separation once achieved are similar to those discussed in 1 above.

3. Maintaining Low Numbers of Fish

The major problem in gravel pit lakes seems to be that, in successful species, reproduction is too efficient. Populations of gravel pit roach and bream are commonly composed of large numbers of relatively slow growing fish. The potential production would be more profitably utilized if these populations were composed of fewer but faster growing fish. The best balance between density and growth would depend on the desires of the anglers concerned. Two methods are available to achieve this aim, culling and natural predation. Culling can be carried out by a variety of techniques such as netting and electrofishing. It would be possible, from a knowledge of the existing population density and growth rate, to calculate the necessary 'fishing (culling) mortality'. However, it is probable that such a management programme would be very expensive. Alternatively, population density can be reduced by adding predators such as pike and perch. Again, the difficulties in achieving the necessary balance between predator and prey density are likely to be very great. Bennett (1944) suggests the density of largemouth bass (predator) necessary to eliminate the possibility of overpopulation of other coexisting fish (prey). However, the ratios of predator and prey suggested by Bennett are different from those preferred by Swingle and Smith (1941). Considerably more work is necessary in Britain before any such natural balance of coexisting populations can be achieved.

In those gravel pit lakes studied in this work, both carp and tench are represented by very few year classes. Their population structure is typically biased towards older and larger fish. It appears, therefore, that either reproduction or recruitment is unsuccessful in most years. Such fish make good angling in reasonably large waters (e.g. Farnborough 18(a) and Darenth 39) because of their large size and relatively high density. Managed lakes, free of other cyprinids, could be stocked with carp or tench of the desired size and provide angling of a predictable quality. Restocking might be necessary on occasion. Undesirable species could be controlled by a combination of small-mesh gill nets and seine nets and predators.

If, as is suggested in this thesis, coexisting species of coarse fish do compete for a common resource with a resultant decrease in growth rate, an efficient management programme for gravel pit lakes must include adequate control of those species least desirable in the fishery.

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APPENDIX 1

Back-calculation growth statistics

(a) = separate year-class data

(b) = composite year-class data

Back-calculated mean lengths-at-age are shown graphically in Figs 3 - 32 (Survey) and 34 - 39 (Series 2).

Year Class	Age	Mean Length (cm)	S.E.	Sample Size
Yateley 3a+b Roach 24.1.72				
(a) 0+	1	6.16	0.16	25
1+	1	5.85	0.15	12
	2	9.30	0.29	
2+	1	7.93	0.08	27
	2	13.15	0.24	
	3	18.52	0.34	
4+	1	5.53	0.15	7
	2	10.66	0.37	
	3	17.39	0.59	
	4	21.15	0.71	
	5	24.84	0.73	
5+	1	5.38	-	1
	2	11.23	-	
	3	18.15	-	
	4	21.61	-	
	5	23.47	-	
	6	25.86		
(b)	1	6.62	0.12	72
	2	11.76	0.30	47
	3	18.29	0.29	35
	4	21.21	0.62	8
	5	24.67	0.66	8
	6	25.86	-	1

Year Class	Age	Mean Length (cm)	S.E.	Sample Size
Yateley 5 Roach 1.11.71				
(a) 1+	1	6.33	0.09	41
	2	9.01	0.17	
3+	1	5.47	0.12	6
	2	8.59	0.51	
	3	12.48	0.78	
	4	16.23	0.58	
4+	1	5.23	-	1
	2	9.79	-	
	3	14.11	-	
	4	17.71	-	
	5	20.11	-	
(b)	1	6.20	0.09	48
	2	8.89	0.16	48
	3	12.67	0.70	7
	4	16.44	0.53	7
	5	20.11	-	1

Yateley 9 Roach 28.2.72

(a)	0+	1	4.84	0.09	8
	1+	1	4.49	0.11	32
		2	8.29	0.25	
(b)		1	4.57	0.09	40
		2	8.29	0.25	32

Bedfont 11 Roach 17.10.72

(a)	0+	1	4.99	0.31	9
	1+	1	6.78	0.12	30
		2	9.03	0.26	
	2+	1	6.64	0.23	4
		2	10.51	0.46	
		3	13.51	1.04	
	3+	1	6.36	0.13	11
		2	12.06	0.19	
		3	16.05	0.39	
		4	18.30	0.49	
	4+	1	5.97	-	1
		2	12.64	-	
		3	17.72	-	
		4	20.12	-	
		5	20.39	-	
	6+	1	6.11	0.13	2
		2	10.11	0.93	
		3	14.92	1.20	
		4	19.72	2.00	
		5	22.66	2.00	
		6	24.53	2.00	
		7	25.46	2.14	
(b)		1	6.37	0.12	57
		2	9.97	0.26	48
		3	15.45	0.43	18
		4	18.64	0.47	14
		5	21.90	1.38	3
		6	24.53	2.00	2
		7	25.46	2.14	2

Chertsey 12 Roach 16.6.72

(a)	1+	1	4.98	0.14	11
		+	6.44	0.19	
	2+	1	3.99	0.11	11
		2	8.37	0.24	
		+	9.68	0.15	
	3+	1	3.62	0.16	5
		2	7.18	0.17	
		3	11.15	0.36	
		+	11.71	0.33	

	4+	1	4.41	-	1
		2	9.22	-	
		3	13.75	-	
		4	18.84	-	
		+	19.41	-	
(b)		1	4.33	0.13	28
		2	8.07	0.22	17
		3	11.58	0.53	6
		4	18.84	-	1

Thorpe 13 Roach 23.10.72

(a)	0+	1	6.52	0.08	27
	1+	1	5.89	0.09	20
		2	9.84	0.25	
	2+	1	6.15	0.16	11
		2	8.86	0.27	
		3	13.43	0.39	
	3+	1	6.67	-	1
		2	10.19	-	
		3	12.95	-	
		4	17.97	-	
(b)		1	6.24	0.07	59
		2	9.51	0.20	32
		3	13.39	0.37	12
		4	17.97	-	1

Farnborough 18(a) Roach 20.3.72

(a)	1+	1	7.24	0.10	22
		2	9.19	0.17	
	2+	1	7.34	0.22	14
		2	10.32	0.34	
		3	11.74	0.39	
	3+	1	6.68	0.27	7
		2	11.45	0.22	
		3	14.11	0.46	
		4	15.59	0.68	
	4+	1	7.08	0.21	3
		2	11.11	0.58	
		3	14.66	1.05	
		4	16.36	0.64	
		5	17.33	1.22	
	5+	1	6.92	1.21	2
		2	12.85	0.61	
		3	15.15	0.48	
		4	17.33	0.73	
		5	18.66	1.33	
		6	19.38	1.57	

(b)		1	7.17	0.09	48
		2	10.13	0.20	48
		3	12.98	0.38	26
		4	16.07	0.46	12
		5	14.39	3.66	5
		6	19.38	1.57	2

Sutton-at-Hone 35 Roach 9.12.72

(a)	2+	1	6.87	0.65	2
		2	10.78	1.44	
		3	12.22	1.31	
	3+	1	5.69	-	1
		2	9.87	-	
		3	12.48	-	
		4	13.52	-	
	4+	1	5.96	0.10	4
		2	10.39	0.37	
		3	13.72	0.22	
		4	15.22	0.43	
		5	17.43	0.56	
	5+	1	6.99	-	1
		2	12.22	-	
		3	15.35	-	
		4	17.44	-	
		5	20.83	-	
		6	22.66	-	
	6+	1	5.69	0.26	3
		2	9.00	0.38	
		3	14.83	0.54	
		4	20.22	0.38	
		5	22.74	0.35	
		6	24.31	0.17	
		7	26.14	0.35	
	7+	1	5.84	0.09	9
		2	10.39	0.29	
		3	15.03	0.34	
		4	19.79	0.34	
		5	22.39	0.30	
		6	24.05	0.33	
		7	25.88	0.54	
		8	27.04	0.56	
	8+	1	7.26	-	1
		2	12.48	-	
		3	15.09	-	
		4	18.22	-	
		5	22.39	-	
		6	23.44	-	
		7	26.31	-	
		8	27.62	-	
		9	28.14		

(b)		1	6.05	0.13	21
		2	10.39	0.25	21
		3	14.38	0.29	21
		4	18.34	0.55	19
		5	21.27	0.53	18

		6	23.96	0.24	14
		7	25.97	0.38	13
		8	27.10	-	1
		9	28.14	-	1

Sutton-at-Hone 36 Roach 3.7.72

(a)	0+	+	4.91	-	1
	1+	1	5.87	0.16	9
		+	7.46	0.39	
	4	1	6.99	0.15	3
		2	10.91	0.39	
		3	14.57	0.15	
		4	17.79	0.09	
		+	17.96	0.00	
	7+	1	6.18	0.14	7
		2	8.57	0.18	
		3	11.73	0.29	
		4	14.79	0.48	
		5	16.73	0.76	
		6	18.26	0.75	
		7	19.75	0.77	
		+	20.12	0.59	
	8+	1	6.22	0.11	4
		2	8.89	0.25	
		3	12.28	0.43	
		4	14.70	0.59	
		5	16.39	0.87	
		6	18.29	0.99	
		7	19.85	1.09	
		8	21.42	1.01	
		+	21.42	1.01	
(b)		1	6.12	0.12	24
		2	8.49	0.29	23
		3	12.49	0.36	14
		4	15.40	0.44	14
		5	16.89	0.46	14
		6	18.27	0.57	11
		7	19.79	0.60	11
		8	20.59	0.53	11

Darenth 38 Roach 16.4.72

(a)	1+	1	9.51	0.07	47
		2	12.26	0.13	
	4+	1	8.65	-	1
		2	11.15	-	
		3	13.63	-	
		4	15.06	-	
		5	17.02	-	
(b)		1	9.49	0.07	48
		2	12.24	0.13	48
		3	13.64	-	1
		4	15.06	-	1
		5	17.02	-	1

Darenth 39 Roach 12.6.72

(a)	0+	1	3.51	0.51	2
	1+	1	6.41	0.06	17
		2	6.58	0.11	
	2+	1	6.62	0.09	10
		2	10.19	0.19	
		3	11.22	0.19	
	3+	1	6.59	-	1
		2	13.02	-	
		3	18.42	-	
		4	19.19	-	
	8+	1	5.57	-	1
		2	10.71	-	
		3	12.76	-	
		4	14.82	1	
		5	16.10	-	
		6	17.91	-	
		7	18.93	-	
		8	19.70	-	
		9	21.22	-	
(b)		1	6.46	0.06	31
		2	10.47	0.28	12
		3	15.59	2.83	2
		4	14.81	-	1
		5	16.10	-	1
		6	17.90	-	1
		7	18.93	-	1
		8	19.70	-	1

Darenth 40 Roach 12.6.72

(a)	1+	1	7.49	0.29	3
		+	7.62	0.36	
	2+	1	7.34	0.44	11
		2	10.97	0.69	
		+	11.11	0.66	
	3+	1	5.41	0.12	4
		2	8.95	0.30	
		3	13.22	0.42	
		+	13.29	0.41	
	4+	1	6.96	-	1
		2	10.43	-	
		3	14.65	-	
		4	17.87	-	
	7+	1	6.13	0.59	3
		2	9.44	0.89	
		3	12.75	1.09	
		4	15.72	1.61	
		5	18.45	1.84	
		6	21.01	2.19	
		7	22.99	2.20	
	8+	1	5.97	0.10	4
		2	9.38	0.64	
		3	12.91	1.31	

		4	16.08	1.99	
		5	17.69	2.29	
		6	19.49	2.04	
		7	21.04	2.22	
		8	22.52	2.02	
(b)		1	6.69	0.25	26
		2	9.83	0.39	26
		3	12.15	0.45	23
		4	15.21	0.83	12
		5	17.99	1.23	8
		6	20.14	1.40	7
		7	21.04	2.22	4
		8	22.52	2.02	4

Larkfield 41 Roach 18.10.71

(a)	2+	1	5.09	0.10	6
		2	7.18	0.12	
		3	9.23	0.24	
	3+	1	5.69	0.13	6
		2	9.91	0.49	
		3	12.60	0.56	
		4	15.94	0.36	
(b)		1	5.39	0.12	12
		2	8.55	0.48	12
		3	10.92	0.59	12
		4	15.94	0.36	6

Fishers Green 42 Roach 24.4.72

(a)	1+	1	6.16	0.06	17
		2	9.79	0.10	
	3+	1	5.35	0.14	14
		2	7.54	0.14	
		3	9.25	0.18	
		4	12.69	0.22	
(b)		1	5.79	0.10	31
		2	8.77	0.22	31
		3	9.25	0.18	14
		4	12.69	0.22	14

Wraysbury 17 Bream 5.9.72

(a)	0+	1	5.18	0.08	8
	3+	1	6.02	0.42	3
		2	12.83	0.20	
		3	17.67	1.06	
		4	22.52	0.92	
	5+	1	5.91	-	1
		2	9.37	-	
		3	13.87	-	
		4	19.06	-	

		5	25.98	-	
		6	29.78	-	
	6+	1	6.11	0.17	5
		2	10.54	0.82	
		3	15.66	1.44	
		4	20.58	1.72	
		5	25.77	1.55	
		6	31.51	1.71	
		7	35.18	1.60	
(b)		1	5.64	0.14	17
		2	11.17	0.62	9
		3	16.13	0.93	9
		4	21.05	1.03	9
		5	25.80	1.26	6
		6	31.22	1.43	6
		7	35.18	1.60	5

Sutton-at-Hone 35 Bream 8.12.72

(a)	3+	1	5.95	0.20	6
		2	9.06	0.25	
		3	12.01	0.24	
		4	13.98	0.27	
	4+	1	7.35	0.16	2
		2	11.23	0.00	
		3	15.12	0.47	
		4	18.39	0.62	
		5	21.34	0.78	
(b)		1	6.29	0.27	8
		2	9.60	0.40	8
		3	12.79	0.55	8
		4	15.08	0.76	8
		5	21.34	0.78	2

Darenth 40 Bream 12.6.72

(a)	1+	1	4.93	0.08	2
	2+	1	5.17	0.13	14
		2	8.29	0.33	
	3+	1	5.46	0.14	10
		2	10.78	0.34	
		3	15.51	0.34	
	8+	1	5.33	-	1
		2	7.92	-	
		3	10.52	-	
		4	16.02	-	
		5	21.86	-	
		6	26.39	-	
		7	28.34	-	
		8	29.63	-	

(b)		1	5.27	0.09	27
		2	8.95	0.38	27
		3	11.27	0.74	25
		4	15.67	0.29	11
		5	21.86	-	1
		6	26.39	-	1
		7	28.34	-	1
		8	29.63	-	1

Larkfield 41 Bream 18.10.71

(a)	1+	1	3.79	0.00	2
		2	6.70	0.00	
	2+	1	3.52	0.09	17
		2	7.11	0.19	
		3	11.19	0.25	
	3+	1	3.68	0.32	8
		2	7.43	0.27	
		3	10.96	0.37	
		4	13.61	0.45	
	4+	1	3.37	0.42	2
		2	5.87	0.42	
		3	9.82	0.21	
		4	14.39	1.04	
		5	20.63	0.21	
	5+	1	5.38	0.62	2
		2	6.69	0.42	
		3	10.65	0.62	
		4	14.60	0.42	
		5	18.14	0.62	
		6	23.96	0.21	
	6+	1	3.37	0.00	2
		2	7.74	1.46	
		3	11.48	1.87	
		4	16.06	2.29	
		5	20.84	2.08	
		6	24.79	2.29	
		7	29.16	3.74	
(b)		1	3.56	0.10	33
		2	7.10	0.15	33
		3	11.03	0.20	31
		4	14.21	0.43	14
		5	19.87	0.79	6
		6	24.38	0.97	4
		7	29.16	3.74	2

Fishers Green 42 Bream 24.4.72

(a)	0+	1	5.47	0.35	4
	1+	1	5.04	0.12	3
		2	8.10	0.12	
	2+	1	6.17	0.53	7
		2	9.47	0.49	
		3	14.92	0.22	

	3+	1	5.28	0.76	3
		2	10.29	1.21	
		3	14.58	1.09	
		4	18.74	0.80	
	4+	1	4.92	0.00	4
		2	10.32	0.31	
		3	15.38	1.06	
		4	20.05	1.61	
		5	25.65	2.18	
	5+	1	5.10	0.18	2
		2	8.77	0.18	
		3	13.54	0.18	
		4	19.41	1.65	
		5	24.92	2.02	
		6	29.14	2.20	
	6+	1	4.92	-	1
		2	8.59	-	
		3	14.83	-	
		4	20.33	-	
		5	26.20	-	
		6	31.34	-	
		7	33.91	-	
(b)		1	5.45	0.20	24
		2	9.45	0.29	20
		3	14.80	0.32	17
		4	19.56	0.69	10
		5	25.52	1.26	7
		6	29.87	1.47	3
		7	33.91	-	1

Yateley 9 Rudd 28.2.72

(a)	1+	1	3.01	0.47	3
		2	7.24	0.75	
	3+	1	3.48	-	1
		2	9.40	-	
		3	14.47	-	
		4	18.42	-	
	4+	1	2.91	-	1
		2	9.12	-	
		3	12.50	-	
		4	16.73	-	
		5	20.11	-	
(b)		1	3.08	0.28	5
		2	8.04	0.65	5
		3	13.49	0.99	2
		4	16.73	-	1

Kingsmead 15 Rudd 17.5.72

(a)	1+	1	3.96	0.16	15
		2	8.85	0.35	
	2+	1	3.73	0.20	10
		2	8.78	0.29	
		3	12.93	0.38	
	3+	1	3.70	0.39	2
		2	9.88	0.26	
		3	12.12	0.65	
		4	15.01	0.13	
(b)		1	3.85	0.12	27
		2	8.90	0.23	27
		3	12.80	1.38	12
		4	15.01	0.13	2

Sutton-at-Hone 36 Rudd 3.7.72

(a)	1+	1	4.27	0.22	14
		+	5.89	0.33	
	2+	1	4.90	0.54	3
		2	8.82	0.41	
		+	10.35	0.39	
	3+	1	5.02	0.20	14
		2	9.29	0.35	
		3	12.52	0.28	
		+	12.92	0.23	
	4+	1	5.61	-	1
		2	8.29	-	
		3	10.70	-	
		4	15.26	-	
		+	15.26	-	
	5+	1	4.27	-	
		2	9.90	-	
		3	14.99	-	
		4	17.94	-	
		5	18.74	-	
		+	18.74	-	
	7+	1	5.08	-	1
		2	8.02	-	
		3	11.24	-	
		4	13.65	-	
		5	14.72	-	
		6	15.79	-	
		7	16.87	-	
		+	16.87	-	
	8+	1	4.67	0.32	4
		2	7.29	0.29	
		3	9.90	0.19	
		4	12.51	0.17	
		5	14.05	0.23	
		6	15.73	0.47	
		7	17.20	0.62	
		8	17.61	0.55	
		+	17.61	0.55	

(b)		1	4.69	0.13	38
		2	8.83	0.26	24
		3	11.99	0.33	21
		4	13.84	0.79	7
		5	14.94	0.78	6
		6	15.74	0.36	5
		7	17.20	0.62	4
		8	17.61	0.55	4

Darenth 39 Rudd 12.6.72

(a)	2+	1	4.44	0.34	4
		2	8.97	0.60	
		3	9.05	0.61	
	8+	1	4.09	0.17	2
		2	6.42	0.17	
		3	11.40	1.62	
		4	15.34	1.16	
		5	17.43	2.09	
		6	18.48	1.51	
		7	20.80	0.17	
		8	21.96	0.58	
		9	23.58	0.17	
(b)		1	4.33	0.23	6
		2	8.12	0.66	6
		3	11.40	1.62	2
		4	15.35	1.16	2
		5	17.44	2.09	2
		6	18.48	1.51	2
		7	20.80	0.17	2
		8	21.96	0.58	2
		9	23.58	0.17	2

Darenth 40 Rudd 12.6.72

(a)	3+	1	4.33	0.13	8
		2	8.29	0.18	
		3	11.21	0.32	
	4+	1	4.16	0.26	4
		2	8.31	0.41	
		3	10.94	0.33	
		4	12.58	0.54	
	5+	1	4.57	0.36	3
		2	7.84	0.59	
		3	10.57	0.21	
		4	12.44	0.08	
		5	14.00	0.31	
(b)		1	4.33	0.12	15
		2	8.20	0.18	15
		3	11.01	0.20	15
		4	12.52	0.29	7
		5	14.00	0.31	3

Chertsey 12 Bleak 16.6.72

(a)	1+	1	5.36	0.18	13
		+	6.83	0.23	
	2+	1	4.54	0.00	4
		2	9.41	0.16	
		+	9.72	0.16	
(b)		1	5.17	0.16	17
		2	9.41	0.16	4

Fishers Green 42 Bleak 24.4.72

(a)	1+	1	8.36	0.23	14
		2	11.42	0.25	
	2+	1	8.60	0.13	15
		2	10.94	0.18	
		3	12.96	0.21	
(b)		1	8.49	0.13	29
		2	11.17	0.16	29
		3	12.96	0.21	15

Farnborough 18(a) Perch 20.3.72

(a)	0+	1	7.52	0.11	3
	1+	1	7.72	-	1
		2	9.05	-	
	2+	1	6.97	0.12	5
		2	8.55	0.11	
		3	9.78	0.25	
	3+	1	6.84	0.12	12
		2	8.59	0.22	
		3	9.68	0.17	
		4	10.46	0.24	
	7+	2	11.63	-	1
		3	19.49	-	
		4	24.74	-	
		5	30.18	-	
		6	31.59	-	
		7	33.62	-	
		8	34.02	-	
(b)		1	7.22	0.23	22
		2	9.18	0.59	19
		3	10.54	0.84	18
		4	11.97	1.53	13
		5	30.18	-	1
		6	31.59	-	1
		7	33.62	-	1
		8	34.02	-	1

Twyford 32 Perch 17.1.72

(a)	0+	1	7.29	0.14	18
	1+	1	6.29	0.15	17
		2	12.64	0.29	
	3+	1	7.28	0.11	7
		2	10.02	0.15	
		3	14.69	0.38	
		4	19.35	0.38	
	4+	1	6.89	0.99	2
		2	10.55	1.60	
		3	14.54	2.00	
		4	18.87	1.66	
		5	22.66	1.60	
(b)		1	6.89	0.12	44
		2	11.77	0.32	26
		3	14.66	0.44	9
		4	19.24	0.41	9
		5	22.66	1.59	2

Twyford 33 Perch 11.9.72

(a)	0+	1	6.27	0.06	20
	1+	1	8.11	0.09	21
		2	10.73	0.18	
	2+	1	6.52	0.16	9
		2	12.47	0.28	
		3	15.27	0.31	
(b)		1	7.09	0.14	50
		2	11.25	0.21	30
		3	15.27	0.31	9

Farnborough 18(b) Tench 15.1.73

(a)	3+	1	12.35	0.38	14
		2	17.23	0.77	
		3	21.62	0.88	
		4	24.70	0.83	
	4+	1	12.31	0.48	5
		2	18.11	1.03	
		3	24.47	1.48	
		4	28.31	1.26	
		5	30.45	0.92	
(b)		1	12.34	0.29	19
		2	17.46	0.62	19
		3	22.37	0.80	19
		4	25.65	0.77	19
		5	30.45	0.92	5

Farnborough 18(a) Roach Series 2

(a)	0+	1	4.77	0.02	560*
	1+	1	3.56	0.05	40
		2	7.74	0.14	
	2+	1	7.87	0.12	2
		2	9.73	0.12	
		3	11.01	0.00	
	3+	1	6.84	0.18	12
		2	9.32	0.24	
		3	10.72	0.31	
		4	13.19	0.43	
	4+	1	6.59	0.00	2
		2	10.08	0.93	
		3	11.48	1.17	
		4	11.95	1.40	
		5	13.34	1.17	
	5+	1	6.82	0.23	2
		2	10.55	1.40	
		3	12.88	2.33	
		4	14.86	1.51	
		5	16.14	0.93	
		6	19.89	0.35	
(b)		1	4.71	0.19	68
		2	8.34	0.21	59
		3	11.20	0.34	19
		4	13.44	0.44	17
		5	15.58	1.15	5
		6	18.55	0.69	3
		7	20.80	-	1
		8	22.90	-	1

Twyford 32 Roach Series 2

(a)	0+	1	9.56	0.14	27
	1+	1	4.39	0.04	33
		2	13.07	0.16	
	3+	1	3.64	-	1
		2	7.36	-	
		3	9.60	-	
		4	11.83	-	
	5+	1	5.63	0.00	3
		2	9.35	0.50	
		3	15.96	0.22	
		4	22.66	0.30	
		5	24.56	0.33	
		6	29.35	1.06	
(b)		1	6.59	0.32	66
		2	12.43	0.28	39
		3	15.09	1.13	6
		4	21.04	1.87	6
		5	24.56	0.33	3
		6	29.35	1.06	3

* from length-frequency distribution

Darenth 39 Roach Series 2

(a)	0+	1	6.31*	0.03	357
	1+	1	5.52	0.05	69
		2	10.55	0.13	
	2+	1	6.56	-	1
		2	10.98	-	
		3	16.96	-	
	3+	1	6.06	0.23	11
		2	9.55	0.37	
		3	12.67	0.75	
		4	16.13	1.13	
	4+	1	7.08	0.45	3
		2	11.93	1.42	
		3	14.79	2.04	
		4	17.39	2.31	
		5	19.91	1.79	
(b)		1	5.81	0.06	114
		2	10.48	0.13	84
		3	13.38	0.73	15
		4	16.40	0.99	14
		5	19.91	1.79	3

Darenth 40 Roach Series 2

(a)	1+	1	4.10	0.06	47
		2	6.98	0.12	
	2+	1	3.82	0.12	5
		2	6.11	0.21	
		3	9.12	0.48	
	3+	1	4.07	0.09	21
		2	7.32	0.25	
		3	10.14	0.30	
		4	12.38	0.28	
	4+	1	4.69	0.17	13
		2	7.78	0.26	
		3	11.86	0.40	
		4	14.07	0.40	
		5	15.21	0.48	
(b)		1	4.16	0.05	86
		2	7.13	0.10	86
		3	10.58	0.26	39
		4	13.02	0.27	34
		5	15.21	0.48	13

* from length-frequency distribution

Larkfield 41 Roach Series 2

(a)	0+	1	5.83	0.08	3
	1+	1	4.57	0.05	28
		2	6.81	0.11	
	2+	1	4.57	0.04	22
		2	6.52	0.11	
		3	9.33	0.26	
	3+	1	4.67	-	1
		2	8.15	-	
		3	10.61	-	
		4	13.30	-	
	4+	1	4.59	0.17	8
		2	6.65	0.33	
		3	9.43	0.35	
		4	11.70	0.33	
		5	14.17	0.37	
	7+	1	4.56	-	1
		2	5.91	-	
		3	8.37	-	
		4	11.06	-	
		5	12.85	-	
		6	14.42	-	
		7	15.76	-	
		8	18.45	-	
(b)		1	4.63	0.05	63
		2	6.69	0.08	60
		3	9.36	0.21	32
		4	11.80	0.31	10
		5	14.02	0.36	9
		6	14.42	-	1
		7	15.76	-	1
		8	18.45	-	1

Larkfield 41 Bream Series 2

(a)	0+	1	6.45	0.09	14
	1+	1	5.99	-	1
		2	8.88	-	
	2+	1	5.11	0.05	32
		2	6.51	0.09	
		3	8.97	0.12	
	3+	1	5.24	0.12	18
		2	7.00	0.17	
		3	8.44	0.23	
		4	11.16	0.27	
	4+	1	5.42	0.06	30
		2	7.16	0.11	
		3	9.01	0.16	
		4	10.22	0.16	
		5	12.83	0.19	

5+	1	4.95	-	1
	2	7.31	-	
	3	9.66	-	
	4	12.55	-	
	5	13.86	-	
	6	14.90		
6+	1	5.73	0.15	3
	2	8.09	0.45	
	3	9.66	0.15	
	4	11.76	0.61	
	5	13.77	0.38	
	6	15.34	0.31	
	7	16.91	0.38	
(b)	1	5.44	0.06	99
	2	6.94	0.08	85
	3	8.90	0.09	84
	4	10.68	0.16	52
	5	12.94	0.17	34
	6	15.23	0.25	4
	7	16.91	0.38	3

Regression Coefficients for Log_{10} Wet Weight (gm) × Log_{10} Fork Length (cm)

LAKE	SPECIES	A	B	T3*	N*
18(a)	Tench	-1.660	2.893	-0.649	29
"	"	-0.694	2.208	-1.516	27
"	Roach	-1.874	2.963	-1.121	83
32	Roach	-2.120	3.276	1.855	44
	Perch	-2.214	3.345	2.891	15
39	Roach	-2.072	3.259	7.429	115
	Bream	-1.736	2.945	-0.448	44
40	Roach	-2.143	3.286	9.413	87
	Bream	-2.226	3.350	5.798	46
41	Roach	-2.227	3.402	10.908	64
	Bream	-2.297	3.445	8.850	96

* T3 = Student's t for B - 3.0

* N = Sample Size

Regression Coefficients for Fork Length (cm) × Posterior Scale Radius (Arbitrary Units)

LAKE	SPECIES	A	B	TL*	N*
18(a)	Roach	1.927	0.233	-0.853	69
32	Roach	1.417	0.258	-0.243	40
39	Roach	1.621	0.260	-4.283	111
40	Roach	1.808	0.239	-0.769	86
41	Roach	2.545	0.224	0.602	63
	Bream	3.376	0.262	0.681	99

* TL = Student's t for deviation from linearity

* N = Sample size

Seasonal Growth of Roach in Yateley 4

(a) 1972 Year Class

Date of Capture	Sample Size	Mean Fork Length (cm)	S.E.
9. 4.73	205	6.02	0.02
3. 5.73	266	6.15	0.02
5. 6.73	404	6.47	0.02
6. 7.73	171	7.99	0.05
10. 8.73	225	9.02	0.07
6. 9.73	104	9.67	0.08
4.10.73	102	10.15	0.10
5.11.73	457	10.41	0.05
6.12.73	149	9.84	0.07
4. 1.74	100	9.86	0.09

(b) 1973 Year Class

Date of Capture	Sample Size	Mean Fork Length (cm)	S.E.
6. 7.73	77	2.35	0.03
10. 8.73	27	4.45	0.06
6. 9.73	96	5.86	0.05
4.10.73	100	6.02	0.04
5.11.73	457	6.25	0.02
6.12.73	305	6.38	0.02
4. 1.74	20	6.36	0.08

APPENDIX 2

CAPTURE-RECAPTURE STATISTICS

KEY TO THE SYMBOLS USED IN THE TABLES

S1/2/2	=	Numbers of fish newly marked and released on day 1/2/3
C2/3/4	=	Numbers of fish examined for marks on day2/3/4 .
M1	=	Recaptures from Day 1 marking only
M2	=	" " Day 2 " "
M3	=	" " Day 3 " "
Mx+y	=	" " Day x and Day y

Lake: Farnborough 18(a) Series 1 Dates 16.3.73 - 23.3.73

Species	Size	Day 1	Day 2			Day 3			
	Group (cm)	S1	C2	S2	M1	C3	M1	M1+2	M2
Roach	>6.0	271	1356	1287	46	658	32	2	103
Tench ♂	all sizes	34	111	104	7	102	5	0	17
Tench ♀	all sizes	28	111	103	8	118	7	1	20
Perch	all sizes	24	62	13	14	21	4	1	3
Gudgeon	all sizes	5	46	44	2	89	2	2	5

Lake: Farnborough 18(a) Series 2 Dates: 12.10.73 - 26.10.73

Species	Size	Day 1	Day 2			Day 3			
	Group	S1	C2	S2	M1	C3	M1	M1+2	M2
Roach	6.10 cm	142	17	17	0	13	0	0	1
"	>10 cm	220	114	97	17	253	12	5	22
Tench ♂	all sizes	63	42	38	4	140	17	4	17
Tench ♀	all sizes	64	50	43	7	124	20	5	19
Perch	<9.5 cm	110	86	80	6	22			1
"	>9.5 cm	11	1	1	0	3			0
Gudgeon	all sizes	49	22	20	2	61			1
Carp	all sizes	8	0	0	0	1	0	0	0
Rudd	all sizes	32	4	4	0	9	1	0	0
Dace	all sizes	0	0			1			
Roach-rudd hybrids	all sizes	1	1	1	0	2	1	0	0

Lake: Twyford 32 Series 1 Dates 29.1.73 - 6.3.73

Species	Size Group (cm)	Day 1	Day 2			Day 3					Day 4				
		S1	C2	S2	M1	C3	S3	M1	M1+2	M2	C4	M1	M2	M1+2	M3
Roach	<5.5	0	67	67	0	0	0	0	0	0	0	0	0	0	0
"	10.0-27.0	7	5	2	3	1	0	0	0	1	3	0	0	0	0
Perch	<8.5	42	101	95	4	30	28	0	0	2	4	0	0	0	0
"	>8.5	24	31	28	3	40	39	1	0	0	38	3	2	2	0
Bleak	8.0-14.0	128	100	19	79	28	2	2	21	3	11	2	0	3	0
Dace	9.0-19.0	17	5	2	3	1	1	0	0	0	13	4	0	0	0
Chubb	6.0-34.0	4	2	1	1	0	0	0	0	0	1	0	0	0	0
Pike	<30.0	20	40	36	3	96	92	0	0	4	40	4	0	0	1
"	30.0-80.0	18	18	16	2	12	8	1	0	3	26	1	2	0	1

Lake: Twyford 32 Series 2 Dates: 10.10.73 - 24.10.73

Species	Size Group	Day 1	Day 2			Day 3			
		S1	C2	S2	M1	C3	M1	M1+2	M2
Roach	<11.0 cm	117	23	23	0	58	1	0	2
"	11-16 cm	668	48	23	25	220	59	0	4
"	>20 cm	3	1	1	0	7	0	0	0
Perch	all sizes	239	33	24	9	48	13	0	2
Bleak	"	12	5	4	1	2	0	1	0
Dace	"	5	0	0	0	1	1	0	0
Gudgeon	"	0	0	0	0	1	0	0	0
Tench	"	11	4	2	2	5	1	0	0
"	"	15	5	5	0	6	1	0	0
Pike	"	1	6	6	0	7	0	0	1

Lake: Twyford 33 Series 1 Dates 4.12.72 - 18.12.72

Species	Size Group (cm)	Day 1	Day 2			Day 3			
		S1	C2	S2	M1	C3	M1	M1+2	M2
Pike	<20.0	0	3	3	0	0	0	0	0
"	>28.0	6	11	10	1	7	0	0	0
Perch	< 8.5	18	21	11	0	19	0	0	0
"	> 8.5	119	27	21	6	86	4	0	1
Roach	19.0-24.0	0	1	1	0	3	0	0	0

Lake: Twyford 33 Series 2 Dates: 17.1.74 - 31.1.74

Species	Size Group (cm)	Day 1	Day 2			Day 3	
		S1	C2	S2	M1	C3	M1
Pike	12-16	15	0	0	0	0	0
"	37.3-68.5	10	5	4	1	4	1
Perch	8-15	3	1	0	0	1	0
"	23.3-35.7	11	10	6	4	2*	0
Roach	8.6-8.8	1	1	0	0	0	0
Dace	15.2-17.4	3	0	0	0	0	0

* includes one perch (23.3 cm) caught in a gill net on 5.2.74

Lake: Darenth 39 Series 1 Dates: 25.6.73 - 17.7.73

Species	Size Group (cm)	Day 1	Day 1			Day 3					Day 4			
		S1	C2	S2	M1	C3	S3	M1	M1+2	M2	C4	M1	M2	M3
Roach	>5.5	170	318	283	0	281	236	0	0	0	278	0	4	0
Bream	5.0-32.0	7	16	16	0	26	19	0	0	0	343	0	0	0
Rudd	25.0-31.0	1	1	1	0	0	0	0	0	0	4	0	0	0
Tench	35.0-41.0	2	0	0	0	0	0	0	0	0	0	0	0	0
Carp	26.0-61.0	4	0	0	0	3	3	0	0	0	2	0	0	0
Chubb	29.0-42.0	2	0	0	0	0	0	0	0	0	5	0	0	0

Lake: Darenth 39 Series 2 Dates: 2.11.73 - 16.11.73

Species	Size Group (cm)	Day 1	Day 2			Day 3					Day 4					
		S1	C2	S2	M1	C3	S3	M1	M1+2	M2	C4	M1	M1+2	M1+3	M2	M3
Roach	<7.4	119	38	38	0	0	0	0	0	0	191	0	0	0	0	0
"	7.4-14.0	346	163	150	13	52	44	2	0	6	145	11	1	2	2	2
"	7.4-9.8	160	52	46	6	20	18	0	0	2	69	3	0	1	1	1
"	9.8-14.0	186	111	104	7	32	26	2	0	4	76	8	1	1	1	1
"	>14.0	45	21	18	3	13	13	0	0	0	11	2	0	0	0	0
Bream	8-22	415	36	36	0	10	0	0	0	0	66	10	0	0	3	0
"	22.0-50	32	10	10	0	12	11	0	0	1	6	1	1	0	0	0
"	>50.0	3	0			0					0					
Rudd	25.0-28.0	1	0			2	2	0	0	0	0					
Tench	35.6	1	0			0					0					
Chubb	26.0-43.0	1	1	1	0	0					0					
Carp	34.0-60.0	3	2	2	0	0					0					
Pike	43.0-72.0	1	0			0					3	0	0	0	0	0
Gudgeon		18	3	3	0	1	1	0	0	0	10	1	0	0	0	0

Lake: Darenth 40   Series 1   Dates: 12.4.74 - 30.4.73

Species	Size Group (cm)	Day 1	Day 2			Day 3			
		S1	C2	S2	M1	C3	M1	M1+2	M2
Roach	all sizes	365	523	251	242	165	13	64	64
Bream	>5.0	406	305	70	228	79	4	51	18
Rudd	all sizes	160	145	24	121	70	10	50	10
Gudgeon	"	51	56	49	7	73	7	0	5
Chubb	"	41	33	14	19	13	2	5	0
Perch	"	19	38	24	14	18	2	6	9
Dace	"	5	2	0	2	0	0	0	0
Carp	"	5	2	1	1	0	0	0	0
Minnow	"	6	15	13	2	6	2	0	3
Tench	"	5	1	1	0	1	0	0	0

Series 2 data given in Table 17, p.

Lake: Larkfield 41 Series 1 Dates: 22.5.73 - 18.6.73

Species	Size Group (cm)	Day 1	Day 2			Day 3					Day 4						
		S1	C2	S2	M1	C3	S3	M1	M1+2	M2	C4	M1	M2	M3	M1+2	M1+3	M2+3
Roach	9.0	216	16	15	1	204	180	0	0	4	233	0	1	0	0	0	0
"	9.0-26.0	55	277	241	1	37	28	3	1	6	30	2	3	3	1	0	0
Bream	8.0	111	111	111	0	618	106	0	0	0	186	1	0	0	0	0	0
"	8.0-28.0	477	169	158	11	277	139	12	0	18	153	6	6	3	4	1	1
Perch	6.0-25.0	7	35	35	0	39	27	1	0	11	37	1	4	2	0	1	1
Tench	30.0-41.0	4	2	2	0	6	4	1	0	1	2	0	0	0	0	0	0
Pike	21.0-67.0	14	11	7	4	13	9	3	0	1	10	0	0	0	1	0	0
Carp	56.0-65.0	5	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Rudd	all sizes	7	12	12	0	24	23	1	0	0	11	0	0	1	0	0	0

Lake: Larkfield 41 Series 2 Dates: 5.12.73 - 19.12.73

Species	Size Group (cm)	Day 1	Day 2			Day 3			
		S1	C2	S2	M1	C3	M1	M1+2	M2
Roach	<8.2	160	1006	984	22	850	2	0	52
"	8.2–12.0	37	144	137	7	62	8	3	30
"	>12.0	17	4	3	1	17	5	0	1
Bream	<7.0	1	63	63	0	44	0	0	0
"	7.0–10.4	94	341	239	2	369	16	0	4
"	10.4–18.0	240	45	41	4	422	28	1	5
Perch	<7.5	748	283	238	45	280	12	1	5
Tench	all sizes	3	3	2	1	0	0	0	0
Carp	"	0	2	2	0	0	0	0	0
Pike	"	6	1	0	1	2*	0	0	0

ESTIMATES OF POPULATION ABUNDANCE

Estimates of population abundance and appropriate standard error are given for each capture-recapture model. No estimate was possible in some cases where recapture data was inadequate.

Lake: Farnborough 18(a) Series 1

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only)	Leslie Method B	Jolly Stochastic Model	'Best' Estimate
		N1	N2	N2	N1	N1	N1	
Roach	>6:0	7824 (1110)	6428 (155)	12505 (119)	12343	-	13218 (2923)	12000
Tench	all sizes	476 (153)	497 (41)	404 (20)	409	360 (146)	328 (319)	400
Tench	"	348 (106)	455 (37)	488 (22)	477	515 (238)	624 (278)	450
Tench	"	864 (202)	962 (56)	986 (31)	978	853 (261)	1259 (422)	850 by addition
Perch	"	100 (22)	151 (14)	68 (8)	76	314 (194)	310 (13)	70
Gudgeon	"	78 (38)	414 (55)	459 (21)	435	383 (311)	1104 (35)	400

Lake: Farnborough 18(a) Series: 2

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only)	Leslie Method B	Jolly Stochastic Model	'Best' Estimate
		N1	N2	N2	N1	N1	N1	
Roach	>6.0	2654 (566)	853 (68)	592 (24)	873	532 (181)	653 (173)	900
Roach	6.0-10.0	2556 -	-	153 (12)	286			300
Roach	>10.0	1405 (296)	661 (56)	458 (21)	606	428 (143)	530 (171)	600
Tench	all sizes	541 (208)	151 (20)	381 (20)	399	319 (154)	399 (227)	400
Tench	"	408 (125)	138 (16)	342 (18)	352	329 (133)	347 (136)	350
Tench	"	984 (255)	293 (25)	780 (28)	806	664 (215)	724 (216)	800
Perch	"	1521 (516)	377 (33)	2036 (45)	1995	4399 (5061)	5133 (5954)	2000
Perch	<9.5	1367	494	994	1024	337	2551	1000
Perch	>9.5	22 -	-	4 (2)	13	-	3 (0.8)	16
Gudgeon	all sizes	375 (175)	194 (37)	383 (20)	382	6242 (7445)	62 (50)	380

Lake: Twyford 32 Series: 1

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch N2	Triple Catch (marked deaths only N1	Leslie Method B		Jolly Stochastic Model		'Best Estimate
		N1	N2			N1	N2	N1	N2	
Roach Days 1,2,3	10.0–27.0	10 (3)	3 (1)	1 (1)	7	2.5 (1)	–	–	–	12
Roach Days (1+2),3,4	"	12	2 (1)	–	–	–	–	–	–	12 (known minimum)
Perch Days 1,2,3	all sizes	1097 (355)	2343 (177)	681 (26)	706	–	–	–	–	
Perch Days 1,2,3	<8.5	856 (341)	782 (65)	646 (25)	656	80 (32)	–	–	–	700
Perch Days (1+2),3,4	"	1457 (692)	75 (9)	289 (17)	402	–	–	–	–	~500
Perch Days 1,2,3	>8.5	192 (80)	635 (91)	224 (15)	220	–	–	–	–	220
Perch Days (1+2),3,4	"	1127 (635)	195 (26)	5596 (75)	5378	–	–	287 (216)	5640 (7067)	–
Bleak Days 1,2,3	all sizes	161 (8)	107 (3)	137 (12)	156	–	–	–	–	150
Bleak Days (1+2),3,4	"	242 (12)	56 (7)	11 (3)	226	–	–	113 (8)	135 (118)	200
Pike Days (1+2),3,4	<30.0	1144 (455	656 (57)	3569 (60)	3444	30 (13)	7449 (8443)	560 (427)	9312 (10823)	3500
Pike Days 1,2,3	>30.0	114 (52)	46 (8)	25 (5)	39	48 (47)	96 (112)	–	–	40
Pike Days (1+2),3,4	"	100 (33)	70 (16)	37 (6)	60	–	–	82 (67)	120 (128)	

Lake: Twyford 32 Series: 2

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only)	Leslie Method B	Jolly Stochastic Model	'Best' Estimate
		N1	N2	N2	N1	N1	N1	
Roach	>11.0	2808 (1944)	339 (61)	184 (14)	293	264 (372	287 (410	300
Roach	11.0-16.0	1258 (166)	165 (20)	511 (23)	908	1074 (500)	1117 (495)	1000
Perch	all sizes	812 (206)	101 (14)	353 (19)	488	737 (569)	819 (622)	500
Bleak	all sizes	72 (46)	5 (0)	30 (5)	37	-	30 (40)	40
Tench	"	18 (6)	12 (4)	3 (2)	12	-	12 -	12
Tench	"	90 (58)	18 (5)	30 (5)	40	-	30 (40)	40
Tench	"	86 (36)	36 (9)	46 (7)	58	-	90 (34)	52 by summation
Pike	"	7 (5)	24 (7)	21 (5)	19	-	42 (40)	20

Lake: Twyford 33 Series: 1

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only)	Leslie Method B	Jolly Stochastic Model	'Best' Estimate
		N1	N2	N2	N1	N1	N1	
Pike	28-81	36 (18.9)	22 (4.2)	20	22	-	71 (91)	24 (total caught)
Perch	all sizes	959 (313.9)	848 (110.1)	448 (21.1)	521	1083 (1218.1)	1264 (1422)	700
"	>8.5	476 (146)	391 (146)	168 (13)	245	439 (485)	513 (562)	300
"	<8.5	396 (274)	210 (35)	242 (16)	249	-	-	400 by subtraction

Lake: Twyford 33 Series 2 Dates 17.1.74 - 31.1.74

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only)	Leslie Method B	Jolly Stochastic Model	'Best' Estimate
		N1	N2	N2	N1	N1	N1	
Pike	37.3-68.5	30 (14.1)	12 (3.5)	12 (12.0)	18	-	30 (40.1)	~20
Perch	23.3-35.7	24 (7.3)	30 (5.5)	13 (13.2)	18	-	35 (35.3)	~24

Lake: Darenth 39   Series: 2

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only	Leslie Method B		Jolly Stochastic Model		'Best' Estimate
		N1	N2	N2	N1	N1	N2	N1	N2	
Roach Days 1,2,3	7.4-14.0	4053 (1001)	959 (65)	502 (22)	805	-	-	-	-	-
Roach Days (1+2),3,4	7.4-14.0	2997 (864)	399 (50)	1381 (37)	1656	783 (552)	1097 (675)	3115 (1483)	1235 (755)	1500
Roach Days (1+2),3,4	7.4-9.8	1484 (687)	200 (40)	315 (18)	482	44 (15)	280 (265)	652 (506)	286 (264)	480
Roach Days 1,2,3	9.8-14.0	2836 (914)	570 (43)	634 (25)	778	-	-	-	-	-
Roach Days (1+2),3,4	9.8-14.0	1400 (439)	189 (29)	674 (26)	828	100 (71)	4190 (3310)	3606 (2184)	885 (716)	7000
Bream Days (1+2),3,4	8.0 22.0	4961 (3345)	61 (17)	1100 (33)	1451	-	-	3600 (4040)	660 (762)	1500
Bream Days (1+2),3,4	22.0-50.0	63 (21)	4 (2)	3 (2)	43	1 (0.3)	21 (26)	110 (133)	6 (6)	50
Bream Days (1+2),3,4	8.0-50.0	3204 (1702)	68 (17)	858 (29)	1219	-	-	-	-	1550 by summation

Lake: Darenth 40 Series 1

Species	Size Group (cm)	Adjusted Lincoln Index N1	Adjusted Lincoln Index N2	Bailey Triple Catch N2	Triple Catch (marked deaths only) N1	Leslie Method B N1	Jolly Stochastic Model N1	'Best' Estimate
Roach	all sizes	787 (37)	611 (10)	641 (25)	708	635 (45)	637 (33)	700
Bream	>5.0	542 (18)	329 (5)	270 (16)	474	324 (15)	326 (13)	513*
Rudd	all sizes	191 (7)	145 (0)	156 (12)	185	171 (11)	172 (9)	180
Gudgeon	all sizes	363 (112)	318 (37)	407 (20)	401 (3)	597 (371)	683 (419)	400
Chubb	all sizes	69 (10)	57 (6)	166 (13)	109	53 (20)	55 (19)	100
Perch	all sizes	49 (10)	40 (1)	49 (7)	49	48 (14)	51 (10)	50
Minnow	all sizes	32 (14)	21 (3)	17 (4)	20	10 (4)	-	20
Tench	all sizes	10 (5)	1 -	2 (1)	6	-	-	8

* Total number caught

Series 2 estimates given in TABLE 18, p.

Lake: Larkfield 41 Series 1

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple Catch (marked deaths only	Leslie Method B		Jolly Stochastic Model		'Best' Estimate
		N1	N2	N2	N1	N1	N2	N1	N2	
Roach Days 1,2,3	<9.0	1836 (996)	546 (126)	25 (5)	238	-	-	-	-	
Roach Days (1+2),3,4	<9.0	9471 (3819)	15912 (959)	3690 (61)	3831	38 (39)	12410 (1569)	118 (128)	15218 (19515)	4000
Roach Days 1,2,3	9.0–26.0	7645 (4398)	1052 (52)	14356 (120)	14308	-	-	-	-	-
Roach Days (1+2),3,4	9.0–26.0	1124 (291)	114 (15)	159 (13)	413	9714 (9497)	307 (209)	24653 (28144)	341 (241)	400
Bream Days 1,2,3	<8.0	6216 (3557)	22903 (1878)	2968 (54)	3026	-	-	-	-	-
Bream Days (1+2),3,4	<8.0	67161 (38713)	38316 (1324)	53853 (232)	53896	5938 (8992)	143788 (5916)	11877 (16562)	215682 (303804)	60000
Bream Days 1,2,3	8.0–28.0	6757 (1807)	1515 (108)	1413 (38)	1790	-	-	-	-	-
Bream Days (1+2),3,4	8.0–28.0	5694 (949)	1939 (105)	8716 (93)	8379	1741 (753)	7302 (3779)	1838 (687)	8461 (4394)	7000

Lake: Larkfield 41 Series: 2

Species	Size Group (cm)	Adjusted Lincoln Index		Bailey Triple Catch	Triple catch (marked deaths only)	Leslie Method B	Jolly Stochastic Model	'Best' Estimate
		N1	N2	N2	N1	N1	N1	
Roach	<8.2	7005 (1414)	15565 (470)	1625 (40)	1748	2654 (1332)	2775 (1326)	∿7000 by subtraction
Roach	8.2-12.0	670 (217)	318 (19)	881 (30)	869	754 (348)	682 (381)	850
Roach	>12.0	42 (19)	10 (4)	18 (4)	28	42 (48)	84 (103)	40
Roach	all sizes	7973 (1390)	10861 (301)	8973 (95)	8974	8609 (2579)	8896 (2565)	8500
Bream	7.0-10.4	10716 (1687)	6008 (309)	87187 (295)	86516	155268 (3661)	232903 (208760)	87000
Bream	10.4-18.0	2208 (851)	543 (77)	1823 (43)	1864	1926 (1127)	2407 (1508)	2000
Perch	<7.5	4618 (617)	4185 (234)	3183 (56)	3416	3758 (1812)	3842 (1832)	4000
Perch	all sizes	4630 (618)	4230 (237)	3183 (56)	3418	3758 (1812)	3842 (1812)	4000