The functional role of gasterosteus aculeatus in promoting energy flow through its ecosystem

Fox, P. J.

Fox, P. J. (1972) *The functional role of gasterosteus aculeatus in promoting energy flow through its ecosystem*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/9143/

UNIVERSITY OF DURHAM

THE FUNCTIONAL ROLE OF GASTEROSTEUS ACULEATUS IN PROMOTING ENERGY FLOW THROUGH ITS ECOSYSTEM.

by

P. J. Fox

A thesis submitted in part fulfilment of the
degree of M.Sc.

September 1972

CONTENTS

Chapter III

INTRODUCTION

The effective use of mans potential food resources to meet the increasing food demands, must ultimately depend on maximizing the efficiency of crop management policy.

It is clear that management policy for animal "crops" must be designed with the following two aims in mind: 1) to match the optimum stocking rate to the long term carrying capacity of the habitat, together with manipulation of the habitat to raise the capacity; 2) to adjust the cropping level to facilitate maximum sustainable yield without depleting either the habitat or crop species. Before we can effectively manipulate either the environment or the crop to satisfy these two aims, we must first have precise knowledge of the functional role of the crop species within the ecosystem framework and its part in promoting energy flow through the system. This approach will enable us to define the rate at which energy is required by the crop species from its food sources, the rate at which energy is passed to other trophic levels (both carnivore and detritivore) and even more important to make a quantitative estimate of crop mortality by predation. This will provide an indication of the overall effectiveness of crop production.

It is hoped that the method of approach outlined in the dissertation would be applicable to any secondary or tertiary producer which is a potential crop species. Three basic prerequisites are needed for a study of this nature:

1) Laboratory investigations, under as near natural conditions as possible, of growth characteristics and energy budget of the chosen species. This will also provide information on food requirements and conversion efficiencies.

2) Field investigations of crop production and the impact of the crop species on its food.

3) Field estimates of predation and other mortality of the species to measure effectiveness of production.

I chose to study a pond population of the three-spined stickleback (Gasterosteus aculeatus), to investigate the significance of this fish in the pond ecosystem and the magnitude of energy flow through the fish population. It is not suggested that the stickleback is a potential food source for man, but only that it is a species which lends itself readily to experimental manipulation and hence can be used to evolve generally applicable theories. The data obtained on the relationship between Gasterosteus and its ecosystem is used to pose the theoretical problem of raising stickleback productivity artificially.

CHAPTER I

THE ENERGY BUDGET.

For any individual species population, or trophic level, an energy budget may be written of the form:

$$C = A + F$$

and $$A = \Delta B + R + U$$

where C = calories ingested / unit time

A = calories assimilated / unit time

F = calories of faeces / unit time

ΔB = calorific change in biomass / unit time

R = calories used in metabolism / unit time

U = calories excreted in urine / unit time

This has been applied to fish by Warren & Davis (1967).

It has been calculated by Ivlev (1945) that energy lost by kidney and gill excretion (U) is small. Winberg (1956) argued that an error of less than 3% of the energy value of food consumed could be expected if metabolic wastes excreted in this manner were completely disregarded. It was therefore considered reasonable to omit considerations of this parameter in the present study.

1) Measurement of food consumption and other energy parameters.

Several methods have been used to estimate the rates of food consumption by fish in the wild. Winberg (1956) and Mann (1964) assumed that metabolic expenditure of fish in the field was approximately twice that of metabolism measured in the laboratory. Assimilated energy requirements in the field were calculated by adding the energy value of weight increase to that of twice the routine metabolic rate.

Consumed energy was then deduced by assuming that the assimilatory efficiency of consumed food in the field was 80%. Failure to provide a rigid definition of "routine" metabolic rate must restrict the use of this technique in duplicate experiments on other fish species or in other laboratories. Similarly, no consideration appears to have been given to possible changes in metabolic rate through the twenty four hour period. Circadian rhythms of metabolism are commonplace in vertebrates. The doubtful validity of predicting average energy requirements over a long period of time from short-term measurements of metabolic rates is also a major shortcoming of the method adopted by Bajkov (1935). This involved the capture of a fairly large group of fish in the wild. By sampling from this group at regular intervals of time, the rate of disappearance of food from the stomach could be measured. This was claimed to give an indication of the amount of food eaten per day. A far more realistic value would have been obtained had the method been modified by feeding to a wild population food "labelled" with either a radioactive isotope or an indicator species for a brief period of time. Periodic removal of samples from the natural habitat with a minimum of disturbance could then have shown the rate of movement of food through the gut under natural conditions. Clearly, samples should have been taken throughout a full twenty four hour period before making predictions of consumption over long periods.

The nitrogen balance method, used by Gerking (1964), is possibly the most accurate technique developed so far. The rate of nitrogen intake over a period of time can be calculated for captive fish by summing the rates of nitrogen accumulation in growth and the rate of nitrogen loss through defaecation and excretion via kidneys and gills. The Kjeldal method was used for these measurements and it is relatively simple to estimate the percentage of nitrogen in food material. The main advantage of this method is that fish can be taken from the natural habitat at periodic intervals and their rates of excretion measured immediately. The assumption is probably correct that the rate of excretion is a mean value and thus not subject to short term fluctuations of food intake. The effect of handling on rates of excretion is however open to conjecture. Hence,without far more experimental evidence than exists at present, this method must be accepted only with reservation, as is true of other energy balance techniques.

Without a reliable technique of measuring consumption directly, in the field, the most realistic method appears to be one based on the creation of laboratory conditions as near to natural as possible. The relationship may then be measured between growth rate and food consumption from known rations. This may then be used to predict consumption from growth rate observed in the field. As pointed out by Ricker (1968), the reliability of this type of technique will depend on how closely the laboratory conditions approximate to the natural state. For a small fish (such as <u>Gasterosteus</u> used in the present study) it was considered that a relatively natural metabolic rate could be achieved by taking certain precautions regarding fish density, temperature, light conditions and food substrate. A distinct advantage of this method is that values obtained would represent an average over a long period of time. Most previous methods are unavoidably subject to inaccuracies due to short term fluctuations. A further advantage is that precise data could be obtained on the assimilatory efficiency, thus allowing estimation of the energy released back into the ecosystem by defaecation.

In order to compare the physiological states of the laboratory fish with wild fish, fat analyses of both groups were undertaken at the end of the experiment. The fat level is possibly the most effective index for making such a comparison, since it reveals whether growth by weight of wild and laboratory animals should be assigned the same calorific value.

2) Methods.

Measurement of the energy budget of Gasterosteus aculeatus was carried out in a constant temperature room at 14 ± 1°C, (this temperature was chosen as it approximated the mean temperature of the pond used in the field study 15.5 ± 2°C). Human disturbance was reduced to a minimum by isolating the experiment tanks in a light-sealed cupboard. This was illuminated inside by two 15 watt flourescent tubes connected to a time switch. The lighting regime was maintained at the normal August daylight hours, 15 hours light and 9 hours dark. Fish brought into the laboratory were first allowed to acclimatize for one week and then starved for 48 hours before wet weighing. Fish were then fed, either individually or in groups (in the case of young fish), in 3.5 litre tanks. These were blacked out from the side to simulate natural light from above. Water in the tanks was replaced slowly by siphon every 48 hours with natural pond water at 14°C to prevent unnatural build-up of soluble excretory products.

The fish were fed with weighed aliquots of live Daphnia brought regularly from the field. Food aliquots were weighed by drying the surface moisture on the Daphnia with tissue paper; animals were then transfered to dry filter paper before they were brushed into a weighed

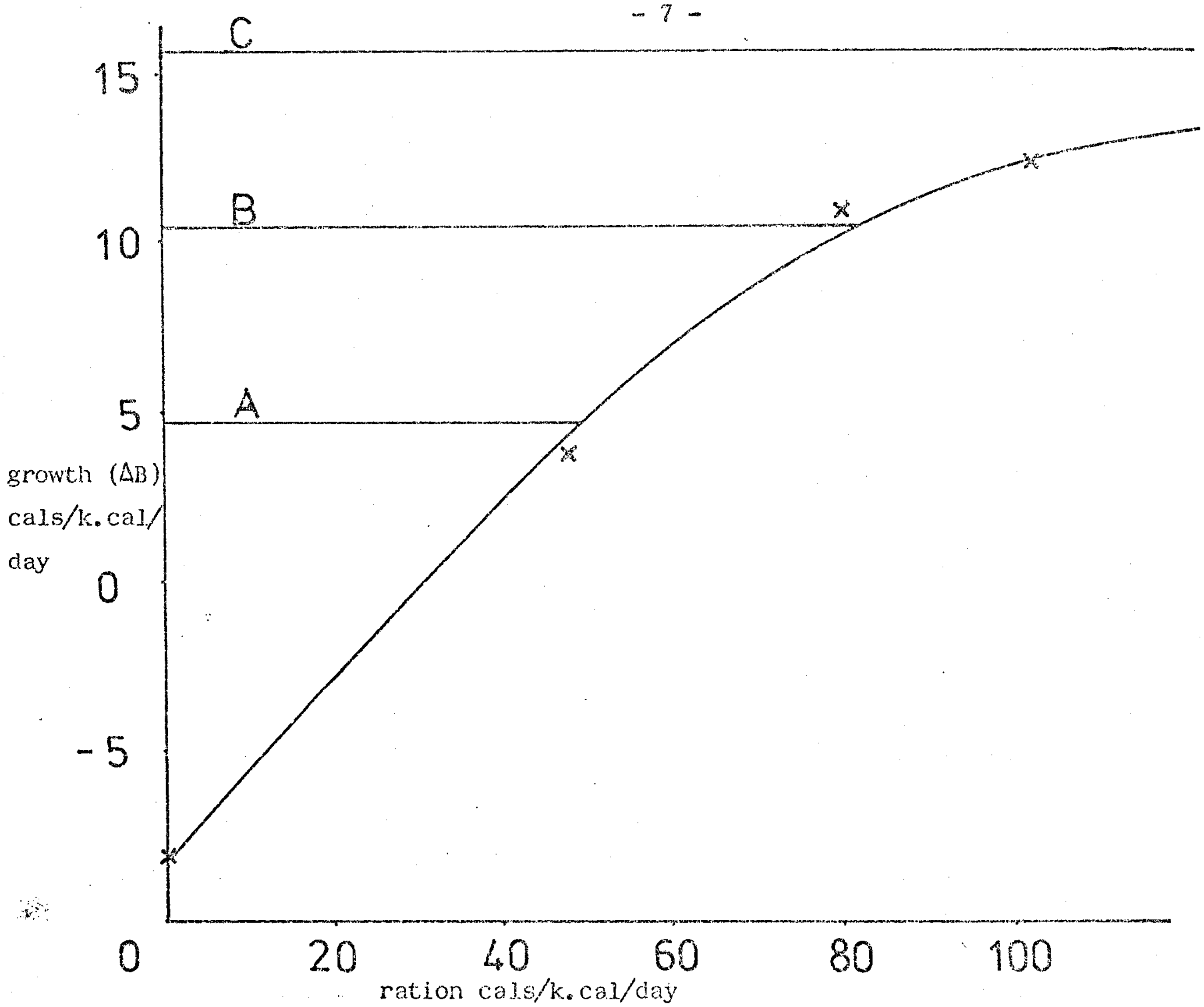


Figure (1) Affect of ration size on growth rate
(A, B, C, growth rates at high, normal & low density)

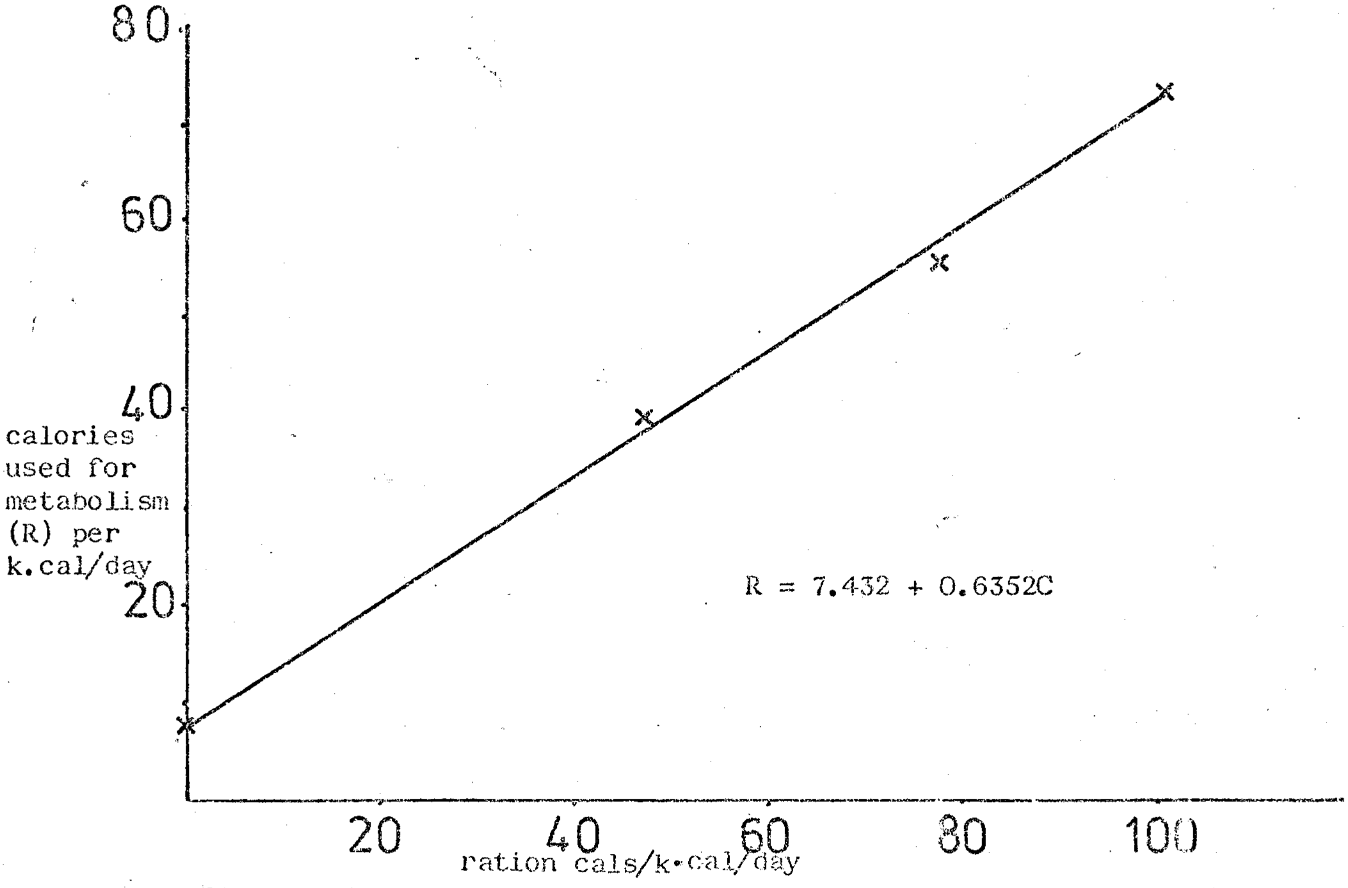


Figure (2) Affect of ration size on energy expenditure tube of cooled water. Subsamples were taken periodically and oven dried for moisture content. With practice it was found that Daphnia could be wet weighed (with a water content of 91%) with an accuracy of ± 1%. Fish fed "ad lib" were given excess of food. All uneaten material was siphoned out through a filter paper after 24 hours. The food was then dried and weighed by the method as that used for fresh Daphnia. Similarly, faeces were removed every 24 hours and oven dried.

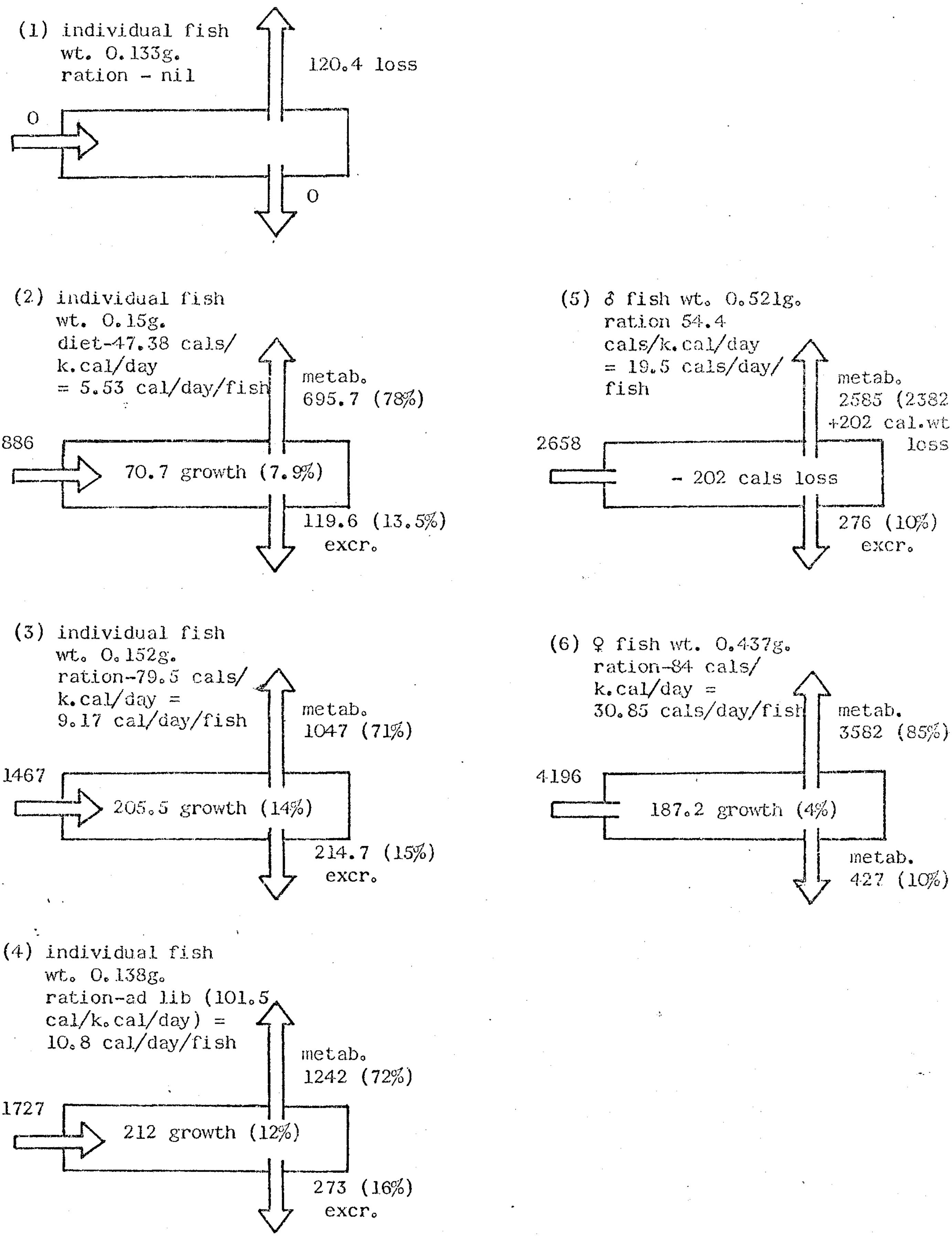
Calorific values of fish, faeces and Daphnia were measured with the Durham exygen microbomb calorimeter. Ash content of all materials was obtained by heating in a muffle furnace at $500^{o}C$ for 48 hours. Fat analysis of the fish was carried out by the Soxlet method of fat extraction from dry material, using petroleum ether.

3) Results and Discussion.

In the analysis of results, it has been assumed that the rate of change of both weight and calorific value of the fish during the experimental period followed a straight line relationship. Thus to calculate the growth rate and feeding level (per unit energy content of fish per day), the average of the initial and final calorific values has been used.

The growth curve shown in fig. (1) for young Gasterosteus was derived from measurements on batches of 10 fish over a period of 20 days. The weights of individual fish varied between 0.10 - 0.16 g. at the start of the experiment. Animals were taken from a field stock approximately twelve weeks old. So that laboratory data could be applied meaningfully to the field experiments, fish were taken from

Figure (3) Energy Budgets



(1) individual fish
wt. 0.133g.
ration - nil

(2) individual fish
wt. 0.15g.
diet-47.38 cals/
k.cal/day
= 5.53 cal/day/fish

(3) individual fish
wt. 0.152g.
ration-79.5 cals/
k.cal/day =
9.17 cal/day/fish

(4) individual fish
wt. 0.138g.
ration-ad lib (101.5
cal/k.cal/day) =
10.8 cal/day/fish

(5) ♂ fish wt. 0.521g.
ration 54.4
cals/k.cal/day
= 19.5 cals/day/
fish

(6) ♀ fish wt. 0.437g.
ration-84 cals/
k.cal/day =
30.85 cals/day/fish

(1) to (4) first season young, age 0

(5) to (6) second season adults, age 1

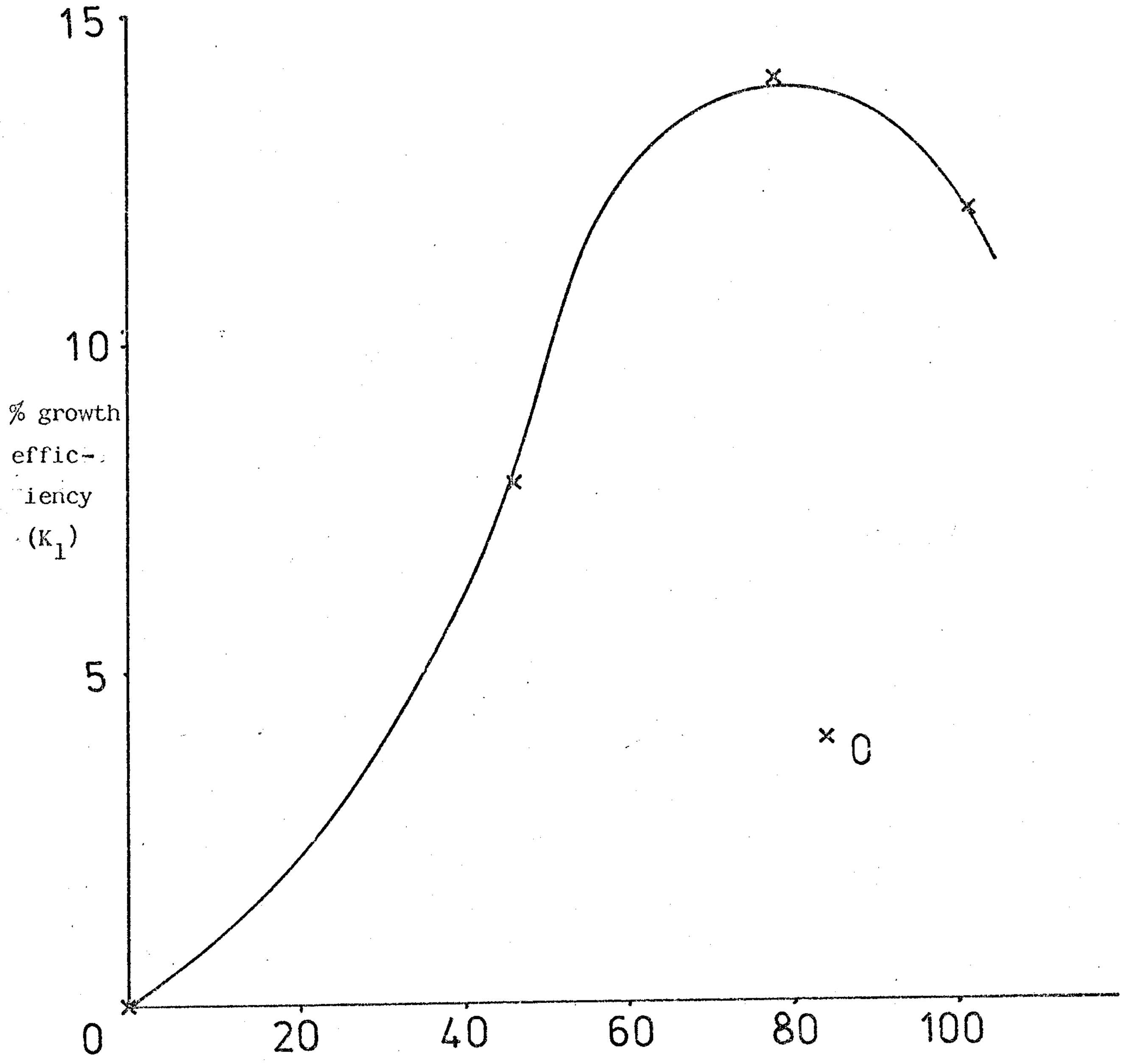


Figure (4) Affect of ration size on growth efficiency of young fish (0 = one year old fish) the same pond as used in the field experiments described later. Furthermore, both laboratory and field experiments were run at the same time of year (mid July - August) and under similar photoperiods.

For comparison the growth rates measured in the field enclosures described in chapter II are superimposed on the laboratory curve in Fig. 1. Energy used for metabolism was calculated by subtracting calories of growth from calories assimilated. When this was plotted against feeding level, a straight line relationship was found, see Fig. 2. The possible implications of this relationship will be discussed later in an appendix.

Energy budgets (in the laboratory) at different ration levels are presented in Fig. 3. It is clear that the proportions of energy used for different functions are highly dependant on the amount of food eaten. It is critical therefore, to select a budget appropriate to the field growth rate (and hence food intake) before computing population energy budgets. Fig. 3 shows that the efficiency of conversion (%) of food (Daphnia) into fish flesh reached a maximum for young fish between 70-80 cals. fed/k.cal. fish/day (fig. 4.) Above this value of food intake the maximum growth rate was approached (fig. 1) and further intake appeared as increased metabolism. Growth efficiency here is considered as Ivlev's (1964) coefficient of growth of the first order (K_1):

$$K_1 = \frac{\Delta B}{C}$$

When budgets 2,3 of the young fish are compared with the energy budgets of one year old fish (budgets 5,6 Fig. 3) at similar feeding levels per unit energy constant of fish, it can be seen that a lower growth efficiency was evident in the older fish (14% against 4% for 80 cals./K.cal./day fed) Fig. 4. A correspondingly higher percentage of energy intake was used for metabolism by older fish.

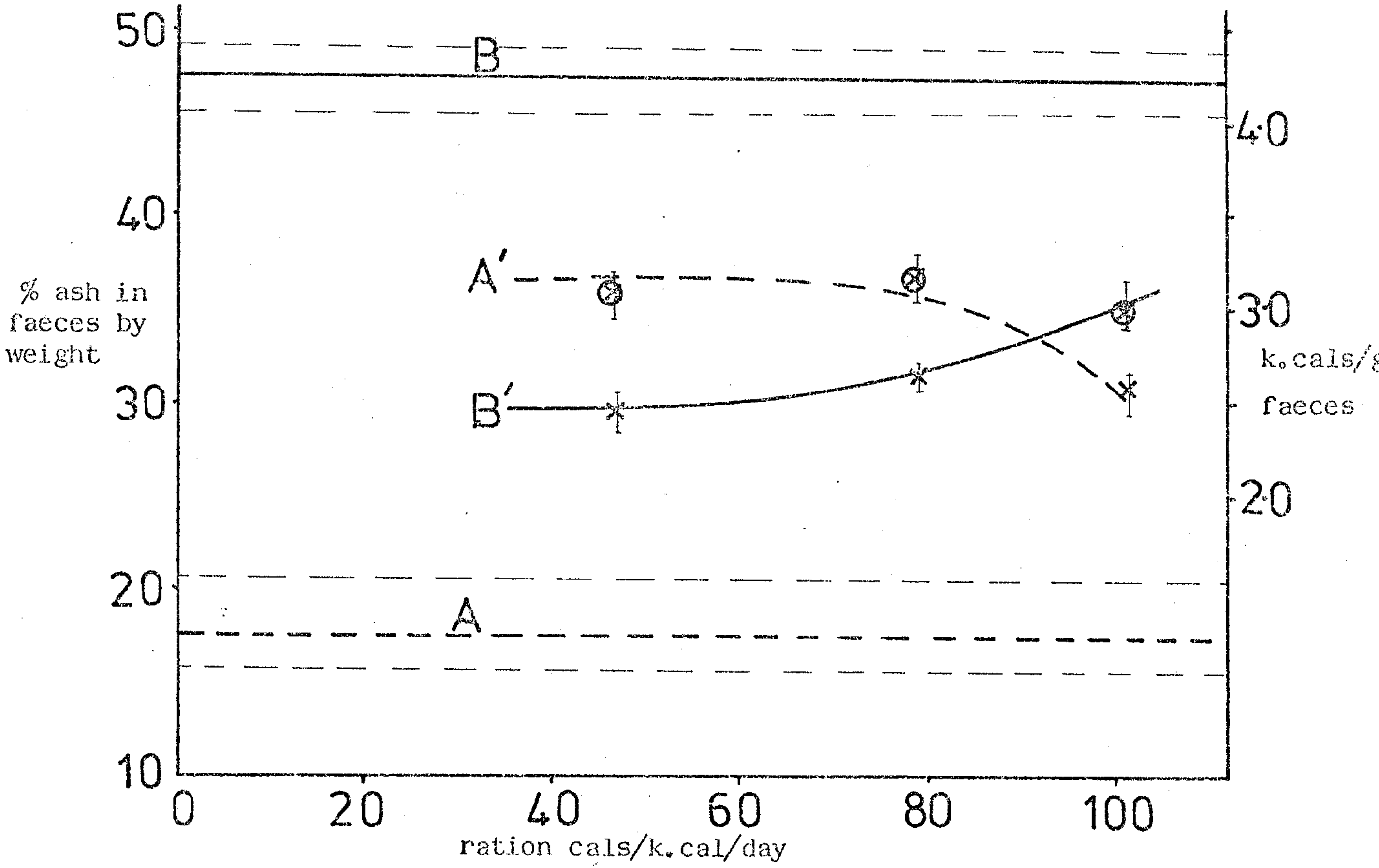


Figure (5) Affects of ration size on energy value of faeces
(A, A′ - ash content of food and faeces respectively)
(B, B′ - caloric values of food and faeces)

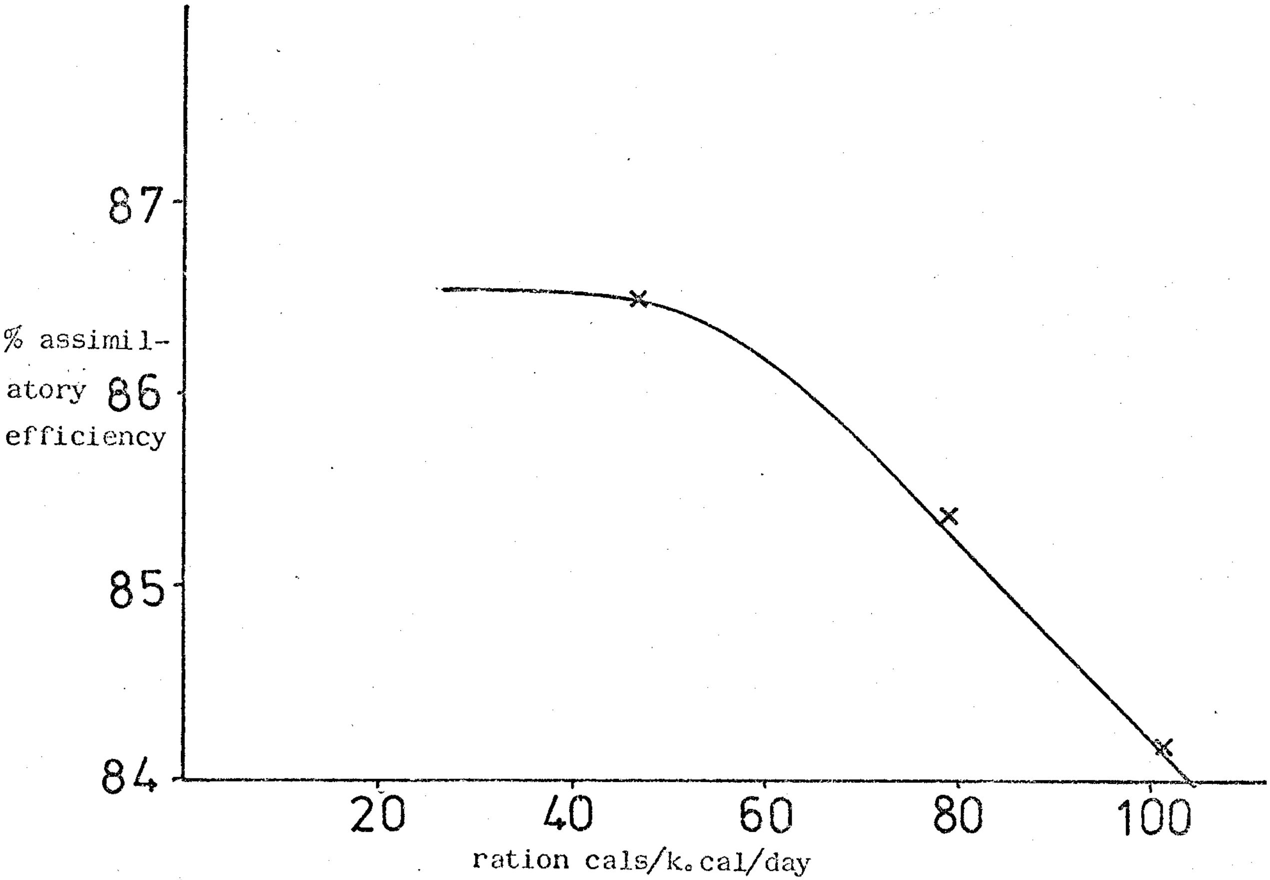


Figure (6) Affects of ration size on assimilatory efficiency

The assimilatory efficiency of young fish (calculated by subtracting calories released as faeces from calorific food intake) varied between 84% and 86.5%. A trend of slightly decreasing efficiency was observed with increase in diet, Fig. 6. The trend was substantiated when both the ash content and number of calories/gm. of faeces are compared with those of the food (Fig. 5). Both the % ash and the calorific value of faeces approaches those of the food at the higher feeding levels, and both curves tend to level off to a maximum divergence between the parameters of faeces and food when the feeding level falls below about 60 cals./K.cal./day. This suggests that the maximum assimilatary efficiency of first season fish fed on Daphnia is approximately 86.5% (the value attained when the feed level drops below 60 cals./k.cal./day). The minimum assimilatory efficiency (84%) was found for fish fed "ad lib". This lower figure may result from the larger volume of food passing through the gut in a given time, rather than a change in the process of digestion.

4) The application of laboratory data to prediction of the energy budget of a field population.

It was assumed earlier that the precautions taken during the experimental proceedure were sufficient for the metabolism (and therefore the growth rates) of fish in both laboratory and field to be directly comparable. However, two results need further consideration before the comparison can be accepted.

Firstly we need to know why the maximum growth rate in the low density field enclosure is greater than the maximum growth rate in the laboratory, Fig. 1. This may well result from a difference in the foods taken in the two situations. Laboratory animals were

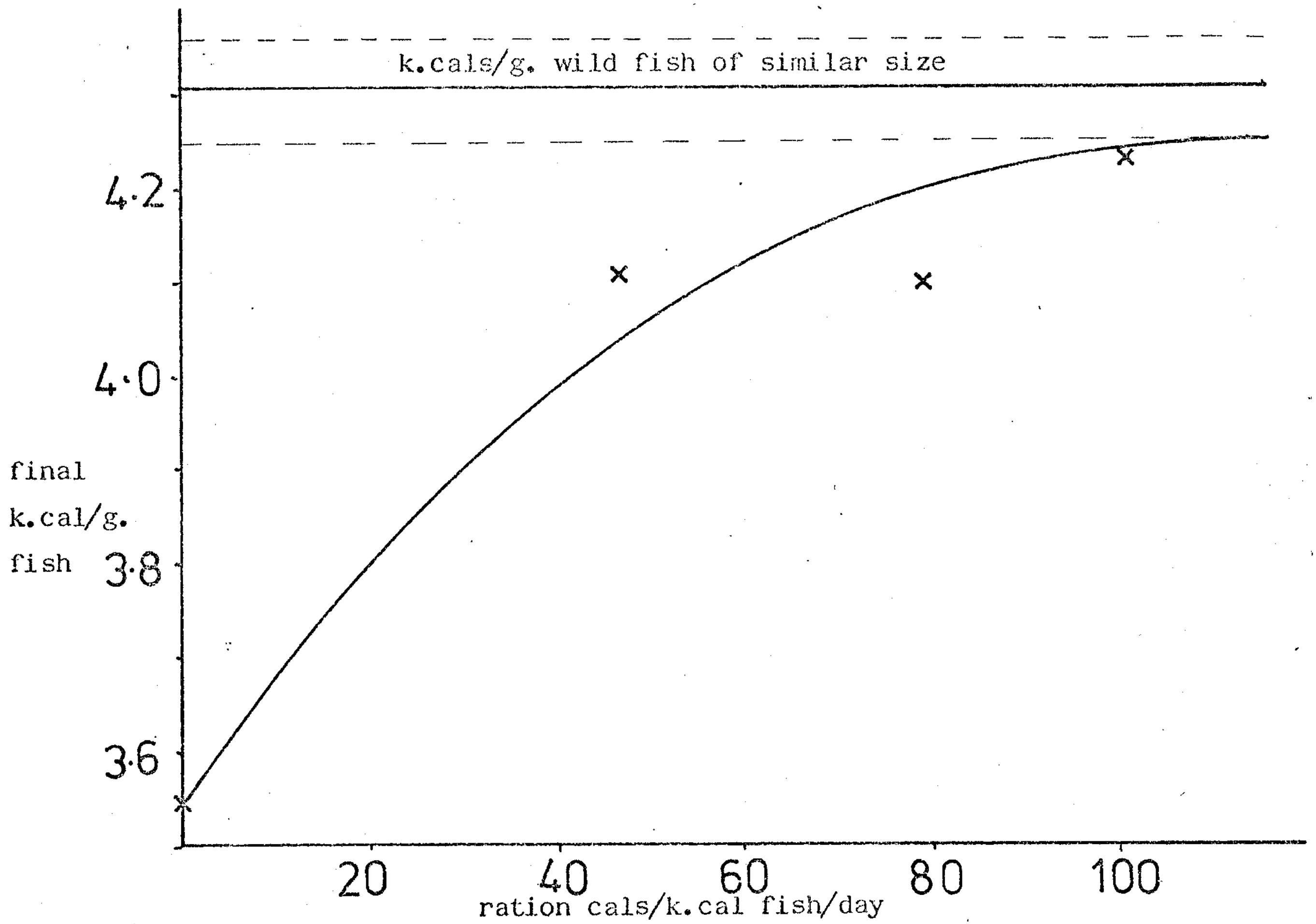


Figure (7) Affect of ration size on final energy value of fish

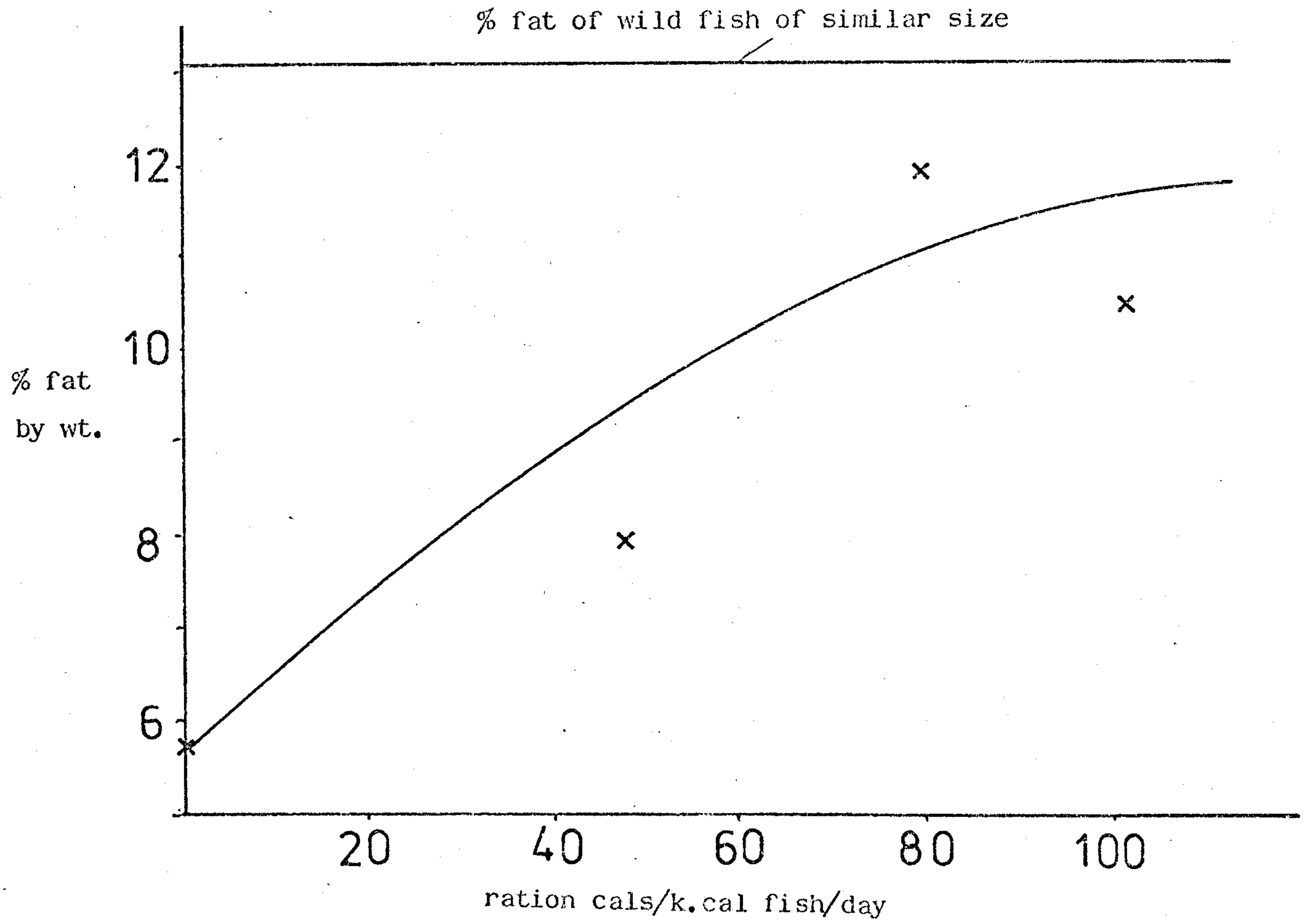


Figure (8)

maintained on Daphnia. This has a fairly low calorific value (4248 cals./g. ± 150) possibly as a result of a high percentage of ash (17.9 ± 3%). Wild fish of similar age eat mainly Ostracods, Chironomid larvae, Ephemeroptera nymphs and small molluscs (see Chapter II). Ostracods have similar calorific values to Daphnia, but those of Chironomids and Ephemeroptera are certainly higher (5102 ± 150 cals./g. and 5200 ± 100 cals./g. respectively (Ricker 1967)). Thus the low density field population with the high growth rate is probably feeding on food of higher calorific value than the laboratory experiments. In order to test this theory, the final physiological states of the laboratory fish were compared with wild fish by means of a fat analysis. The graphs in Fig. 8 (fat as a percentage of dry weight of the fish) and Fig. 7 (final calorific value) show that the laboratory fish fed "ad lib" on Daphnia have slightly lower values than the field animals. Since the total weight intake of fish fed "ad lib" will be limited by the size of the stomach and the rate of passage of food, the maximum growth rate in the laboratory might well have been restricted to a level proportional to the calorific value of the food (assuming similar assimilation efficiencies for different food). This phenomenon will not affect the relationship between growth and calorific intake below "ad lib" feeding, and by this argument, laboratory feeding levels below "ad lib" should still be applicable to field growth data. The second and related problem pertinant to the estimation of food intake from measured growth rates concerns the fundamental reasons for differences in growth. Are the differences in field growth rates between the three populations of varying densities due to different food intakes, or do they result from similar intakes but different rates of metabolic expenditure?

It is likely that fish subjected to high densities will exhibit unusual patterns of behaviour not found in normal density populations. It could be argued that an unnatural hierarchical structure may result in higher metabolic expenditure which would decrease the growth rate. Normally, a 'pecking order' is of distinct survival value to individuals at both the top and the bottom. Lack (1966 p.276) states that "Those higher in the order obtain food with little fighting, whilst those lower down save time on fights they would otherwise lose, and energy can be conserved for searching elsewhere". Murton, Isaacson and Westwood (1963) found that in pigeons, juveniles lower in the hierarchy are displaced by adults in dispute. Despite this, juveniles pecked for food as often as adults and even walked a shorter distance. This implies that they were less selective and took food rejected by adults. Obviously under normal conditions, where a hierarchy exists, there would appear to be no detrimental affect of increased energy expenditure in individuals lower in the chain, as these either move elsewhere or change to sub-optimal food.

Under enclosed conditions the situation is probably different. Barnett (1955) found that rats enclosed at high density often lost weight if they were sub-dominant. By analysis of the size of the adrenal cortex he concluded that this exhaustion was not merely a consequence of violent exercise but of more complex nervous and endocrine changes. This is an important alternative viewpoint because it stresses that although sub-dominant individuals may be able to withdraw to relatively secluded parts of the habitat so that their level of activity is not severely altered, changes in endocrine balance can shift the energy budget in favour of catabolic processes. It must be remembered that animal density in Barnett's experiment was abnormally high, between sixteen to thirty rats per square metre. Under these conditions it is hardly surprising that pathological symptoms were observed.

In my study, the number of fish in the in the high density enclosure (130 fish/sq.m.) was only double the normal pond density (65 fish/sq.m.) and it is doubtful that the conditions described by Barnett are applicable to the situation. Furthermore, young Gasterosteus form shoals at the age used in the experiment. Although the average pond density was 65 fish per square metre, shoals containing up to two hundred young fish were often observed occupying an area of a quarter of a square metre at any one time. The shoaling density was therefore far higher than the average fish density even in the high density enclosure. In addition to this shoaling was still observed in this enclosure with no visible abnormalities. It is therefore unlikely that metabolism was raised at the higher stocking density used.

Further evidence that food was the most probable factor restricting growth rate, can be seen by comparing the indices of stomach content presented in Table 8, Chapter II. Stomachs of fish taken from the high density enclosure were consistently only 40 - 60 % as full as those of the fish kept at normal density. Thus it may be safely assumed that the differences in growth rate observed in the field at the three specified densities resulted primarily from 1) food limitation at the higher densities and 2) a choice of optimal food types from a super-abundant supply at the low density. It was therefore considered justifiable to estimate calorific intake in the field from the laboratory curve of calorific intake versus growth rate, whenever the field growth rate fell below the point at which the laboratory fish were fed "ad lib".

If a fish population consists of individuals of different year classes, it would be necessary to know the relevant energy budgets and feeding levels of each component year class in the population before a population budget could be constructed. The total energy budget could then be calculated by summing the total energy flow through each component allowing for mortality. Fortunately, the majority of Gasterosteus in my study pond spawned in early April of their second summer, and died soon afterwards when just over one year old. Therefore, during the two months when my field experiment was in progress (July - August), the population energy budget was equivalent to that of first season (young) fish. The energy budget of a single fish of average weight on the median day of the experiment can now be calculated:

From the curve in Fig. 1. it can be deduced that the approximate daily calorific intake required to produce the growth rate of 10.5 cals./k.cal./day observed in the "normal" density fish population was 80 calories per k.cal. of fish. The appropriate energy budget for a daily intake of this magnitude is budget (3) of Fig. 3. However, the weight of an average fish in the "normal" population was 0.1243 g., not 0.152 g. as in the last experiment. Hence the final energy flow per day through the average fish on the median day of the experiment was as shown in Fig. 9.

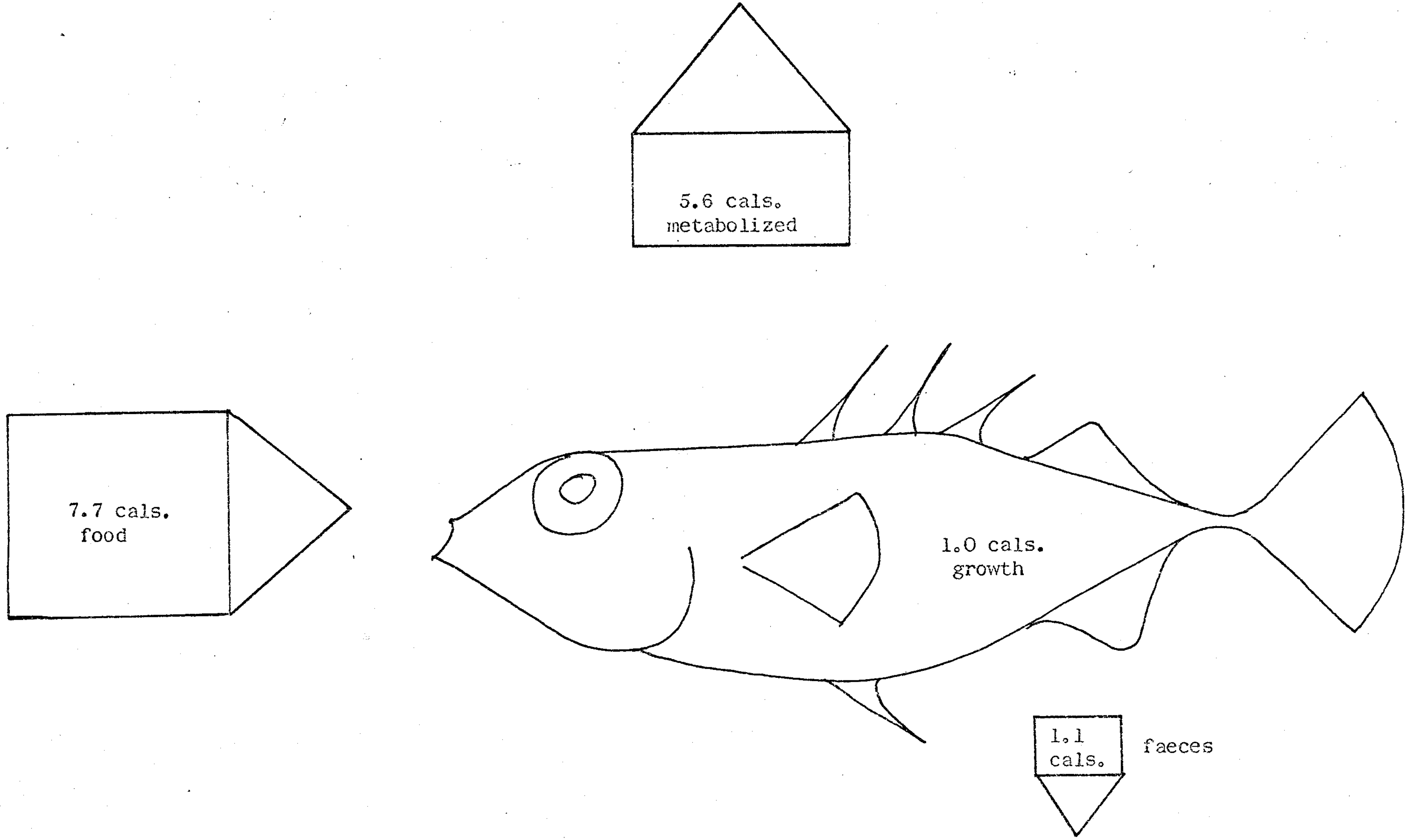


FIGURE (9) Energy flow per day through a fish of average size on the median day (21 August)

Wt. - 0.1243 g. (96.29 cals)

APPENDIX

POSSIBLE IMPLICATIONS OF THE METABOLISM / FOOD INTAKE GRAPH (FIG. 2)

When energy used for metabolism was plotted against calorific intake a straight line relationship was observed, as Fig. 2. Basically this shows that the fish is able to conserve energy when fed on low rations by reducing its rate of metabolic expenditure. This type of relationship is known in many other animals, but the fact that it appears to be a straight line in Gasterosteus could have useful implications. It is possible that all fish have such a relationship peculiar to the species or age group, at least under laboratory conditions. If this is so,then two values, the slope and intercept of the line could characterize the entire feeding energetics of that species age group at all feeding levels. Palaheimo and Dickie (1966) observed a straight line relationship between the log of growth efficiency and feeding level. The physiological basis for both these two lines is probably essentially the same because if the assimilatory efficiency is relatively constant, food conversion efficiency and metabolic expenditure are obviously interdependant. With Palaheimo and Dickiés curve, the relationship was linear only between very narrow limits of food intake in the middle of the range. The relationship shown in Fig. 2. is clearly more useful than Palaheimo and Dickie's equation because it is linear for all feeding values between starvation and "ad lib". If we assume that the slope of the line characterises the fish species or age group, it is possible that the intercept is demonstrative of the metabolic level of the fish. If these two values are known from laboratory measurements, a single experiment, viz. starving fish under specified conditions and measuring the loss in weight, would enable the entire set of energy budgets to be defined as if the fish had been fed different rations under these conditions.

If these statements are found to be correct, this plot could be a highly effective tool in fish ecology. At the present time it is impossible to ascertain acurately, the metabolic rate or energy budget of fish in the wild state. It would seem relatively simple to develop a technique whereby fish could be enclosed in a completely wild situation in the absence of food. The resultant loss in weight over a known period of time * could then be used to measure the field metabolic rate and the respective energy budgets. It would be necessary to know the calorific value of the fish in the wild and certain assumptions would have to be made about body components which are being used up during starvation to provide energy. Without these corrections, considerable error could be introduced.

Another important relationship which could be established from the regression equation of the graph is a formula linking food intake, growth rate and fish size. This formula can be derived as follows:-

It can be seen that the relationship in Fig. 2 is described by:

$$R = A - \Delta B = a + b\ c \qquad (1)$$

where a = a constant (intercept)
b = the slope
All values A, B, C are in
cals./k.cal.fish/day.

The assimilatory efficiency varies very little (Fig. 5). Using an average of 85%, no more than 2% inaccuracy will be incured.

Thus:

$$\frac{A}{C} = 0.85 \qquad (2)$$

by substituting (2) into (1)

$$0.85C - B = a + bc$$

$$C(0.85 - b) = a + B$$

$$C = \frac{a + B}{0.85 - b} \text{ cals.food/k.cal.fish/day} \qquad (3)$$

For young Gasterosteus in July / August it was found that:

$$R = 7.432 + 0.6352C$$

$$C = \frac{7.43 + B}{0.85 - 0.635} = \frac{7.43 + B}{0.215}$$

If, therefore, we know the calorific value of the weight increase B, and the mean calorific value of the fish, we can calculate the amount of food eaten per day.

---

* Ivlev (1961) showed that the rate of loss in weight during starvation is initially steady and high for several days, but then begins to decrease. The period for which the energy used for metabolism during starvation lies on the same line, which relates metabolism and consumption at higher feeding levels, will thus be rather short. That is, the longer a fish is left starving the more its metabolism value will deviate from the straight line (Fig. 2). A compromise must be chosen between the period of time needed to give significant weight loss and the period of time before the metabolic rate deviates significantly from the straight line.

CHAPTER II

FIELD EXPERIMENTS

1) Description of site

Browney Pond lies about 4 miles south west of Durham City. It is approximately 40 metres long by 17 metres wide. (See Fig. 10). The southern and western sides of the pond are surrounded by a bank one metre high. The north end is overhung by a dense growth of small Alders (*Alnus glutinosa*) with *Juncus* spp. at the water level. The pond is not natural but was dug out in the 1920's as a reservoir for a nearby colliery.

It has an unusually high biotic potential made possible by the contours of the bottom. Half of the area of the pond is occupied by a shallow shelf which supports a fairly diverse standing crop and vegetation, including a dense growth of *Elodea canadensis*. The remainder of the pond is dominated by a deep profundal zone with poor vegetation and invertebrate fauna (see Fig. 10). The dimensions of this profundal zone would, under the conditions of an average pond be entirely inadequate to support a large population of Perch (*Perca fluviatile*). In Browney Pond, however, the Perch density is exceptionally high (approximately one fish per two square metres of surface). It must be assumed that the large "shelf" area with its correspondingly high standing crop of invertebrates and stickleback, provided the food reservoir necessary to maintain large predatory fish. Thus for a pond of this size, the diverse nature of its physical structure provided an unusually wide selection of ecological niches.

Two experimental enclosures, measuring two metres square, were

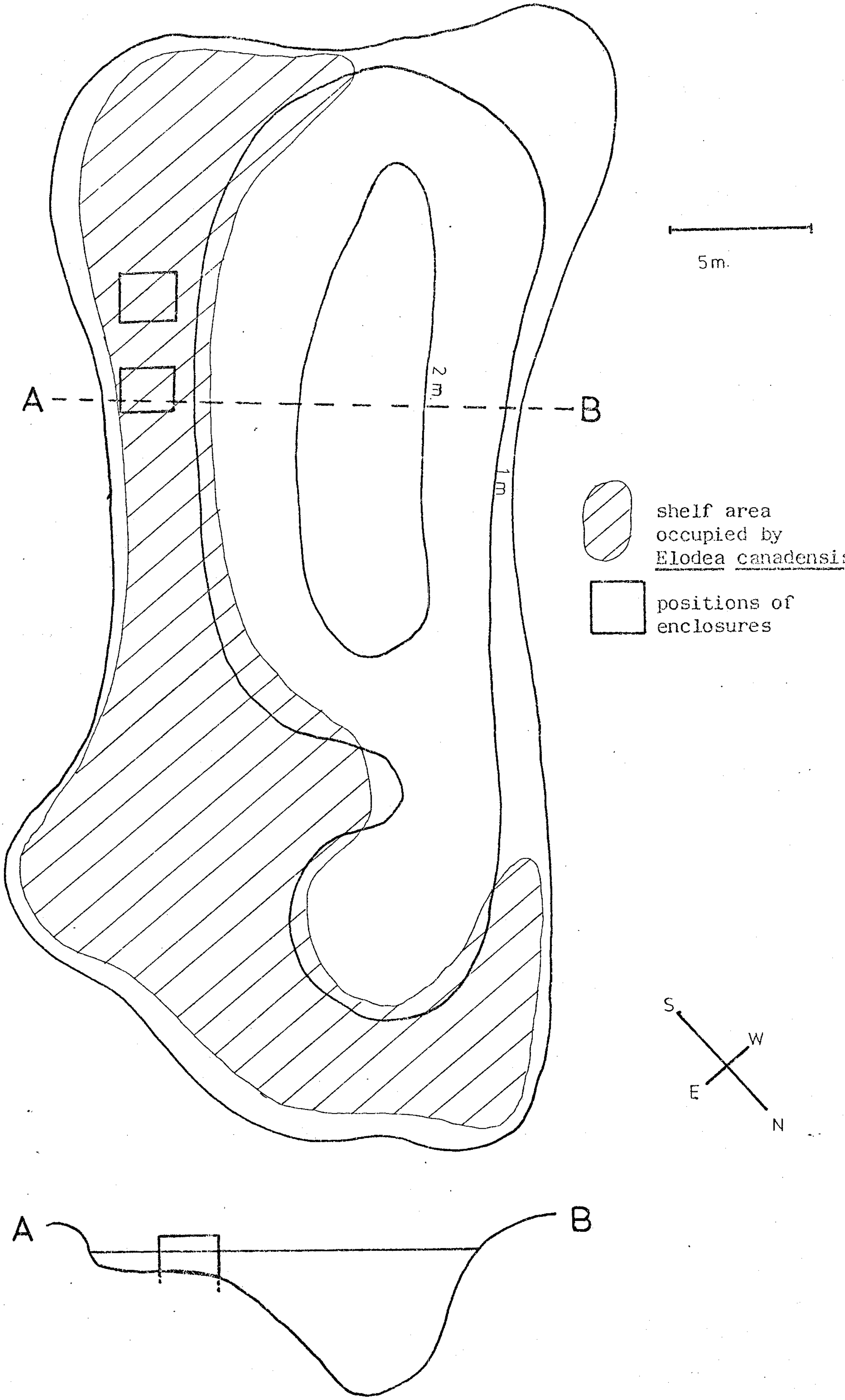


Figure (10) Physical structure of Browney Pond

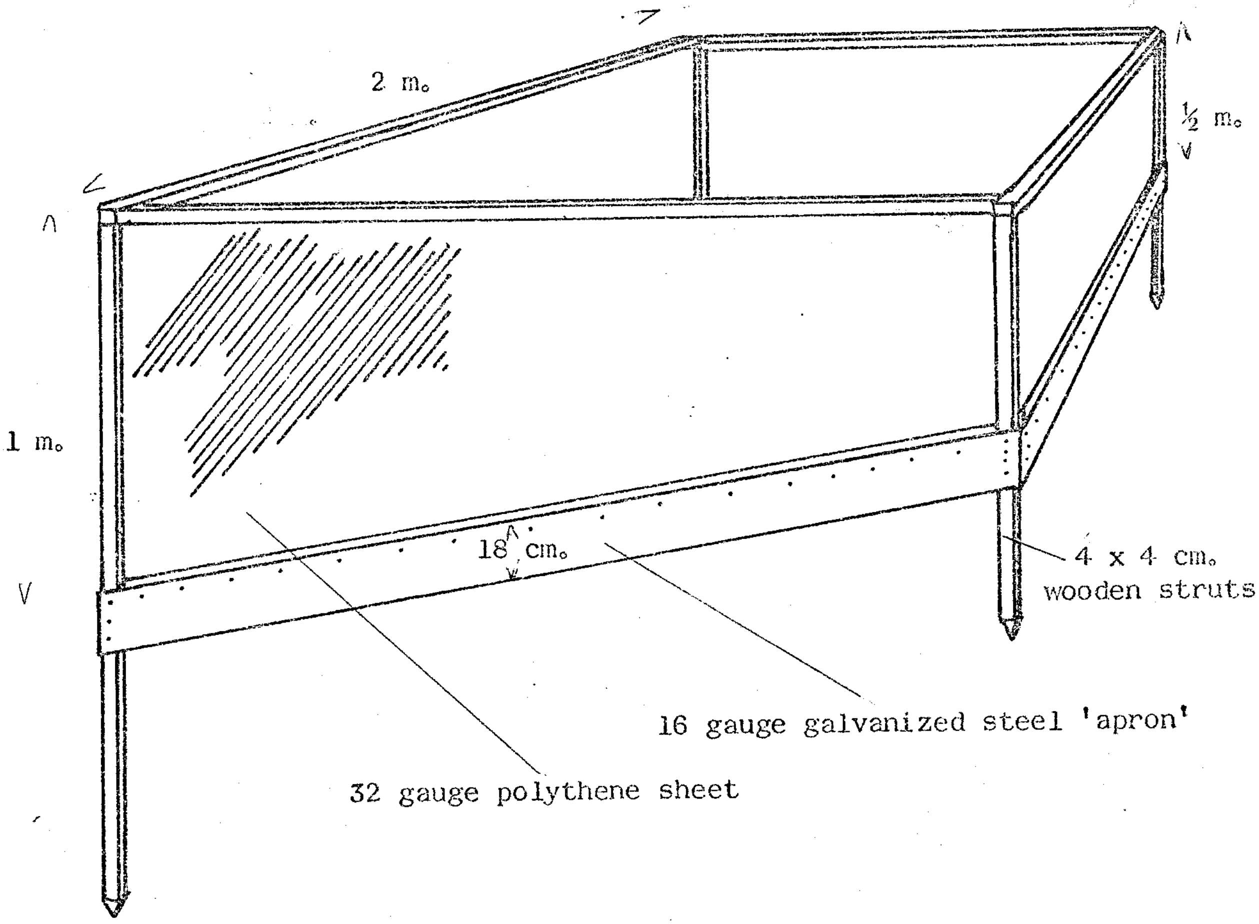


Figure (11) Construction of enclosures

PLATE I

The enclosures before placing in situ.

PLATE II

PLATE III

Enclosures in use looking North

PLATE IV

Pond aspect looking South.

constructed as shown in Fig. 11. These were situated at points (1) and (2) in Fig. 10, see also Plates 1, 2, 3 & 4. The galvanized steel strip around the bottom edge was pushed firmly into the muddy substratum and mud was piled up about 15 cm. around the outside to isolate the enclosed fauna. When the enclosures were in place, the tops projected about 20 cm. out of the water. The total fish population was completely netted from both enclosures and counted to give estimates of the initial density of stickleback in the pond. The vegetation and remaining fauna were left to settle for four days before restocking with stickleback at known densities on 19th July '72. Enclosure (1) was stocked at double the normal pond density (137 fish/sq.m.) and enclosure (2) at half the normal density (32 fish/sq.m.).

2) Fish growth rate

(i) Methods and results

Size distributions of a representative sample of *Gasterosteus* were measured before and after the 6 - 7 weeks experimental periods. Fish length was measured in the field by "pricking" onto waxed graph paper the positions of snout and tail fork. Fig. 12 (a) shows the length frequency distributions on 19th July when the enclosures were set up. The distributions measured 40 - 48 days after stocking at each respective density are also shown in this figure. To calculate the mean weight of each size class, a length *vs*. wet weight relationship was obtained from fish measuring between 10 to 45 mm. (Wet weights were taken after first drying off surface moisture). It was found that the relationship assumed a straight line after a logarithmic transformation was applied to both variables. By regression it was found that the length - weight relationship of *Gasterosteus* between 10 - 45 mm.

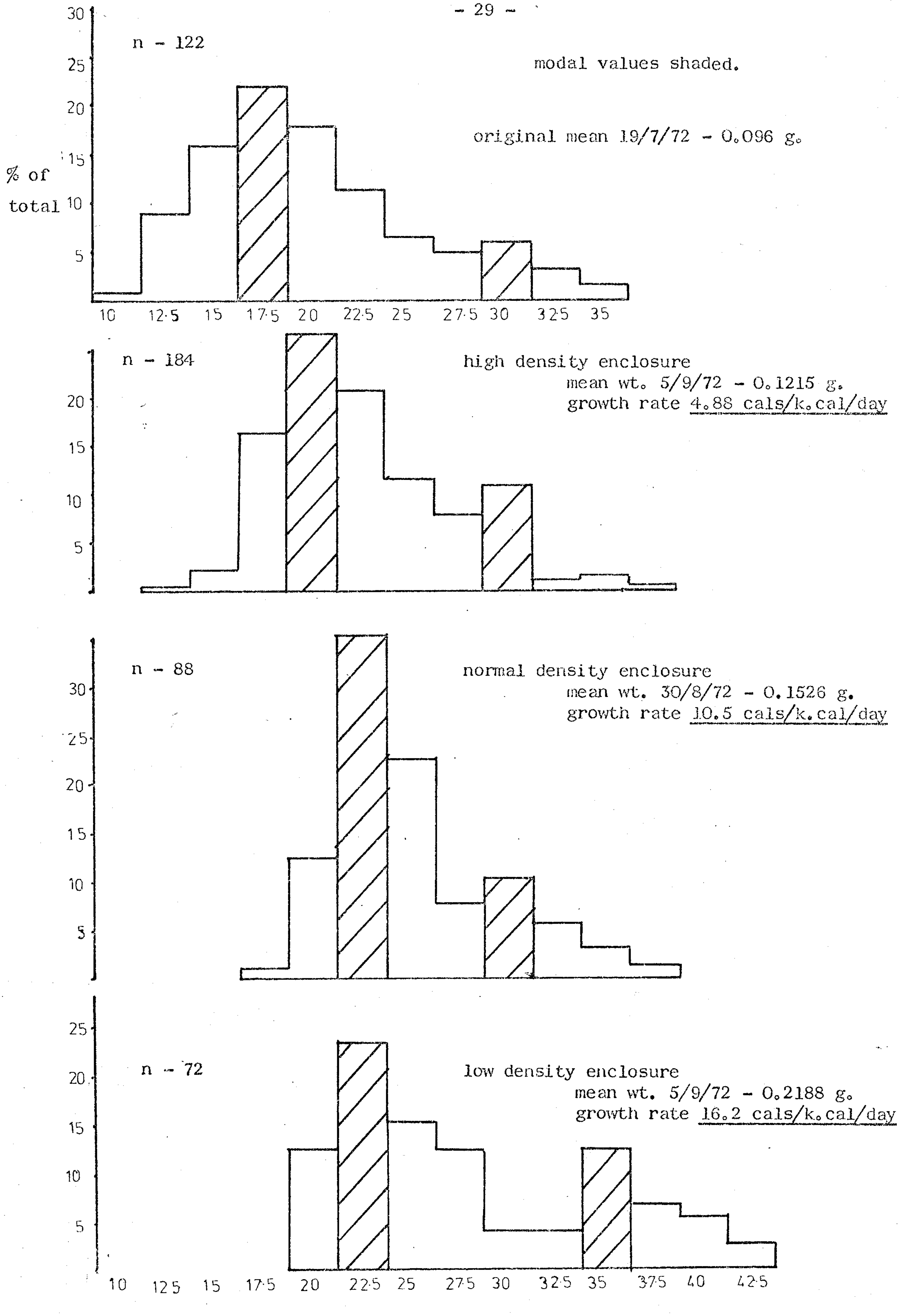


Figure (12) Length frequency histograms of young Gasterosteus

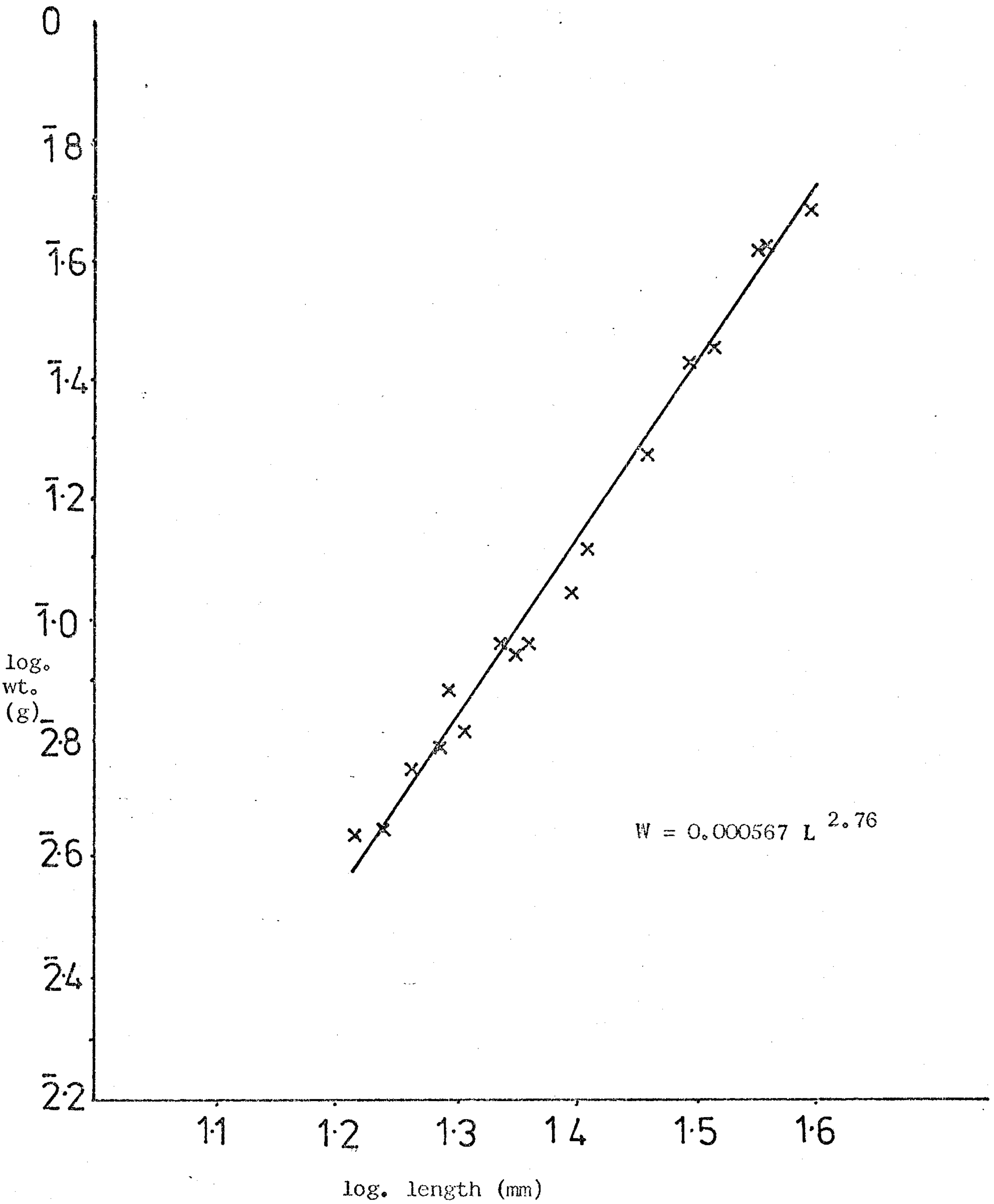


Figure (13) Length/weight regression of young Gasterosteus between 10 - 45 mm. length conformed to the formula:-

$$W = .000567\ L^{2.76}$$

(where weight (W) is in gms. and length (L) is in mm.)

The regression line is plotted in Fig. 13.

The mean weight of each size class (from Fig. 13) was then multiplied by the number of fish of that size class in the sample, the total weights of each size class were then summed. The growth rate (cal.growth/k.cal.fish/day) was calculated assuming linear growth between 19th July and 30th August.

(ii) Discussion of results of growth in the field

The graphs of growth rates at different fish densities (Fig. 14 & 15) show that there is an inverse relationship between fish density and mean growth rate measured over the whole period. It is probable that the initial growth rate was lower and that as mortality occured the rate speeded up. It is likely that this effect was more pronounced in the high density enclosure so the true growth curve is probably nearer the dotted curves in Fig. 14.

It is possible to conclude from this data, that the maximum mean growth rate attained by Gasterosteus, kept at artificially low density in Browney Pond during August 1972, was approximately 16 cals./k.cal./day. The normal fish population found in the pond during this month grew at a rate below this value.

It was argued in Chapter 1 that the fish within both enclosures were kept at insufficiently high densities to cause changes in metabolic rate through behavioral effects. This suggests that the submaximal growth rate observed in normal density fish is caused by a restriction imposed by fish density on the daily calorific intake.

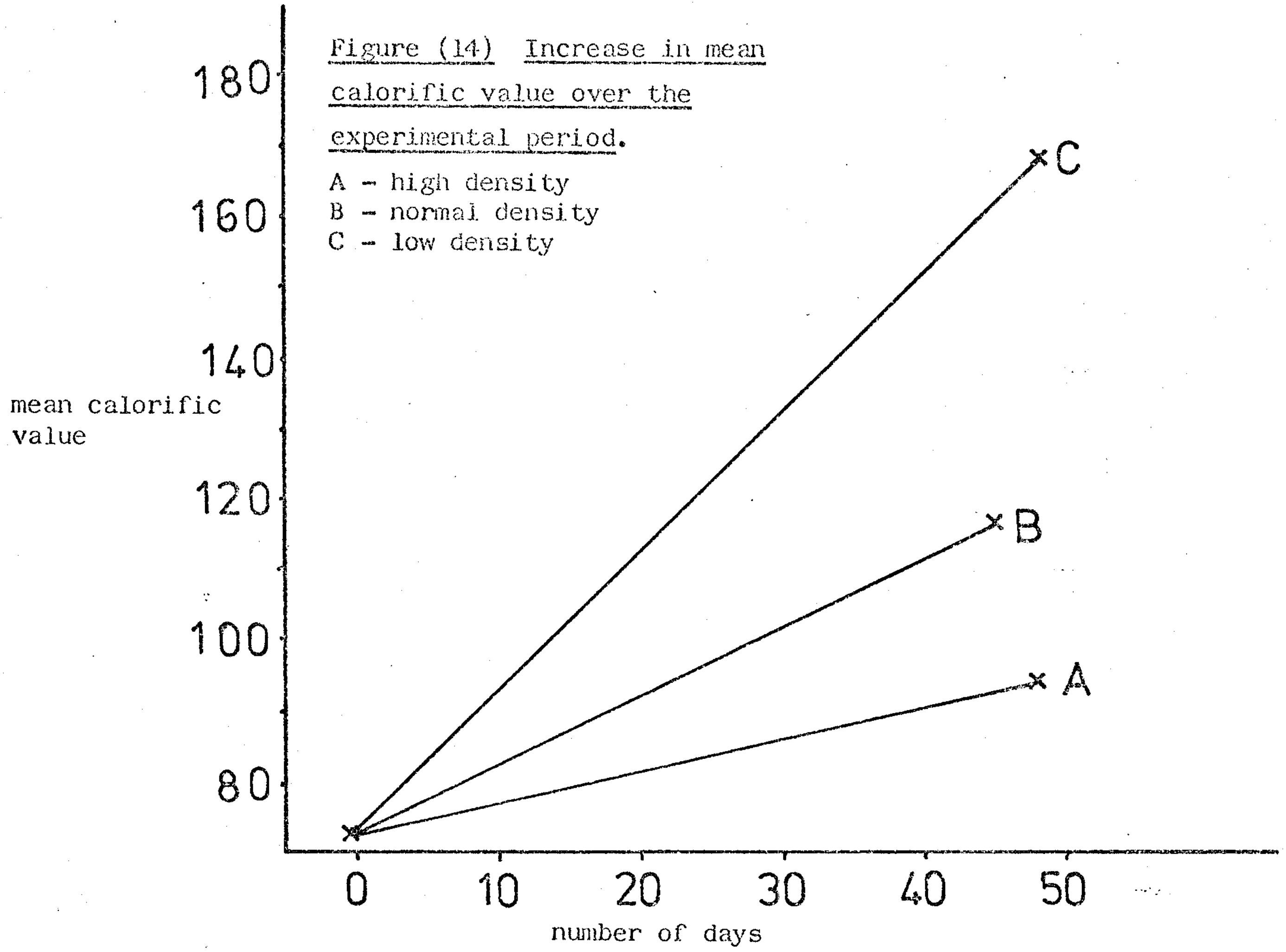


Figure (14) Increase in mean calorific value over the experimental period.

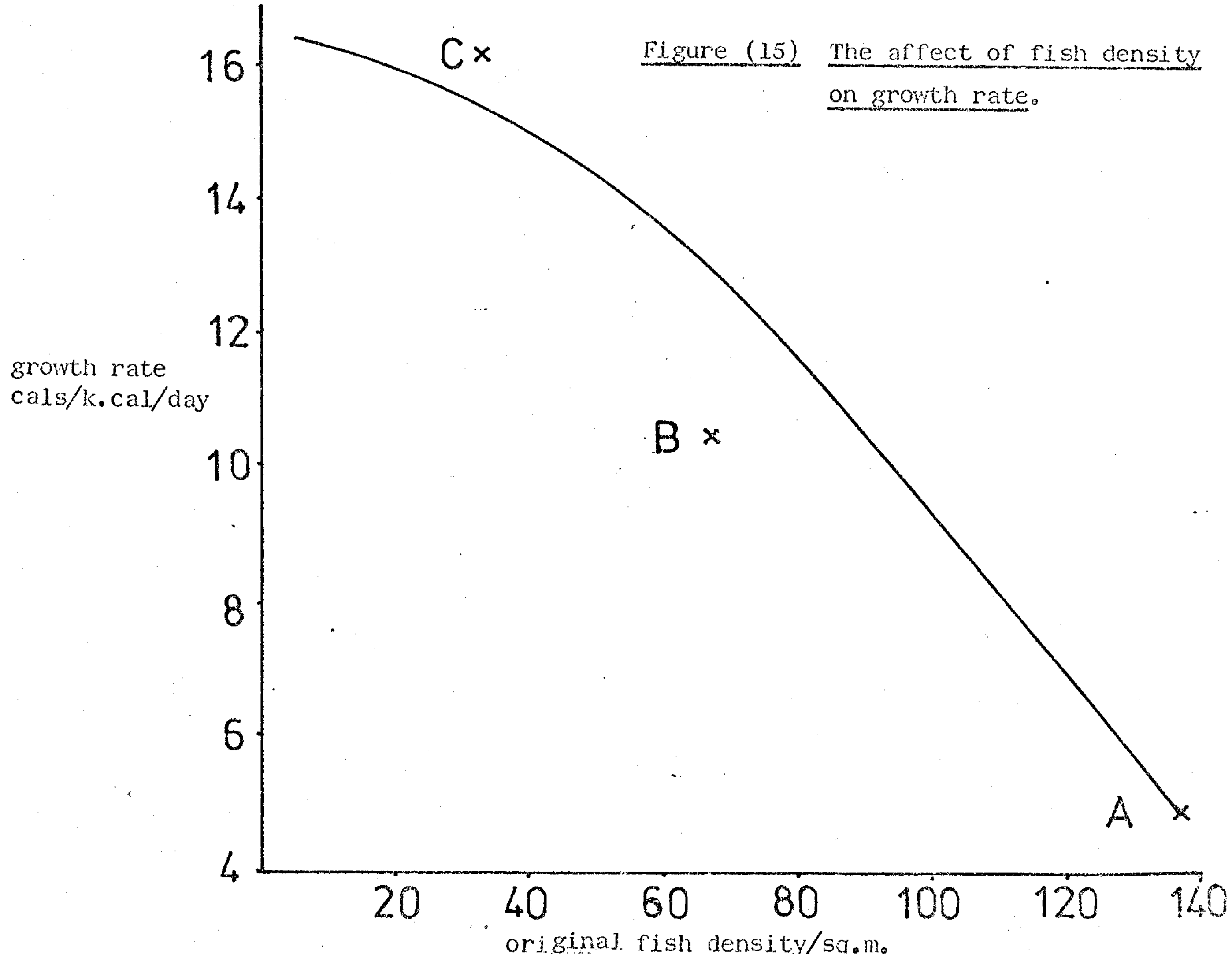


Figure (15) The affect of fish density on growth rate.

3) Mortality

Estimates of the magnitude of the various sources of mortality are necessary before a population energy budget can be constructed. Reliable quantitative estimates of predation are probably the most difficult of all energy values to obtain. Predation rates in the field can usually be measured only by incidental observations or numerical records of prey contained in a predators gut at any one time. Analytical methods are usually of a semi-quantitative nature and estimates of predation rate can usually be reliably used only to a first order of magnitude. Dempster (1966), using the precipitin test on predacious groud beetles, obtained semi-quantitative measurements of predation on larvae of *Pieris rapae*. He estimated the time for which anti *Pieris* antigen gave a positive reaction with the gut contents of a predator after it had eaten a *Pieris* larva. Supported by laboratory feeding data, he was able to show that the chance of a positive reaction representing more than one feed was small. Thus the total number of positive tests on a sample of predators gave an indication of the number of larvae taken during the feeding period.

The major predator of stickleback in Browney Pond was Perch. *Dytiscus* and other predacious water beetles were very rare in the pond, so it was assumed that mortality during August from invertebrate predators was sufficiently small to be neglected.

The total population of Perch was estimated by the mark and recapture method using simple Lincoln index. Repeated fishing with hook and line was carried out to sample the population, and fish were individually marked by clipping the spines of the dorsal fin in the manner shown in Fig. 16. The Lincoln index method assumes that the marking of an animal in no way alters the probability of it being

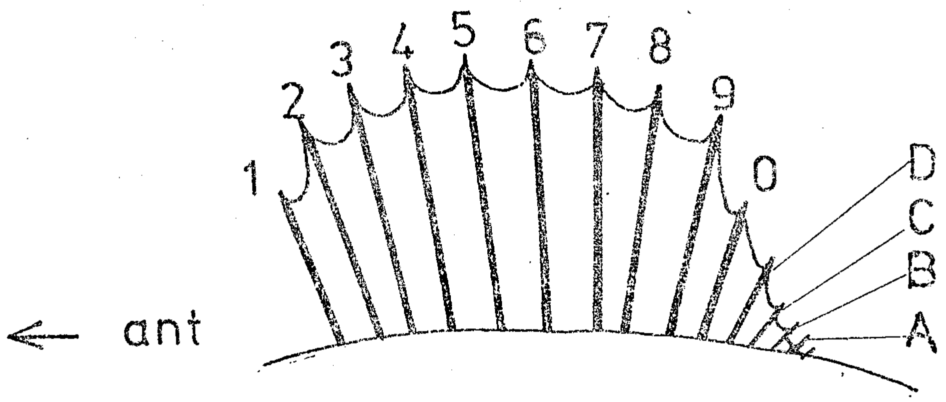
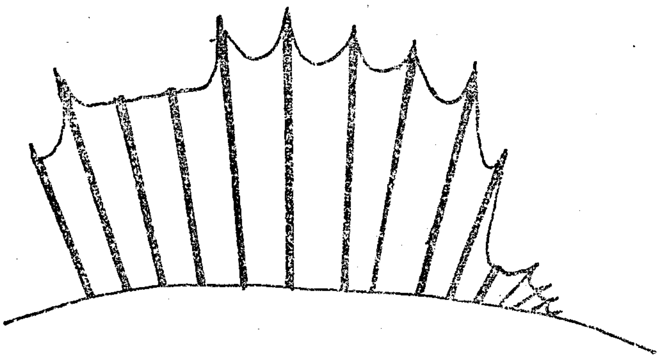


Figure (16) Method of marking perch by clipping of dorsal fin

nos. 1 - 10 clip respective number
nos. 10 - 19 clip respective number + A
nos. 20 - 29 clip respective number + B
nos. 30 - 39 clip respective number + C
nos. 40 - 49 clip respective number + D

Thus number 43 would be:-



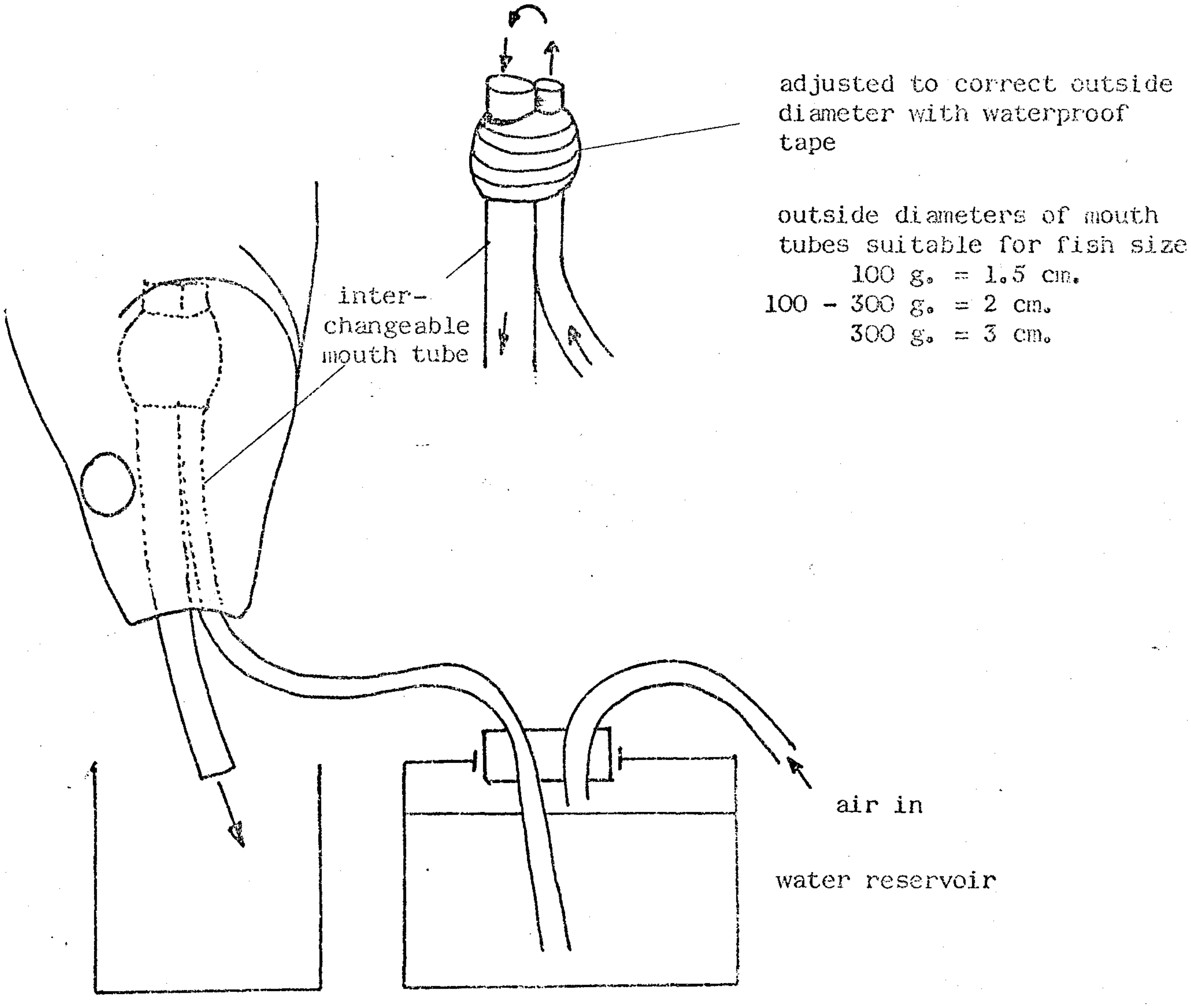


Figure (17) Construction of stomach pump

PLATE V

Method of stomach pumping of Perch.

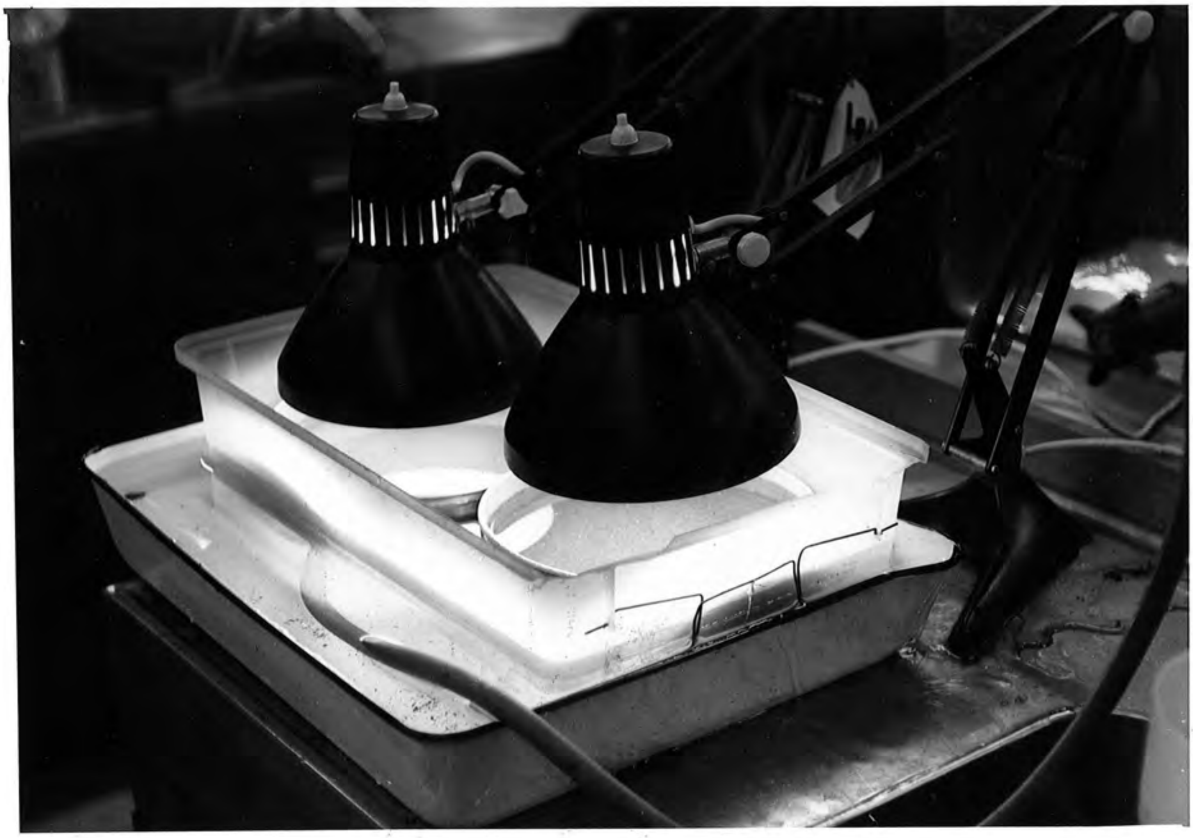


PLATE VI

Apparatus used for extraction of Oligochaetes.

recaptured and that the marked animals distribute themselves randomly in the population. Clearly neither of these two pre-requisites could be satisfied with fish and this method of capture. It was therefore considered that by releasing marked individuals and fishing from the entire area of the pond, a random distribution could at least be approached. Because of the phenomenon of "hook shyness" it was considered necessary to mark between a quarter and a third of the total population before the total estimate could be tentatively accepted. With these precautions it was felt that applications of the Lincoln index was justified.

To avoid depleting the population of these fish unduly, a stomach pump was designed and constructed in the manner shown in Fig. 17. This was operated by inserting the double tube through the oesophagus and into the stomach (see Plate 5). Water could then be forced in at low pressure from the reservoir attached to a standard tyre foot pump. Stomach contents were simultaneously ejected through the larger outlet tube. It was found that about 100 cc. of water were sufficient to completely empty the stomach. Unfortunately there was insufficient time to carry out tests on the long term effects of stomach pumping. It can be tentatively assumed, however, that these were negligible as 2 of the 44 fish pumped in this way were recaptured and pumped again.

Results and discussion

The data given in table (1) shows that six fishing operations were necessary before the ratio of marked to unmarked fish in the sample approached 25%. Had a more effective and random method of sampling been available the data would have been more reliable,

TABLE 1

MARK RECAPTURE DATA OF ADULT PERCH

Date	Sample no.	no. of fish caught	no. recaptures in sample	no. unmarked	no. injured	no. marked & released	total no. marked & released	N ± S.E. (N)
5/8/72	1	8	0	8	0	8	8	-
10/8/72	2	6	0	6	0	6	14	-
12/8/72	3	13	0	13	2	11	25	-
15/8/72	4	13	1	12	1	11	36	325 ± 306
19/8/72	5	14	3	11	3	8	44	168 ± 82
26/8/72	6	11	4	7	0	7	51	121 ± 46
3/9/72	7	23	6	17	0	0	51	197 ± 55
5/9/72	8	8	2	6	0	0	51	

however, it will be assumed that the combined total of the last two fishing operations give the most realistic population estimate. Since the method of capture involved food bait, the method was selective for fish in the process of feeding. For the purpose of estimation of predation rates, it was necessary to assume that all fish in the pond fed simultaneously.

Table II Results of stomach pumping

Perch Size	Total No. of stomachs pumped.	Total No. of stomachs containing stickleback		Total No. of stickleback	Perch No. Stickle.No.
> 200 gm.	16	4	25%	5	3.2
< 200 gm.	30	7	23%	8	3.7
					(mean 3.5)

It was found that Perch fed primarily at two periods during the day, once in early morning and again in late afternoon. Their stomachs usually emptied between feeding periods. The results presented in Table II were taken from samples caught during both feeding periods and are the totals from 44 fish taken on four seperate dates (10 fish per day) during the experimental period (July-August).

In two cases skeletal remains of stickleback were the only items present in the Perch's stomach. It is therefore probable that a small bony fish such as stickleback, eaten during either of the feeding periods will remain in the stomach until the end of that feeding period. Without further data on the time of retention, we will assume that the average stickleback/perch ratio represents the mean number of stickleback taken by a Perch in any one feeding period. (This will clearly be a minimum value as a Perch will have two opportunities of taking food during a day.

We can now say that the minimum number of stickleback taken from the pond, during any one day, by the Perch population present during July - August 1972 approximates to:

$\frac{N}{P}$ where N is the estimated number of Perch and P is the Perch per Stickleback ratio of the stomach.

$= \underline{\underline{56 \pm 16}}$ stickleback/day

Natural Mortality

The population of Gasterosteus was found to be restricted to the shallow weedy area around the "shelf" section of the pond. It was considered that the most accurate method of estimating the mean population density was to use the enclosures before and after the experiment to isolate temporarily an area of the "shelf". The enclosures were placed at four different positions in turn along the shelf, on 18th August and again on 6th September upon completion of the field experiment. The fish were then completely netted out from the four square metres of enclosed weed and counted. It was observed that the instinctive behaviour of stickleback when frightened, was to dart into the nearest patch of weed and remain still rather than swim away. It could therefore be assumed that the error incurred in my population estimates, due to fish swimming away as the enclosure was brought down, was small.

The mortality of fish within the enclosures whilst the density experiment was in progress was deduced from the fall in numbers.

Table III Mortality at different densities

	Normal density (outside enlosures)	High density	Low density
Original density	67.12 ± 15/sq.m.	137.5/sq.m.	32.5/sq.m.
Final density	17.12 ± 5/sq.m.	62.5/sq.m.	18.0/sq.m.
Mortality	50.0/sq.m.	75/sq.m.	14.5/sq.m.
% Mortality	74%	54%	44%
Length of experiment	45 days	48 days	48 days

It should be noted that the results for normal density are the combined mortality figures for natural mortality and predation. Within the two enclosures mortality represents natural mortality only, as the mojor fish predators were excluded from the enclosures.

It appears from the enclosure results that the natural mortality rate was slightly dependant on fish density. It is possible that the natural mortality for the fish at normal density should lie between these two values. We can safely accept the maximum natural mortality observed (that of the high density enclosure group) as the upper limit likely to be encountered under normal density conditions. The difference between this and the observed mortality under normal conditions was about 20% . There are two possible explanations for this:-

1) that this figure represents the true percentage of predation of sticklebacks by perch,

2) that there had been a migration of part of the population to a different area of the pond.

If we refer to the size distributions (Fig. 12) we can see that all the histograms can be divided into a major component and a minor component displaced to the right, (this division was probably caused by conditions such as weather during the reproductive process). If we consider the modal values of the two components we can see that those of the major component of the normal and low density size distributions, have been displaced equally during the experimental period. However, the displacement of the modal values of the minor component appears to be different. We could either presume that larger animals in the distribution enjoy benefits not encountered by smaller size groups when subjected to low density conditions, or we could assume that some migration of the upper size classes has taken place in the normal situation which is prevented by the enclosure in the low density situation. However, it was difficult to envisage any area in the pond to which they could move that had not been sampled by the enclosures. Furthermore, a sample of fish taken from the very edge of the shelf by means of a large hand net had a size distribution closely similar to that illustrated in Fig. 12. The probability that these fish had moved away from the weed and into deeper water is discounted, because they would have been devoured immediately by perch.

It has been stated above that the large, highly productive "shelf" area is likely to act as a food reservoir for the large perch population. On clear days, perch could be observed swimming onto the "shelf" presumably to feed, and it is possible that during these feeding movements, the larger sizes of stickleback are selectively "cropped" from the "shelf". It was not possible to obtain a large enough size distribution from perch stomach contents to prove this but all fish remains found in the perch were above 30 mm. in length, ie. of the upper size component.

It must be concluded that the difference between the maximum possible natural mortality and the apparent observed mortality in normal density fish in the field, was due primarily to predation and not migration out of the area.

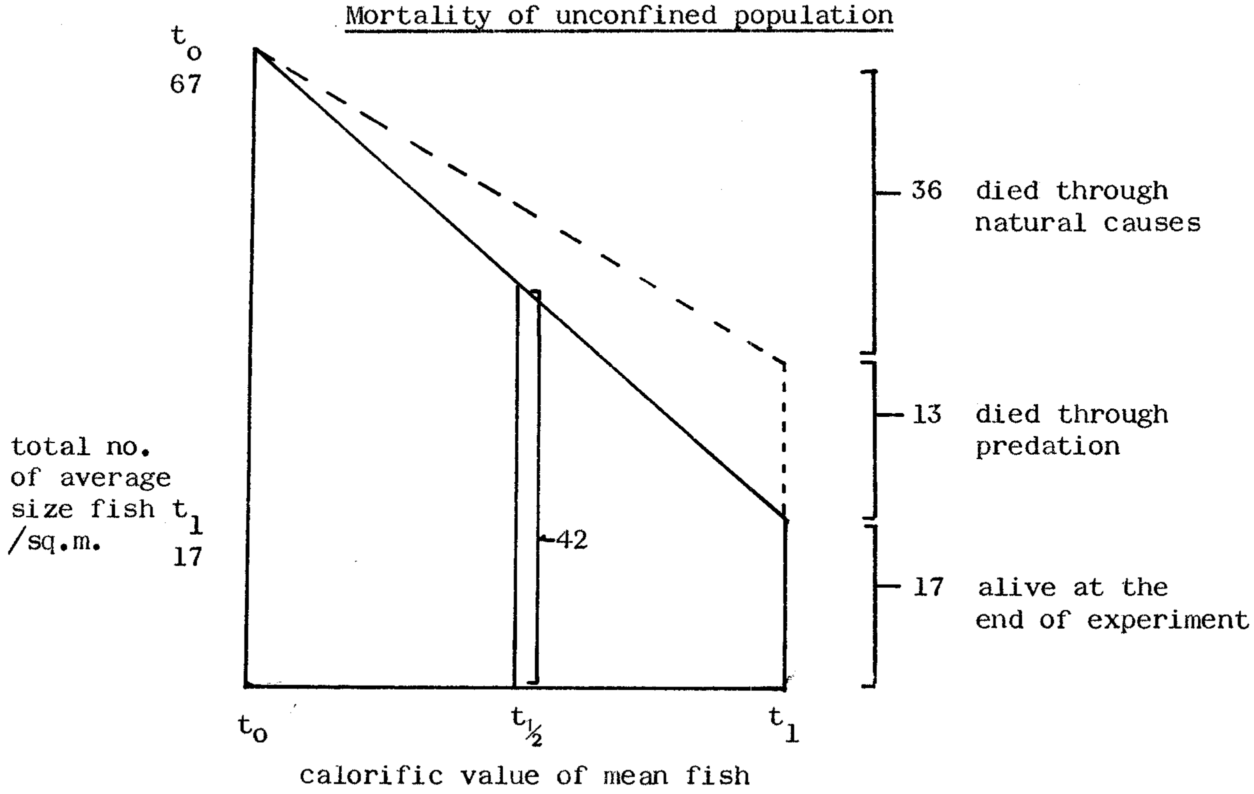
It has been shown that predation by perch can account for about 56 stickleback/day from the pond. Over the 48 days of the experiment this represents 2688 fish. The "shelf" area, ie. the area supporting the entire stickleback population, was estimated to occupy 256 square metres. This means that perch must have consumed a minimum of about 10 sticklebacks/sq.metre (— $\frac{2688}{256}$). When this value is subtracted from the observed mortality a figure of 59% is obtained for the "natural" mortality. Considering the inaccuracies involved in the estimations of predation by perch, this value of 59% agrees favourably with the highest natural mortality value possible of 54%. As the predation estimates were restricted at each stage to the minimum values possible, it was to be expected that the estimated value of 59% should fall slightly above the observed value.

We are now able to add to the population budget the values of energy fed to the decomposer level, by natural mortality, and energy fed to the next trophic level by predation during the study period.

If we represent the mortality of the natural unconfined population graphically, we obtain Fig. 18.

FIGURE 18

Mortality of unconfined population



where t_o = start of experiment

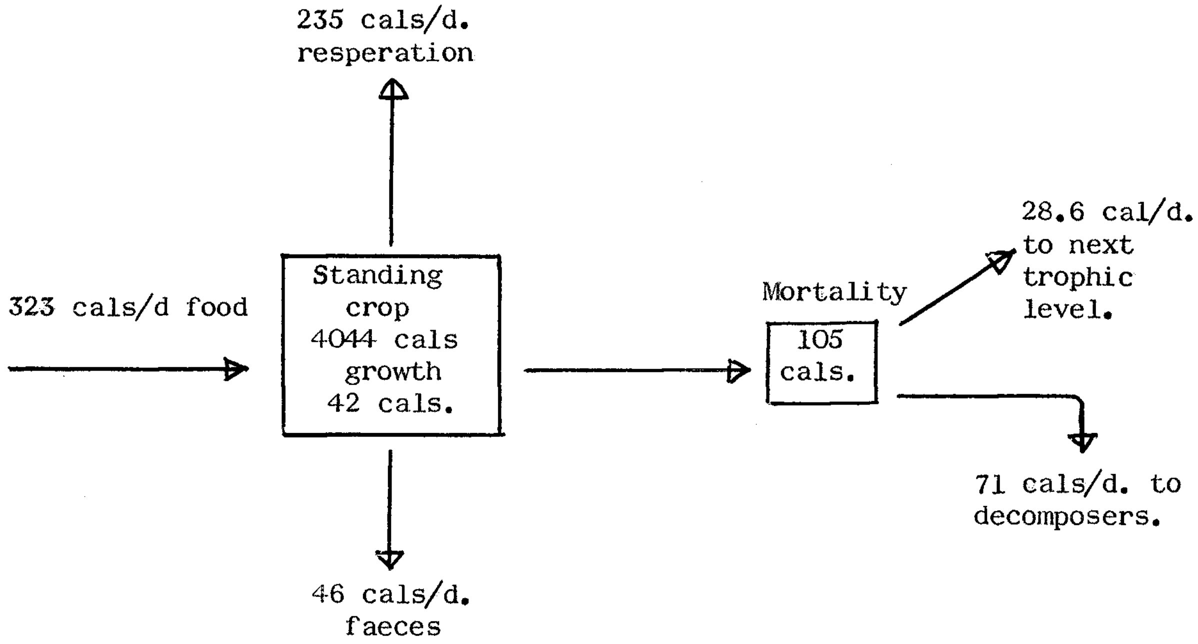
t_1 = end of experiment

$t_{1/2}$ = median day

If we know that the natural mortality over this experimental period of 45 days has accounted for 50% (33 fish/sq.metre) of the initial number, we can assume that, on average $\frac{33}{45}$ fish will die per day = 0.74.

Similarly we know that mortality due to predation is 20% (13 individuals per sq. metre) and we can say that $(\frac{13}{45})$ = 0.297 fish will die in this way every day in one square metre.

We can see from Fig. 18 that the number of fish surviving on the median day will be 42. From Fig. 9 (Chapter I) we saw that the mean calorific value of an average fish on the median day was 96.29 cals. (from 0.1243 g. wet weight). The standing crop of fish on the median day is thus (42 x 96.29) = 4044 calories/sq.metre. If 0.74 fish (71.2 cals.) die from natural causes and 0.297 fish (28.59 cals.) are fed to the next trophic level sq.m/day, we are able to modify the energy budget for individual fish given in Fig. 9, Chapter I, to give the total population energy budget on the median day.



4) Food relationships

In the laboratory experiments described in Chapter I, the daily calorific intake of fish in the field was calculated. In order to evaluate the relative energy flow from each dietory constituent in the wild, I investigated how the diet was divided among the various food items available in the pond.

Methods

Several methods have been proposed for the estimation of stomach contents of fish. Direct enumeration or frequency of occurance of constituent food groups are methods often used. These demonstrate the species taken but give no information on the relative biomass of the component groups. Volumetric and gravimetric methods outlined by Windell (in Ricker 1968) can be used accurately only on stomachs of large fish and even then are of limited value for conversion into caloric values.

For my project, a semi-micro method was developed, which should be applicable to any small animal with a stomach capacity of 0.1 to 20 mg. The results of this method gave information on the percentage (of dry weight) of each component of the stomach contents, and also provided comparable indices of stomach "fulness".

Fish removed from the pond were killed immediately in 90% alcohol. The stomachs of between ten and fifteen fish were carefully dissected out by cutting through the anterior and posterior sphincter muscles, thus the volume of food relative to the size of the fish was kept constant. The stomachs were then placed on to a microscope slide and the contents squeezed out under a drop of water. The food of each stomach in turn was then sorted into major groups under a binocular microscope with dissecting needles, so that a particular food group from all the stomachs lay in a longitudinal row along the slide. The slides were then placed in a convector oven and dried for twenty four hours, on each occasion they were handled with rubber gloves. The initial weight of the slide was taken to 0.1 mg. Each group row was then removed in turn by means of a razor blade and the corresponding weight loss was measured between the removal of each group.

This method is effective only if the stomach contents have been little digested. Clearly there is a possibility of error in this method since softer, more delicate organisms will be digested more rapidly than more chitinous species. However, it was found that this error could be minimized by manipulating the time of collection to occur in the middle of a feeding period (ie. early morning or mid afternoon). At this time the number of partially digested organisms represented less than 10% by weight of the total stomach contents. In order to allow for error due to possible differences in food selection at different times of the day, half the samples were removed during the morning feed and half during the afternoon feed.

To obtain information on the amount of food available in the stickleback's habitat in Browney Pond, an estimate of the invertebrate standing crop was made at the end of July. A cylindrical core sampler was constructed (centre of Plate 3), which could be pushed into the bottom mud to enclose completely a column of water 1000 sq.cm. in cross section. Weed was extracted first by cutting it at the base with scissors and removing it to a bucket. The free swimming and mud surface fauna were then removed by stirring the contents of the cylinder vigarously and netting continually with a 100 mesh/inch plankton net, for approximately thirty minutes. The material which had been

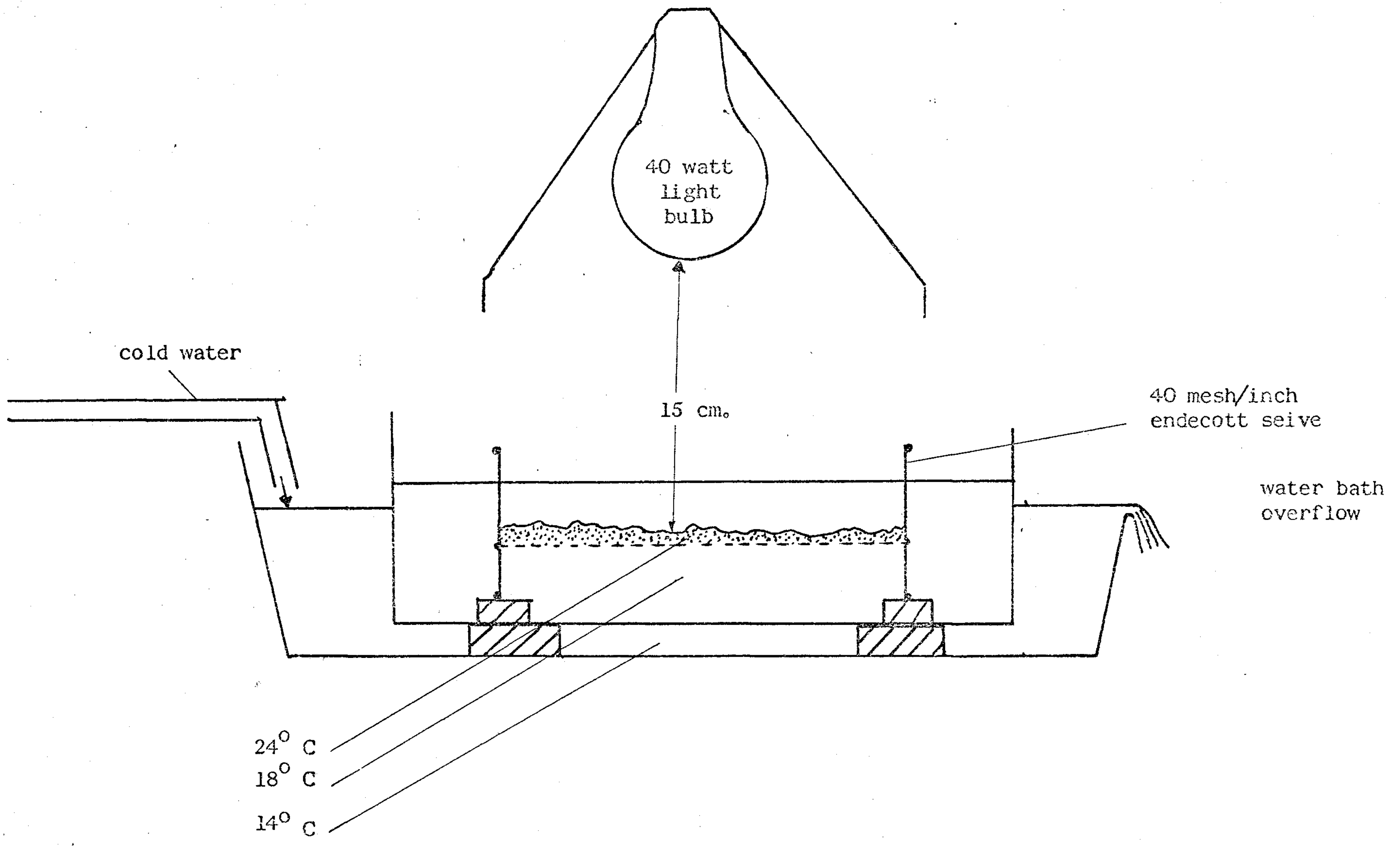


Figure (19a) Apparatus used for extraction of Oligochaeta removed was taken to the laboratory and washed through fine Endecott seives (mesh sizes (1) 10, (2) 40, (3) 100 mesh/inch) to remove silt. The contents were then hand sorted.

Oligochaetes were extracted with a temperature gradient through water, using apparatus constructed as shown in Fig. 19 (also Plate 6). By hand sorting a subsample of the seived material (after extraction) it was found that the apparatus was approximately 95% efficient. It was found that Ostracods and other micro-zooplankton could be floated out efficiently from subsamples of the fine silt retained by the 100 mesh seive, by adding concentrated magnesium sulphate solution. These formed a "scum" which was decanted into a large container and could then be stirred vigarously before subsampling. The subsamples were filtered through a Buchner funnel using filter paper ruled off into squares. The papers were then removed and the zooplankton counted under a binocular microscope. A wet weight/dry weight correction factor was obtained for zooplankton by oven drying five hundred individuals.

Results and discussion on food relationships

The total invertebrate standing crop at the end of July is shown in Table 4. This crop is representative only of that area occupied by the stickleback population during August. It may be seen that more than 75% by weight of the total standing crop is represented by four groups, namely; Molluscs; zooplankton; Chironomids and Oligochaetes (in decreasing order of significance). If we now refer to the stomach analysis of normal density fish (Table 5), we can see that molluscs and zooplankton were the chief dietory constituents,

TABLE IV

INVERTEBRATE STANDING CROP OF BROWNEY POND " SHELF" AREA (END OF JULY)

	Mean dry weights of five core samples of 1000 sq.cm wt.g.	± S.E.	Calorific values k.cals/g.dry wt.	Total k.calories per sq. metre	% of total caloric composition
Chironomids	0.09248	± 0.0320 g.	5.1	4.716	13.5 %
Trichoptera	0.06246	± 0.014 g.	5.781	3.611	10.4 %
Molluscs (without shell)	0.2369	± 0.134 g.	5.0	11.845	34%
Ephemeroptera	0.02332	± 0.0111 g.	5.151	1.201	3.4%
Coleoptera + Hemiptera	0.0230	± 0.009 g.	4.981	1.146	3.3%
As~~s~~ellus	0.0023	± 0.0017 g.	4.241	0.097	0.3%
Leeches	0.0144	± 0.0140 g.	4.6	0.662	2.0%
Odonata	0.003	± 0.0025 g.	5.041	0.151	0.4%
Oligochaetes	0.0756	± 0.0300 g.	5.555	4.199	12%
Zooplankton	0.163	± 0.085 g.	4.4	7.172	20%

TOTAL 0.6965 gms per 1000 sq.cm.

= 6.965 gms per sq. metre

TOTAL 34.8 k.cals per sq. metre

TABLE V

STOMACH ANALYSIS OF FISH KEPT AT NORMAL DENSITY

fish ength mm.	Slide (1)										dry wt.g.	%
	30	30	30	25	28	30	26	25	24	30		
Molluscs	x	x		x	T	x	x		x	x	.0046	43%
Chironomids	T	T		T	T				T	T	.0005	4.7%
Ephemeroptera			x	T		x		x			.0009	8.4%
Zooplankton	x	x	x	x	x	x	x		x	x	.0045	42.4%
Surface & terrest. flies etc.								x			.0001	0.9%

10 fish = 0.0106

= 1.06 mg/fish

fish ength mm.	Slide (2)								dry wt.g.	%
	23	25	24	24	23	25	25	25		
Molluscs	x	x	x	x	x	x	x	x	.0042	56%
Chironomids		x	T		T	T	T	T	.0004	5.3%
Ephemeroptera	T	x				T	T		.0004	5.3%
Zooplankton	x	x	x	x	x	x	x	x	.0026	34%
Surface & terrest. flies etc.										0%

8 fish = 0.0075

= 0.9 mg/fish

fish ength mm.	Slide (3)										dry wt.g.	%
	25	30	25	32	32	34	28	30	24	26		
Molluscs	x	x	x		x	x	T	x	x	x	.0041	47%
Chironomids		x	x			T		T		x	.0006	7.2%
Ephemeroptera				x		T	x				.0005	6.0%
Zooplankton	x	x	x	x		x	x	x	x		.0035	39%
Surface & terrest. flies etc.												0%

10 fish = 0.0089

= 0.89 mg/fish

x = present in significant amounts

T = only a trace present

Mean stomach contents = 0·96 mg

TABLE VI

STOMACH ANALYSIS OF FISH KEPT AT HIGH DENSITY

	Slide (1)												Slide (2)												Slide (3)											
ish ngth mm.	30	30	32	32	32	29	31	30	35	30	dry wt.g.	%	25	30	28	30	32	30	26	25	29	30	dry wt.g.	%	25	28	30	25	32	27	35	35	32	26	dry wt.g.	%
Molluscs							x				.0012	17%							x				.0008	20%		x				x					.0011	16.7%
Chiron-omids				T	T	T		T			.0003	4.2%			T	T	T		T	T		T	.0002	5.1%	T			T	T					T	.0003	4.0%
Ephem-eroptera		T	T	x						T	.0009	12.8%		x	x	T				x			.0004	10.2%		T			T						.0008	10.2%
Zoo-plankton	T		T	T	x	x	x	T	x	T	.0036	51%	x		x	x					x		.0019	48.7%	x		x		x	x		T		x	.0038	50.1%
Surface & terrest. flies etc.		x		x				x		x	.0010	14.2%		x		x		x				x	.0006	15.3%							x	x	x		.0016	21.1%
										Total	.0070											Total	.0039											Total	.0076	

+ 4 fish empty
14 fish = 0.5 mg/fish

+ 6 fish empty
16 fish = 0.24 mg/fish

+ 3 fish empty
13 fish = 0.58 mg/fish

TOTAL: 43 fish mean .43 mg/fish

TABLE VII

STOMACH ANALYSIS OF FISH KEPT AT LOW DENSITY

fish length mm.	Slide (1)								dry wt.g.	%	Slide (2)										dry wt.g.	%
	34	28	33	33	27	30	26	34			25	35	30	28	26	30	32	28	25	20		
Molluscs	T	T	x			x		x	0.0020	33.3%	T	x	T				x	x		x	0.0033	33%
Chiron-omids	x	x		x	x	T	x	x	0.0013	21.6%		T		x	T			x		x	0.0020	20.2%
Ephem-eroptera	x	x	x	x		T			0.0011	18.5%			x		x	x	x		x		0.0018	18.18%
Zoo-plankton	T	T		T	x	x	x	T	0.0014	23.3	x	x		x			x	T	x		0.0028	28.28%
Surface & terrest. flies etc.										0%												0%

8 fish = 0.0058

= 0.7 mg/fish

10 fish = 0.0099

= 0.99 mg/fish

Mean stomach contents = 0.87 mg

in terms of dry weight, with Chironomids third. Table 8 shows the proportions of these constituents in terms of calories and indicates that the chief constituent was zooplankton.

Table VIII Average of total stomach constituents

	Normal density			High density			Low density		
	Average total cals in stomach		% of total cals.	Average total cals in stomach		% of total cals.	Average total cals in stomach		% of total cals.
	Wt.mg.	cals		Wt.mg.	cals		Wt.mg.	cals	
Molluscs	0.460	2.3	50.9%	~~0.032~~ 0.072	~~0.162~~ 0.360	~~8.0%~~ 18.0%	0.29	1.45	~~19.1%~~ 35.0%
Chironomids	0.053	0.27	5.97%	0.019	0.094	~~5.2%~~ 4.0%	0.18	0.918	~~24.1%~~ 21.0%
Ephemeroptera	0.065	0.33	7.3%	~~0.075~~ 0.049	0.25	~~13.8%~~ 12.0%	0.16	0.824	~~24.1%~~ 19.0%
Zooplankton	0.378	1.6	35.42%	~~0.332~~ 0.216	0.95	~~52.4%~~ 47%	0.23	1.012	~~32.0%~~ 24.0%
Surface & terrest. flies etc.	0.003	0.017	0.37%	~~0.114~~ 0.074	~~0.36~~ 0.347	~~20.0%~~ 17%			0.0%
Mean total in stomach	0.959 mg.	4.517 cals		0.429 ~~0.539~~ mg.	1.998 ~~1.796~~ cals		0.86 mg.	4.204 cals	

In Chapter I, Fig. 1, it was shown that the daily calorific requirements of a young fish growing at 10.5 cals/k.cal/day, (the field growth rate during August), was 80 cals/k.cal/day. Therefore, the daily requirements of an average fish (of calorific content 95.97 cals) on the median day would be 7.68 cals. From the total calories present in the stomach of normal density fish, given above, we can see that on the day the samples were taken (end of August) the average Gasterosteus filled its stomach approximately twice.

The effect of fish density on food selection

When fish were subjected to high density the main dietory constituents changed from molluscs and zooplankton to zooplankton and surface flies (Table 6 & 8). The fall in the percentage of molluscs taken was probably due to exhaustion of the edible size range of this food substrate. The standing crop of zooplankton was high (Table 4) and probably had a much faster rate of turnover than that of other invertebrates. Thus it could withstand higher predation pressure without over-exploitation. Examination of the guts of larger Gasterosteus occuring at normal density, showed that surface and terrestrial flies etc., did not usually occur in the stomachs until fish were over 35-40 mm. in length. It therefore seems likely that high density induced surface feeding in fish of smaller size.

Further evidence that food supplies (of suitable size range or palatability) were restricted in the pond at these fish densities, is offered by the indices of stomach fullness (Table 8), which show that the stomachs of high density fish were approximately half as full as normal density fish. When the fish density was reduced to half "normal", the percentage of Chironomids and Ephemeroptera nymphs in the diet rose above normal. It is possible that these two groups were optimal food, which would explain the much higher growth rate in the low density enclosure, as was suggested in Chapter I. It is clear that the index of stomach fullness for low density fish is no higher than that for normal density fish, which supports the argument that the increased growth of this group is not caused by a greater volume of food.consumed.

CHAPTER III

THE FUNCTIONAL ROLE OF GASTEROSTEUS IN PROMOTING ENERGY FLOW THROUGH THE BROWNEY POND ECOSYSTEM DURING AUGUST 1972

Although Gasterosteus represented only about 10% of the total standing crop (of approximately 50 k.cals/sq.m.) in August, it is clear that it played a major role in the flow of energy through the ecosystem. From Figure 19 it can be seen that Gasterosteus represented about 66% of the biomass of the secondary consumer trophic level.

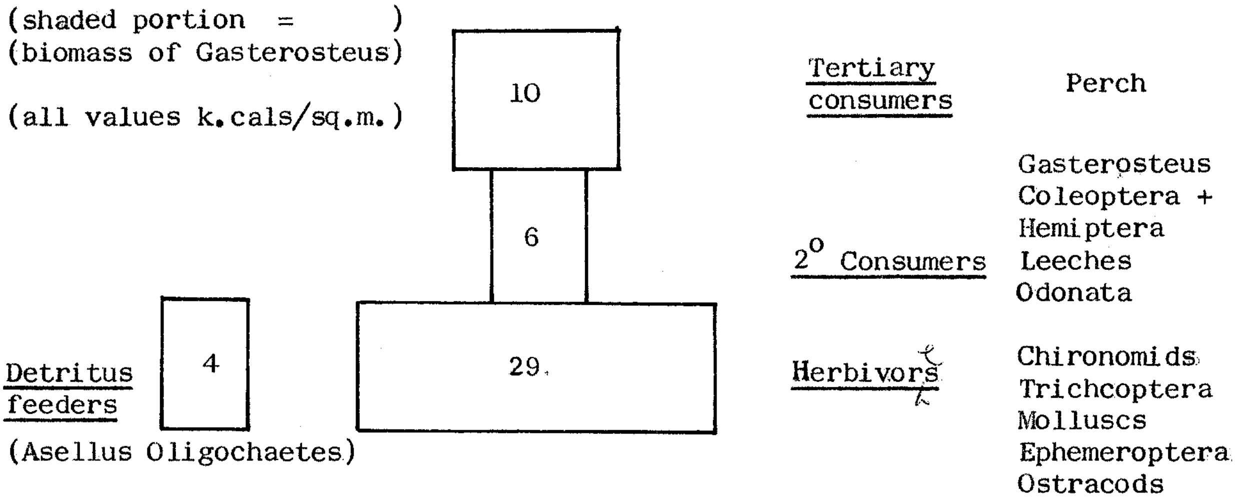
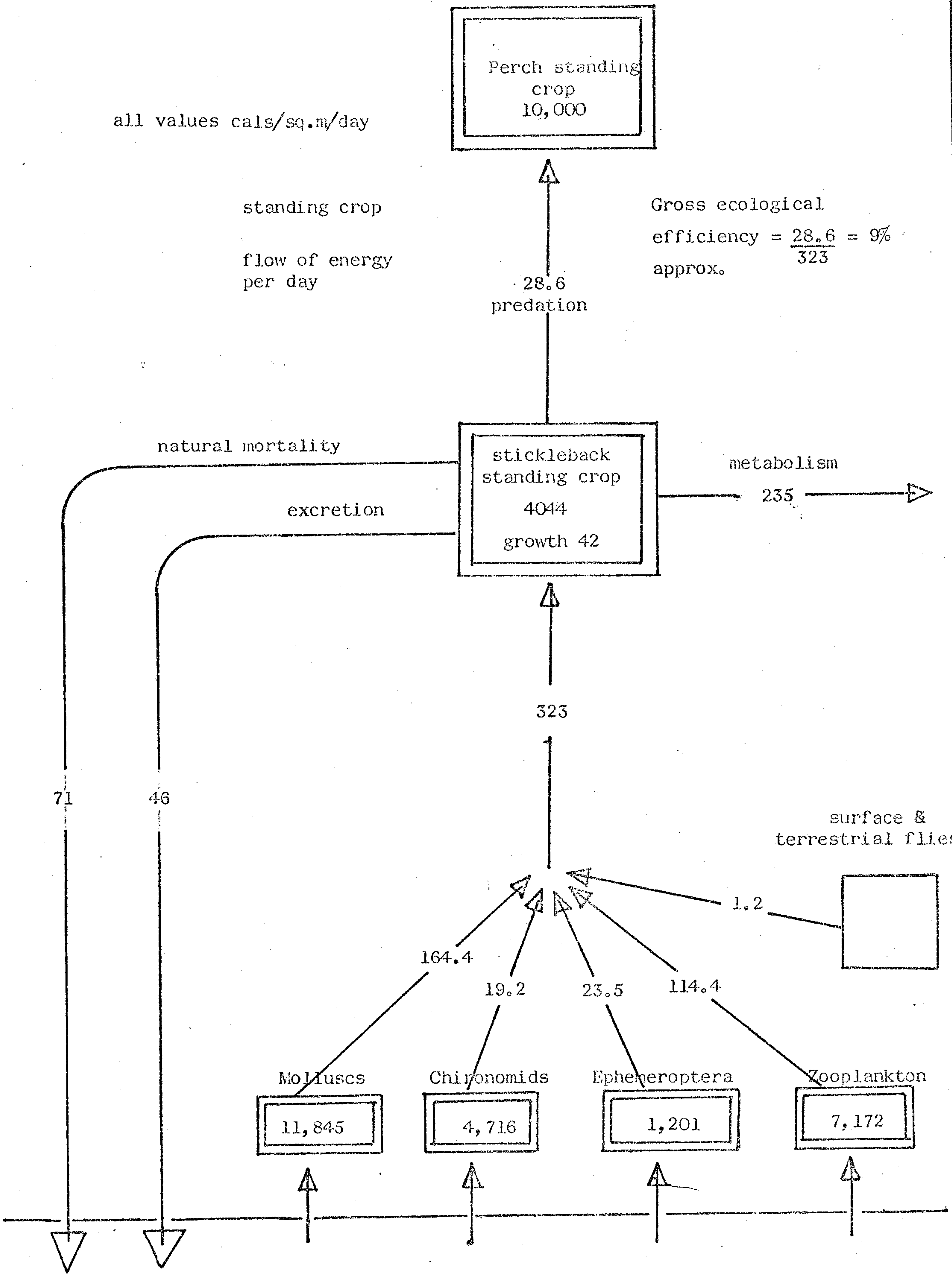


Figure 19 Trophic structure of ecosystem

The component values for each energy pathway, derived from each of the preceeding chapters, have been used to construct the total daily population energy budget for Gasterosteus in August (Fig. 20). Under the normal fish densities in the pond the major pathway of energy into the stickleback population was via the mollusc and zooplankton components of the benthos. A respiratory loss ratio from Gasterosteus $\left(\frac{\text{Respiration}}{\text{growth}}\right)$ of about 5.5 : 1 was evident. This is

Figure 20 The total population energy budget



all values cals/sq.m/day

Gross ecological efficiency = $\frac{28.6}{323}$ = 9% approx.

low when compared with another carnivorous poikilotherm, Bleak (*Alburnus alburnas*), which had a ratio of about 12.8 : 1 (Mann 1964). Mann's data, however, was derived over a complete twelve-month period and it is likely that, in summer, the respiration / growth ratio would be lower than in winter, when growth is much retarded.

Approximately 36% of the energy fed to the *Gasterosteus* population was returned to the ecosystem by natural mortality and excretion. The energy would become available to the decomposers and detritus feeders present in the bottom sediments. In agreement, a high standing crop (12% of the total energy) of detritivores, mainly Oligochaetes and Asellus, was found in the pond at this time of year.

The gross ecological efficiency, defined as:-

$$\frac{\text{calories of prey consumed by predator}}{\text{calories of food consumed by prey}}$$

was about 9% $\left(\frac{28.6}{323}\right)$ for this food chain. This compares favourably with 13% observed by Slobodkin (1959) on a *Chlamydomonas* *Daphnia* chain, 7% for *Artemia* / *Hydra* (Slobodkin 1962) and 9% for total berbivores at Root Springs (Teal 1957). This efficiency for stickleback - perch energy transfer in Browney Pond during August therefore supports Slobodkin's (1964) theory that gross ecological efficiencies in natural ecosystems are of the order of 10%.

A THEORETICAL PROBLEM

It was the intention of this project to identify and investigate critical pathways of energy flow through a fish population, to facilitate theoretical manipulation of the species to raise its productivity.

1) Manipulation of density

Allen curves for the three experimental densities are given in Fig. 21. In the form shown, they are not really comparable as the fish at normal density, (unlike those in the enclosures) were subject to natural predation by perch. In section 3 of Chapter II the mortality from this source of predation was estimated to be approximately 20% at the pond stickleback density during August. If we assume that the total mortality could be reduced by 20% with total removal of perch from the pond, we must correct the Allen curve for normal density by adding the 20% mortality to the final fish number. This will give us a final number of 30.5 fish/sq.m. (dashed line in Fig. 21) If we assume that mortality between the start and end of the experiment took place at a constant rate , we can deduce total fish production by counting the squares under the Allen curves, between time (0) and time (1)after the method of Allen (1950). The total production figures, plotted against initial stock density, are given in Fig. 22. We can see that the total production was surprisingly constant over a wide range of densities.

It is clear from this data that by modifying the population density, little change in the overall fish production could be achieved. With the existing food ecology in Browney Pond it is therefore unlikely that Gasterosteus production could be raised much above about 44 cals/

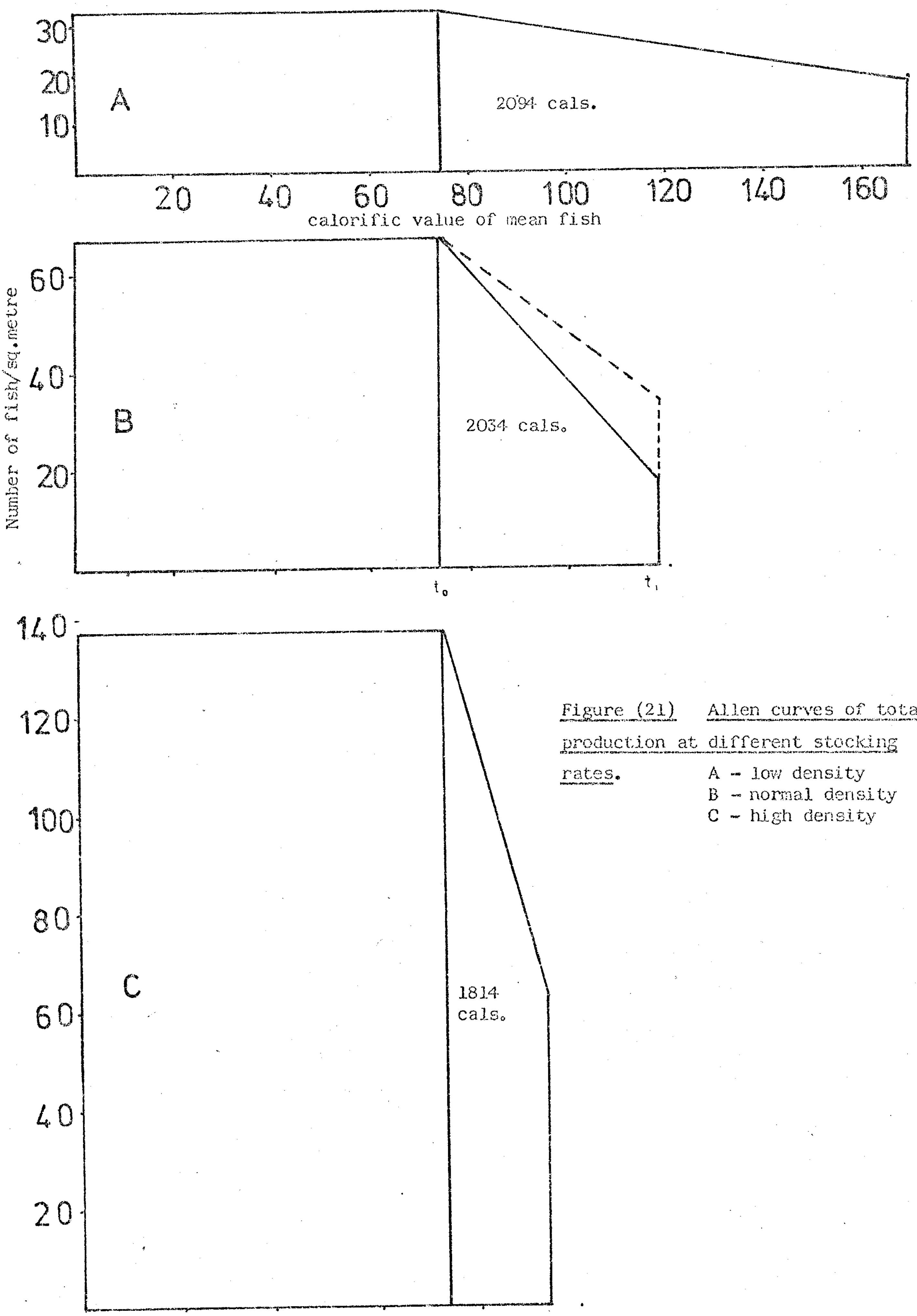


Figure (21) Allen curves of total production at different stocking rates.
A - low density
B - normal density
C - high density

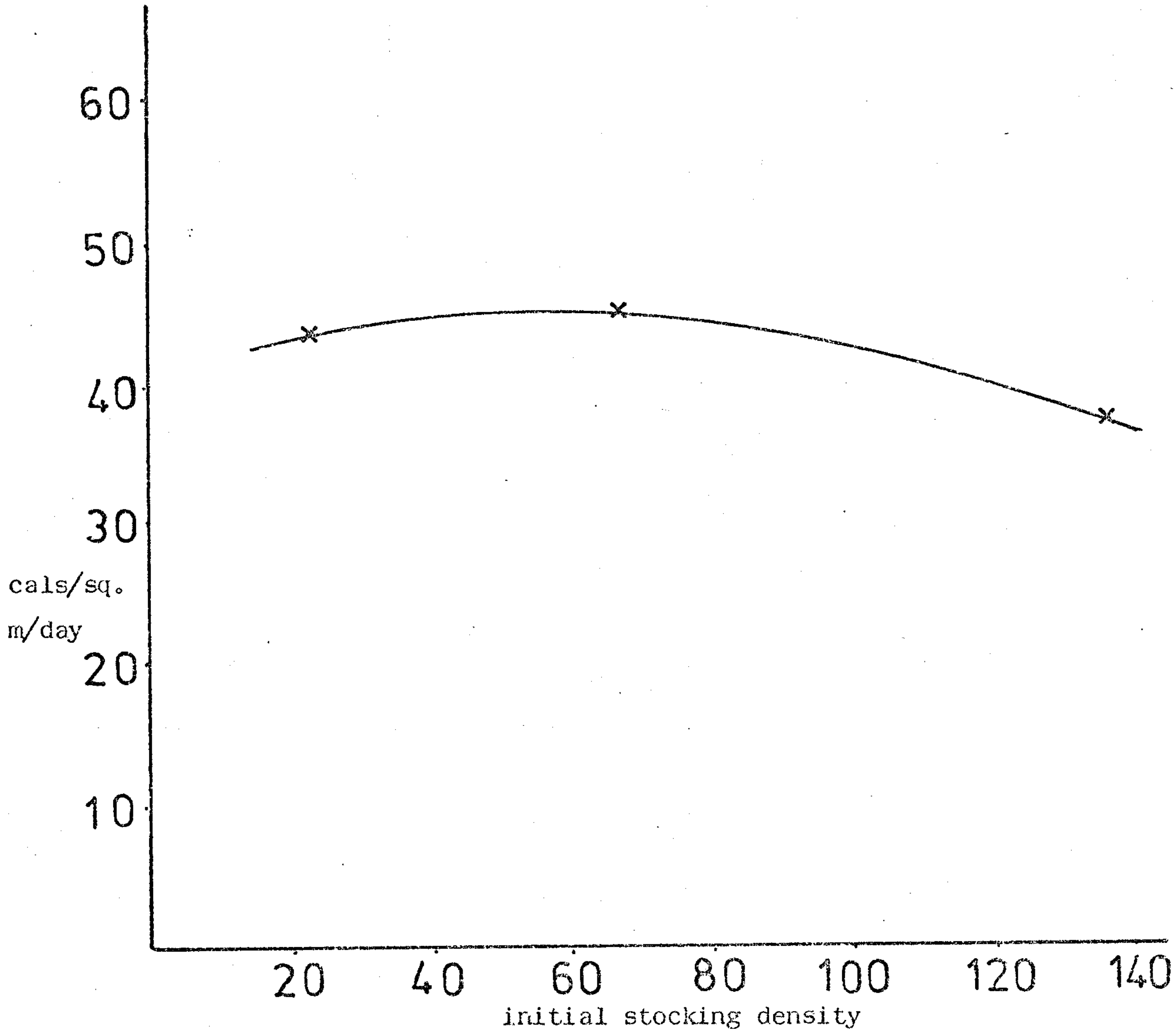


Figure (22) The affect of initial stocking density on total stickleback production sq.metre/day($\frac{2000}{45}$) during August. Whether this situation is prevalent throughout the year is doubtful. If growth slows down and mortality increases with decreasing temperature towards winter, it must be stressed that August was probably the month with: a) the greatest stickleback standing crop and b) the greatest energy turnover rate, therefore, from the point of view of cropping a univoltine species such as Gasterosteus, this period is the most important. So far I have considered cropping for maximum possible biomass. If on the other hand, Gasterosteus were a coarse fish with angling potentialities, the requirements would not be maximum production but maximum individual size at the expense of productive efficiency. It is probable that the growth rate achieved in the low density enclosure was approaching the maximum attainable for this pond during August, therefore, this density would be the optimum for promoting the greatest growth in the maximum number of fish.

2) Manipulation of food

It has been shown that food availability was almost certainly the major factor restricting growth rate at high densities, and that the percentage composition of the diet that gave rise to the highest growth rate (at low density) was different from that of fish at normal density. In particular, at low fish densities, fewer molluscs and more high - calorie foods such as Chironomids and Ephemeroptera (Table 8) were taken. The importance of zooplankton remained relatively similar at all densities. It seems therefore that manipulation of the habitat to improve growth or reproductive conditions for either molluscs or zooplankton would not increase growth of Gasterosteus in any way. However, if the productivity of optimal foods such as Chironomids or Ephemeroptera could be increased, there is no reason why the growth rate and hence production of fish at high density should not approach those at either of the two lower densities. (The high natural mortality rate at high density is probably a manifestation of food shortage).

Many Chironomids are filter feeders, taking suspended particles of algae and bac~~k~~teria (Jonasson and Christianson 1967). Ephemeroptera nymphs are mainly grazers, again taking algae as their principal food, (Jones 1950). Clearly then, a management policy for *Gasterosteus*, if it were a commercial enterprise, should aim to raise the levels of the planktonic algae, which serve as food for these two groups of invertebrates. Tall vegetation surrounding the pond could be cleared to allow unrestriceted passage of sunlight for photosynthesis. Lund (1970) describes how the major restrictions imposed on algae growth are the levels of phosphorous and, to a lesser extent, nitrogen dissolved in water. Phosphorous becomes bound up with cations in anaerobic mud (Hutchinson 1957) thus artificial recycling of nutrients by periodic stirring and oxygenation of the bottom sediments could increase the potential for algal growth. Further investigations would have to be carried out to find the extent to which this type of operation could be maintained before serious and detrimental algal blooming took place.

GENERAL DISCUSSION

The contribution made by a species to the community in which it lives has been a subject of much controversy. This has largely been due to different ideas on how significance is defined and which properties attributed to a species can be defined as useful.

Margalef (1969) has proposed that ecological significance is proportional to the total biomass of a species in that ecosystem. This may well describe the importance of a forest canopy but is clearly inadequate for minor species such as soil anthropods which play an essential role in functioning of the system.

The various forms of diversity index proposed by MacArther (1955) and Margalef (1958) are similarly restrictive as a measure of significance, because the numerical contribution of a species to a diversity index, does not reflect its contribution to the community. Whittaker (1965) suggested that the best single measure of contribution is productivity. Whereas this might be adequate for restricted groups of organisms (eg. green plants) where competition is the main interraction between individuals, it is not applicable to a varacious feeder such as Cactoblastis with a high metabolic rate and low productivity. For similar reasons, Macfadyan (1963) has questioned the adequacy of metabolic rate as a measure of significance.

Probably the most acceptable measure of the contribution of a species has been proposed by Hurlbert (1971): "the significance of a species is the sum of the changes in productivity over all other species which would occur on the removal of that species". This criterion allows for both an increase or decrease in productivity after the removal of either a restrictive or beneficial organism respectively.

Apart from the practical difficulties involved in total removal of a component species from an ecosystem, (especially if that species is small) it gives only an indirect measure of the contribution. It tells nothing of the method by which the contribution is made.

The failure to provide a single unifying criterion may have been due to a failure to recognise the disparate nature of all the commonly accepted values of "usefulness" of a species. It is unlikely that a complex set of variables such as habitat amelioration by a species, competition or shelter should be sufficiently interdependant to provide a single descriptive index. Possibly the most significant factor which has prevented the development of an index of contribution, has been that the classical trophic - dynamic picture developed by Lindeman (1942) of ecosystems, is based on ecologicaly distinct groupings (trophic levels) which do not exist so simply in reality.

The division of ecosystems into groups comprising of herbivors, carnivors and producers is an imposed division, not natural, and implies that there is no energy flow within so called'trophic levels'. Such a description of a community is too inflexible to be of use in attempting to measure the contribution of a single species, which may take its food from several trophic levels. It is undeniable that relatively constant ratios of energy interchange may be taking place between the trophic levels as strictly defined, just as the ratios of the biomass of different levels may be relatively constant. Such empirical data as these however, tell us nothing of the relative importance of different components within a single trophic level.

A more workable model might be a community defined in a cyclical manner, with injection of energy from photosynthetic producers at different points in the cycle (not at a single point) to counteract energy lost through respiration. The groups arranged in the order of energy flow in the cycle would be assemblages of species whose members promote energy flow in a similar manner. By this is meant that all members of species group A will have similar feeding habits, and all feed to a greater or lesser extent on most of the constituents of species group B. Whether the constituents of group B are primary producers, herbivores or carnivores is irrelevent.

With such a community model we could see the magnitude of the real contribution of a species,or group of species,to the maintenance of the functioning of ecosystems. This contribution is measured in terms of energy flow, not physical contributions such as habitat amelioration or shelter.

The fauna of Browney Pond presented in the form of such a model in Fig. 23. This is the simplest possible structure with the minimum of major energy pathways. Similar smaller cycles of energy flow will invariably exist within each of these major divisions, but these need not be considered as we areinterested now only in the role of *Gasterosteus*.

By considering probable values for each energy pathway we can see that proceeding in a clockwise direction:

A = is large - energy mainly from molluscs, Ephemeroptera and zooplankton fed to both *Gasterosteus* and *Perca*

B = is large - decomposition upon mortality and energy lost in defaecation

C = is probably large - bacteria and micro-organisms fed to invertebrate filter feeders (*Chironomids*, *Trichoptera* etc.)

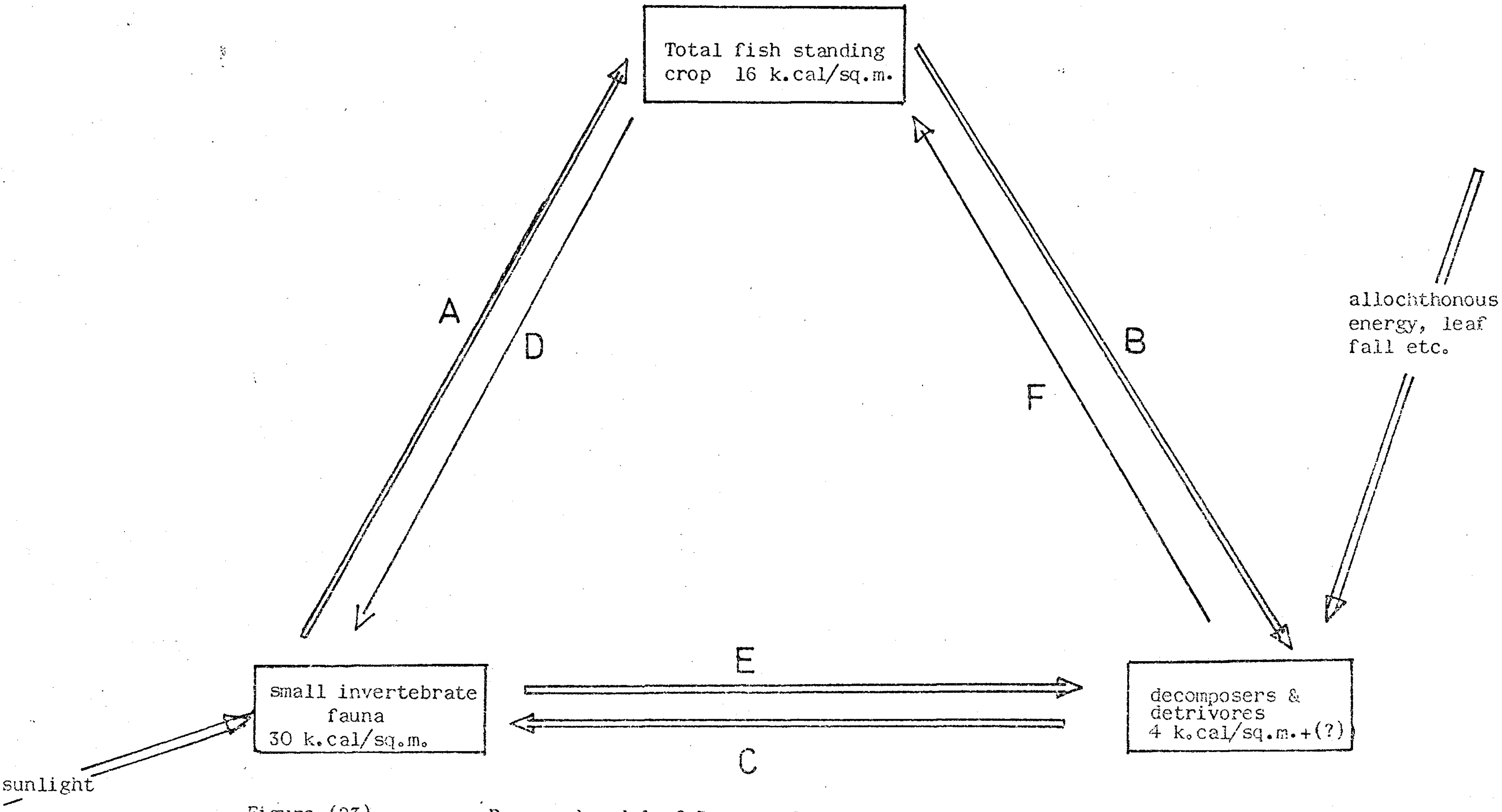


Figure (23) Proposed model of Browney Pond ecosystem.

Proceeding in an anticlockwise direction:

D = is small - probably only predation of small fry by invertebrate predators

E = is large = decomposition and defaecation of invertebrates

F = is probably small - predation by fish on Asellus

The standing crop of Gasterosteus was approximately 40% of the total standing crop of fish on the "shelf" area. If we assume that both species of fish have characteristics of energy intake and output of comparable orders of magnitude, then Gasterosteus will contribute 40% of energy flows A and B. The total standing crop of Gasterosteus was less than 10% of the total energy and the production of the small invertebrate fauna during August was likely to have been higher than that of Gasterosteus. Therefore, the total contribution made by Gasterosteus to the decomposers will have been small compared with that made by the inverterbrate standing crop.

Although we are able to describe the community only in terms of approximate values of energy flow, this type of analysis of the community structure indicates the 'Species contribution' more realistically than classical trophic - dynamic criteria.

Comparable indices of "function" or "contribution" could be derived by expressing the total energy throughput per unit time of a particular species as a percentage of the total throughput of its species group. The data acquired by such an approach could lend itself to mathematical modelling of the system by experimental component analysis (Holling 1966). Slobodkin (1964) was able to show that rates of energy flow into, and out of the trophic levels in Lindeman's model bore an empirical relationship to each other. It is probable that similar empiricsms could be found in an analysis of the sort developed above. It is further possible that unifying concepts derived from empiricsms could be developed along these lines. For instance in most established communities in temperate zones, we find a relatively stable background community of larger, slow growing, long lived species, supported by a comparatively unstable seasoned community generally consisting of smaller, faster growing individuals. Mcneill and Lawson (1970) pointed out that homiotherms and longer lived poikilotherms put more energy into respiration than do short lived poikilotherms. This is because of increased cost of maintenance with little growth.

The stable component will therefore consist of few individuals each of large average biomass, which they may achieve at the expense of low growth efficiency, high maintenance cost and long life time. On the other hand, the transistory component consisting essentially of fast growing individuals might achieve high growth efficiency and low maintenance cost at the expense of small average biomass and short lifetime.

When the ecosystem is considered in this light, it seems possible that the stable component acts as a "long term insurance policy" of slow transfer to the decomposers of large stores of "bound" energy. This "insurance policy" is probably needed by the unstable seasonal component to ensure year to year stability of standing crop energy. Conversely the seasonal component with its higher growth efficiency and faster growth rate, is opportunistic in that it can exploit and assimilate any short term energy source which the stable component would waste. This efficiently assimilated energy can then be passed on to the stable 'reservoir component' at an appropriate rate.

It would be a gross oversimplification to view communities as two completely seperate entities joined by a decomposer group. In reality, the model described above probably represents two extremes between which will be all grades of intermediates. Furthermore, the model does not presuppose that systems consisting of only seansonal species could not exist in a self perpetuating manner, only that in such a state, long term stability of standing crop energy would be unlikely.

CONCLUSIONS

In experiments carried out during July / August 1972:

1) the daily calorific intake of young Gasterosteus aculeatus during August was estimated from laboratory data to be 80 cals food/k.cal fish/day;

2) from field observations this calorific intake was obtained in the following ways: Molluscs 50.9%, Zooplankton 35%, Ephemeroptera 7.3% and Chironomids 6% (expressed as a percentage of the total calorific intake);

3) natural growth rate was found to be 10.5 cals growth/k.cal fish/day. When the fish density was reduced from normal (67 fish/sq.m. on 21 July) to half this density, the growth rate increased to 16.2 cals/k.cal/day. Similarly when the density was doubled the growth rate dropped to 8.8 cals/k.cal/day;

4) estimates of mortality in the field were a) natural mortality 50% in 45 days b) predation by Perch 20% in 45 days.

SUMMARY

A synthesis of the critical pathways of energy flow through a wild population of Gasterosteus aculeatus is presented in an attempt to define the functional role of the species in its ecosystem.

The energy budget and food requirements were calculated from laboratory experiments under or near natural conditions as possible. A natural population was studied during July / August 1972. By means of experimental enclosures, growth rate, mortality and food selectivity under three conditions of population density were measured.

Results obtained from the field experiments were used to propose a theoretical problem of raising Gasterosteus productivity.

The functional role of Gasterosteus in its ecosystem was defined in terms of trophic - dynamic concepts. An alternative, more appropriate, model is proposed for measuring "species significance".

REFERENCES

ALLEN, K. R. (1950) The computation of production in fish populations. N.Z. Sci. Rev. 8, 89.

BAJKOV, A. D. (1935) How to estimate the daily food of fish under natural conditions. Trans. Amer. Fish Soc. 65, 288.

BARNETT, S. A. (1955) Competition among rats. Nature Lond. 175, 126.

GERKING, S. D. (1954) The food turnover of a bluegill population. Ecology 35, 490 - 498.

HOLLING, C. S. (1964) The analysis of complex population processes. Canad. Ent. 96, 335 - 47.

HURLBERT, S. H. (1971) The nonconcept of species diversity. A critique and alternative parameters. Ecology 52 No. 4, 577.

HUTCHINSON, E (1957) A treatise on Liminology.

IVLEV, V. S. (1945) The biological productivity of waters. (Translated by W. E. Ricker) Usp. Sovrem. Biol. 19, 98 - 120.

IVLEV, V. S. (1961) The experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven.

IVLEV, V. S. (1964) Techniques for the investigation of fish physiology. (E. N. Pavlonskii ed.) U.S. Dept. Int. and Nat. Sci. Found. Washington.

JONASSON & CHRISTIANSON (1967) Int. rev. Gen. Hydrobiol.

JONES, J. R. E. (1950) The food of the common insects of the R. Rheidol. J. anim. ecol. 19, 159 - 174.

LACK, D. (1966) Population studies of birds. Oxford Univ. Press.

LINDEMAN, R. L. (1942) The trophic dynamic aspect of ecology. Ecology 23, 399 - 418.

LUND, J. W. G. (1970) Primary production. Wat. treat. exam. 19, 332.

MACARTHER, R. W. (1955) Fluctuations of animal populations and a measure of community.stability. Ecol. 36, 533.

MANN, K. H. (1964) Pattern of energy flow in R. Thames. Archiv. fur. Hydrobio

MARGALEF, (1969) "On certain unifying principles in ecology" Am. Nat. 97, 357

MURTON, ISAACSON & WESTWOOD (1963) The feeding ecology of the woodpigeon.

PALAHEIMO & DICKIE (1966) Food and growth of fishes III. Relations among food, body size and growth efficiency. J. Fish. Res. Bd. Can. 23, 1209 - 1248.

RICKER, W. E. (1968) Methods of assessment of fish production in fresh waters. Ricker (Ed.) Blackwell.

SLOBODKIN, L. B. (1959) Ecology 40, 232.

SLOBODKIN, L. B. (1962) Adv. Ecol. Res. 1, 69 - 101.

SLOBODKIN, L. B. (1964) J. Anim. Ecol. 33, 131 - 48.

TEAL, J. M. (1957) Community metabolism in a temperate cold spring. Ecol. Monog. 27, 283.

WARREN & DAVIS (1967) Laboratory studies on the feeding, bioenergetics and growth of fish. In the "Biological basis of Freshwater fish production (Gerling Cd.) Blackwell.

WHITTAKER, (1965) Dominance, diversity in land plant communities. Science 147, 250.

WINBERG, G. G. (1956) Rate of metabolism and food requirements of fish. F. R. B. transl. 194.

WINDELL, J. T. (1968) Food analysis and rate of digestion (in Ricker meth. assess. of prod. of fish) Blackwell 1968.