

LABORATORY STUDIES ON THE FEEDING, BIOENERGETICS, AND GROWTH OF FISH¹

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INTRODUCTION

An animal is often studied in the laboratory in order to increase understanding of its success or failure in nature. Since a species is successful within the range of environmental conditions to which its structural, physiological, and behavioural characteristics permit it to adapt, these characteristics are examined in relation to important combinations of factors present in the natural environment. The biological problem chosen for study will largely determine the particular physiological and behavioural responses and environmental factors that will be considered in experiments. In studying growth in the laboratory, food consumption and changes in body weight are usually measured under various conditions, but in addition to accumulation in the body the other important fates of the food consumed should also be determined. The quantity and quality of the ration, the metabolic state of the animal, and the energy demands of its maintenance and behavioural activities will largely determine the fates of the food consumed and the growth possible. Factors in the environment, including food, that influence the metabolic state and the activities of the animal should, then, be considered in studies of growth. To increase understanding of the growth of an animal in its natural environment, studies of growth must have a fairly complex conceptual framework. Bioenergetics, as taught by Brody (1945), and Fry's (1947) exposition of the relation between environment and animal activity provide us with this framework.

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BIOENERGETIC APPROACH TO THE STUDY OF GROWTH

Kleiber (1961a) vividly describes the evolution of bioenergetics from its 18th century beginnings in the experiments of Priestley, Scheele & Lavoisier, through the development of calorimetry starting about that time, then through early 20th century arguments concerning Rubner's 'specific dynamic effect,' to its modern concern with biochemistry, nutrition, and growth. In a very personal account, Kleiber (1961b) tells us something of the monumental contribution of Brody and of his own role in the development of this approach to the study of growth, an approach that has contributed greatly to animal husbandry.

Those who are interested in quantifying the feeding and growth relationships of fish owe much to Ivlev (1939a, b, c, 1945, 1947, 1961a, b) for the approaches he has suggested. Winberg (1956) has brought together much of what is known about the bioenergetics and growth of fish; and the importance of the contributions of the Russian workers and of Fry (1957) and his students is apparent.

In the following discussion of energy budgets for fish, and in later discussions of growth efficiencies, various categories of losses and uses of food energy are referred to frequently. We have prepared a diagram (Fig. 1) to help clarify our use of terms. The digestible portion of the consumed food undergoes digestion in the alimentary canal, the remainder being passed out as faeces. The digested materials, here considered assimilated materials (Fig. 1), enter the circulatory system and are distributed about the body. Some portion of the assimilated nitrogenous materials is not metabolized and is lost through the kidneys, gills, and skin. The energy of the remaining assimilated materials has been considered the 'metabolizable energy' by Brody (1945) and Kleiber (1961a), and Brody has termed their energy or heat content their 'physiologic fuel value'. Winberg (1956) uses the expression 'physiologically useful energy' for the energy of metabolizable materials, but this is not strictly correct, for not all of the energy of the metabolizable materials is available for physiological processes and growth. As a result of deamination, which occurs before nitrogen excretion through the kidneys and gills, and other conversion processes, a considerable part of the energy of metabolizable materials is freed and is not available to the organism for useful purposes. It is the other part of the energy of the metabolizable materials which the organism can use that Brody (1945) and Kleiber (1961a) have called the 'net energy' and that can correctly be termed the physiologically useful energy.

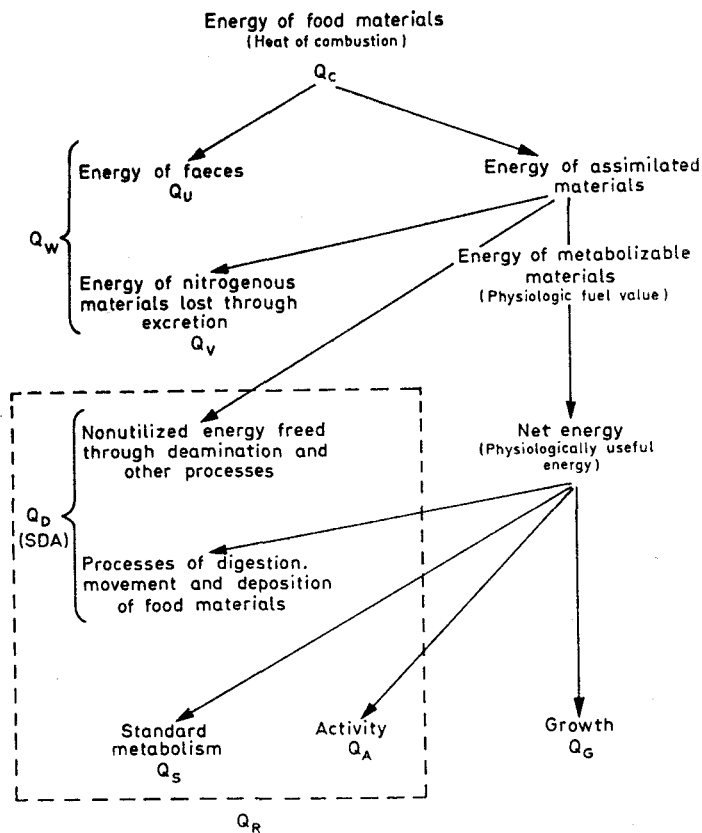


FIG. 1. Categories of losses and uses of the energy of consumed food materials.

The consumption of food by animals results in an increase in their rates of oxygen consumption and heat production. This increase is known as the specific dynamic action (SDA) of the food. In cattle, SDA 'ranges from about 8 per cent of the *metabolizable energy* at 0.5 maintenance to 38 per cent of the metabolizable energy at full feed' (Brody, 1945). It is generally accepted that SDA is not due to energy utilization for digestion, movement, and deposition of food material but represents primarily energy freed and lost through deamination of proteins to be stored as fats or catabolized; corresponding but smaller losses occur with fats and carbohydrates (Brody, 1945). Nevertheless, we cannot assume that none of the increase in the rate of oxygen consumption or heat production after food consumption is due to

utilization of energy for digesting, moving, or depositing of food materials. Accordingly, we will here consider a small part of this increase to result from energy utilization for these purposes (Fig. 1).

In order to represent the losses and utilization of the energy of the food an animal consumes, Ivlev (1939a, b, c, 1945) proposed the following equation, which is a modification of one Terroine & Wurmser (1922) used for microorganisms:

$$Q = Q' + Q_r + Q_t + Q_v + Q_w$$

where

- Q = energy value of food consumed,
- Q' = energy value of materials laid down as growth,
- Q_r = energy value of faecal and nitrogenous wastes,
- Q_t = energy of primary heat,
- Q_v = energy of external work, and
- Q_w = energy of internal work.

The symbols we have used in Fig. 1 differ from those of Ivlev. By 'primary heat,' Ivlev appears to have meant the portion of the energy of metabolizable materials that cannot be utilized by the animal. A major part of this would certainly be SDA, but Ivlev may have been considering primarily heat losses resulting from the inefficiency with which energy-rich materials are utilized through the biochemical processes which make activity of an animal possible. He used oxygen consumption determinations to estimate 'internal' and 'external' work, and measured food consumption, growth, and the energy value of waste products. He then determined primary heat as the difference between the energy value of the food consumed and the sum of the energy values of waste products, oxygen consumption, and growth.

Winberg (1956) objected to the determination of primary heat by this difference. Fundamentally, Winberg's objection was that the organism's total heat production resulting from energy utilization as well as loss comes about through oxygen utilization; and Ivlev, in determining internal and external work by measurements of oxygen consumption, had already accounted for all heat production. SDA is usually estimated by measuring differences in the metabolic rates of fed and unfed animals; and the procedures Ivlev (1939c) and Ivlev & Ivleva (1948) used in some of their experiments could lead to estimates of SDA. This is apparently not recognized by Winberg. We must, however, accept Winberg's objection to Ivlev's (1939a) experiments with sheat-fish (*Silurus glanis*) larvae, and the same objection appears to apply to his experiments with pike, *Esox lucius*, (Ivlev, 1939b), though

our understanding of his methods apparently differs from Winberg's (1956). Ivlev did not always carefully describe his methods. Though we may not completely understand Ivlev's objectives and methods or be entirely satisfied with the clarity or usefulness of his equation, his papers first drew our attention to the possibilities of bioenergetic studies of growth.

Winberg (1956) himself proposes for estimating food consumption rates, the use of a 'balanced equation,' which is equivalent to the following:

$$Q_c = 1.25(Q_r + Q_g)$$

where

Q_c = energy of ration,

Q_r = energy of metabolism,

Q_g = energy of weight increase,

and where the metabolizable energy is assumed to be 0.8 of the energy of the ration. This equation can be expected to yield reasonably accurate estimates of the rates of food consumption of fish in nature only if the estimates for energy of metabolism are based on laboratory experiments with fish expending about as much energy in activity, consuming about as much food, and growing about as fast as those in nature. Winberg's (1956) discussion of the experiments of other workers fails to convince one of the value of using laboratory measurements of 'routine metabolism' in conjunction with growth measurements to estimate the food consumption of fish. To be useful, the concept of routine metabolism needs further definition as to the plane of nutrition and the level of activity of the fish.

Although there may be no entirely adequate way of representing the energy budget of an animal, Ivlev's equation can be rewritten and his definitions refined. Without clear definitions, such an equation loses much of its value, for satisfactory methods of obtaining the necessary data are then less apparent and interpretations may be more questionable. We will begin with the following equation:

$$Q_c - Q_w = Q_g + Q_r \quad (1)$$

where

Q_c = energy value of food consumed,

Q_w = energy value of waste products in faeces, in urine, and lost through gills and skin,

Q_g = total change in energy value of materials of body (growth), and

Q_r = energy metabolically utilized or released in all ways for all purposes.

Now if we let

$$Q_r = Q_s + Q_a + Q_a \quad (2)$$

where

Q_s = energy equivalent to that released in the course of metabolism of unfed and resting fish (standard metabolism),

Q_a = additional energy released in the course of digestion, assimilation, and storage of materials consumed—SDA, and

Q_a = additional energy released in the course of swimming activity,

then, substituting, we can represent the over-all energy budget of a fish for any given period of time in terms which are convenient for our purposes as follows:

$$Q_c - Q_w = Q_g + Q_s + Q_a + Q_a \quad (3)$$

Equation (1) is equivalent to Winberg's balanced equation except that we make no assumption as to the proportion of the consumed food that is metabolizable. Davis & Warren (MS, 1967) separated the waste product term (Q_w) into the energy of faecal material (Q_u) and the energy of materials excreted through the kidneys, gills, and skin (Q_v). From a bioenergetic viewpoint, we have defined growth as the total change in energy value of the materials of the body. It will sometimes be useful to deal with either positive or negative values of this change. From a physiological viewpoint, growth is often defined as the elaboration of protoplasm, and changes in protein content of the body may be considered a more appropriate measurement (Gerking, 1955). Both viewpoints can be usefully combined by substituting a term for protein changes and a term for fat changes in place of Q_g in equations (1) and (3). Use of the bioenergetic viewpoint does not decrease the need for information on changes in body composition to arrive at an understanding of the growth process. The elaboration of sex products can be separated from other changes in body energy value by addition of another term to our equations. The energy metabolically utilized or released in all ways for all purposes (Q_r) is equivalent to total heat production or, with appropriate oxy-calorific conversion, to total oxygen consumption.

We have attempted to define the components of total metabolism in equation (2) so as to make them independent. Standard metabolism is taken to be the metabolic rate of an unfed fish whose activity has been projected to the zero level on a graph of the relationship between its metabolic rate and its activity level (Beamish, 1964; Brett, 1964).

Thus it is approximately equivalent to basal metabolic rate. Routine metabolic rate has been too poorly defined both as to the plane of nutrition and the level of activity of the animal to be useful. Variation in the behaviour of fish under different conditions makes it difficult to associate routine metabolic rate with any particular level of activity. Also because of such variation, the measurement of SDA (Q_a) in fish can perhaps best be made by determining the increase in metabolic rate caused by ingestion of food by a fish required to maintain a fixed low level of swimming activity. From a behavioural point of view, there may be occasions when it would be useful to partition the energy expenditure due to swimming activity (Q_a) into such components as expenditures for capture of food, reproductive activity, and random activity.

The degree of refinement used in budgeting the energy of an animal will depend on the objectives of the research. Reasonably accurate budgeting is only possible under laboratory conditions, but laboratory studies used in conjunction with studies on the behaviour, food habits, and growth of fish in nature can greatly increase our understanding of their bioenergetics and growth.

Basically, two kinds of information can usually be obtained from laboratory studies of the bioenergetics of fish: (1) amount and quality of food consumed, body weight and composition changes, and amounts and kinds of waste products; and (2) amounts of oxygen utilized or of carbon dioxide released. We will delay discussing food quality, body composition, and kinds of wastes, all of which have received too little attention, and consider how information on the heat content or caloric value of food, body, and waste materials might be obtained.

Oxygen-bomb calorimetry should be more widely used by those interested in the feeding and growth of fish. The equipment is not expensive and its use requires relatively little of the experimenter's time. Dry weight measurements without caloric information on the materials involved are not satisfactory for bioenergetic studies. When the protein and fat contents of the materials are known, satisfactory caloric values can be computed using typical conversion factors for protein and fat. The energy value of faecal waste products can perhaps best be determined with wet combustion methods, because some of these wastes will be in solution in the water in which the fish are held. However, excreted nitrogenous wastes will also be present in solution; and we are aware of no method for discrete measurement of the entire amounts of each of these two kinds of wastes. Ammonia and urea

are not oxidized under the conditions of the iodate methods described by Davis & Warren (1965) or Karzinkin & Tarkovskaya (1962), though uric acid and perhaps other nitrogenous wastes are partially oxidized. When the objectives of particular experiments warrant the additional effort, available methods make possible more careful accounting of major components of the nitrogenous wastes.

An oxy-calorific coefficient can be used to convert measurements of the oxygen consumed by fish to the equivalent amounts, in calories, of energy resources oxidized. Although the exact value of the coefficient will depend on the relative amounts of fat, carbohydrate, and protein being metabolized, it will usually be 3.42 cal/mg (4.89 cal/ml) of oxygen consumed plus or minus 1.5 per cent (Winberg, 1956; Kleiber, 1961a; Brody, 1945).

If the terms in equation (3) are taken to represent energy values of materials utilized or lost in different ways over some convenient period of time, say 2-4 weeks, then these values are influenced not only by physiological and behavioural effects of the environmental factors under consideration but also by changes in body weight, unless the animal is receiving only a maintenance ration. There is, of course, considerable interest in the cumulative effects of physiological, behavioural, and weight changes, but there is also great interest in primary changes in rates of energy utilization or loss caused by changes in environmental factors.

In this paper, we will use mean body weight (or energy value) and a unit time of 1 day to convert energy utilizations and losses occurring during experimental periods into rate terms. We have not worked with fish of greatly different size, and such a treatment of the data is adequate for our present purposes. However, there is considerable evidence that growth and metabolism in fish are more nearly proportional to the 0.8 power of weight than to weight alone (Winberg, 1956; Parker & Larkin, 1959; Paloheimo & Dickie, 1966). For the terms in equation (3) to be treated as rates per unit body weight per unit time, for the rates to be additive, and for the equation to balance, all of the rates must be determined as the same function of body size. Strictly, we cannot expect all utilizations and losses of energy to be the same function of body size. Moreover, the value of such equations is that they enable us to compare animals under different environmental conditions, and changes in environmental conditions may change the appropriate function of body size. However, it may sometimes be useful to assume all utilizations and losses of energy to be proportional to the same power function

of weight and to use some mean value such as 0.8 for this power. We could then rewrite equation (3) with rate terms as follows:

$$A_c - A_w = A_g + A_s + A_a + A_a \quad (4)$$

where the Q 's of equation (3) and the A 's of equation (4) are given by

$$Q_i = A_i W^x t, \quad (5)$$

and

$$A_i = \frac{Q_i}{W^x t}, \quad (6)$$

where

W = mean body weight or energy value,

t = time in days,

x = some mean power of W , and

$i = c, w, g, s, d, \text{ or } a.$

We must distinguish between the structural and physiological capacity of a fish to consume food and the amount of food the fish can and will consume under a given set of environmental conditions. Food capacity may be some simple function of weight, as Kleiber (1933, 1961a) has shown it to be for chickens, rabbits, sheep, swine and steers. He found the ratio of food capacity to $W^{0.75}$ to be reasonably constant even between species. For some species of fish, standard metabolism (Q_s) and total metabolism (Q_t) under different conditions of feeding and activity appear to be proportional to about $W^{0.8}$ (Winberg, 1956; Paloheimo & Dickie, 1966; Fry, 1957). If this is true, food handling and activity components of metabolism must also be approximately proportional to $W^{0.8}$, or be in some way compensatory. Job (1955) showed the active metabolic rate ($Q_s + Q_a$ when Q_a is maximal) of brook trout (*Salvelinus fontinalis*) to be proportional to W^x , where $x = 0.75$ to 0.94 depending on temperature. Brett (1965) has demonstrated that with increasing activity the powers of weight that give proportionality increase from 0.78 with no activity to 0.97 at the maximum sustained performance of sockeye salmon (*Oncorhynchus nerka*). With the above considerations in mind, perhaps we can assume that Q_w and Q_a will also be approximately proportional to $W^{0.8}$.

The above cited authors discuss some of these relationships rather thoroughly, and here further consideration need not be given these matters. Our problem is essentially the practical one of representing our data in terms that help to reveal the underlying bioenergetic relationships. At this time, too little is known of the physiology, behaviour and

ecology of fish to make it possible to represent properly the biological interrelationships in mathematical models of bioenergetics and growth, if, indeed, biological complexity will ever permit such simple representation.

ENVIRONMENT, BIOENERGETICS AND SCOPE FOR GROWTH

Our bioenergetic equation describes an animal only under one set of environmental conditions, and a broader conceptual framework is required if the organism-environment complex is to be analyzed effectively. Those of us interested in the autecology of animals are indebted to Fry (1947) for his statement of the relationship between environment and activity, 'The idea of activity as distinct from metabolism and the concept that environment influences activity by acting on metabolism . . .'; for his classification of the environment; and for his concept of 'scope for activity' as the difference between active and standard metabolic rates under given environmental conditions. Growth can be considered an activity, so perhaps the difference between the energy of the food an animal consumes and all other energy utilizations and losses can be defined as the 'scope for growth' under particular environmental circumstances. Scope for growth, as defined, is not strictly equivalent to scope for activity. Food consumption rate is not active metabolic rate, but will be influenced by and will influence metabolic rate. Other metabolic utilizations and losses are not equivalent to standard metabolism. Nevertheless, if we may be permitted this liberty with Fry's concept, we will be able to take advantage of his way of relating the performance of an animal (growth in this instance) to the action of factors in the environment.

Fry classified environmental identities or factors as lethal, masking, directive, controlling (e.g., temperature), limiting (e.g., oxygen), or accessory, according to the manner in which they may influence an organism. A particular identity may act under more than one category of the classification.

Environmental factors such as temperature and oxygen can influence either physiologically or behaviourally the food consumption and the metabolism, and, consequently, the scope for growth of an animal. Food availability and quality are other environmental factors that must be considered. They will influence consumption (Q_c), waste products (Q_w) and some components of metabolism (Q_d and Q_a). Food will not influence standard metabolism (Q_s) except when its lack

reduces the animal to starvation, when it could be considered a lethal factor. Perhaps food can be included within Fry's limiting factor category. Certainly food acts as a directive factor, and one can envision it sometimes acting as a masking or an accessory factor.

Fry (1947) has explained how limiting and controlling factors as well as other possible physiological stressors may act together to determine an animal's scope for activity. The energy budget of an animal provides us with a measure of its scope for growth under particular environmental conditions. Together these approaches provide a conceptual framework for examining the relations between growth and environment.

Hari Sethi of our laboratory has permitted us to use his preliminary data on the bioenergetics and growth of a cichlid (*Cichlasoma bimaculatum*) to illustrate the influence of temperature on scope for growth. Different groups of cichlids, which had been acclimated to the test temperatures of 20, 24, 28, 32, and 36° C while on maintenance rations, were then permitted to feed *ad libitum* on *Tubifex* for 14 days. Other groups were starved for the 14-day period. Weight and caloric determinations were made on subgroups at the beginning of this period, and on the remaining test animals at the end. The weights and caloric values of the *Tubifex* consumed were measured by appropriate methods. The percentages of consumed food lost in faeces were determined by the iodate wet combustion method (Davis & Warren, 1965) for other

TABLE I. Mean percentages of dry weight, range of caloric values and mean caloric value in kilocalories per gram dry weight of experimental materials

Material	Number of samples	Mean percent dry weight	Range of caloric values	Mean caloric value
Midge larvae	6	14.2	4.97-5.33	5.27
Housefly larvae	8	19.9	6.03-6.16	6.11
Housefly adults	11	26.7	4.76-4.79	4.77
Stonefly naiads	19	19.2	4.84-5.48	5.36
Tubificid worms	14	16.2	5.34-5.99	5.49
Trout (<i>Salmo clarki</i>)				
Low ration	7	18.5	4.14-4.49	4.22
Intermediate ration	9	20.5	4.51-4.72	4.54
High ration	12	22.4	4.88-5.17	5.04
Sculpins (<i>Cottus perplexus</i>)	17	23.5	4.74-5.44	5.29
Cichlids (<i>Cichlasoma bimaculatum</i>)	130	—	4.50-5.94	5.15

groups of fish also fed *ad libitum* at the various temperatures. The dry weights as percentages of wet weights and average caloric values of food organisms and fish used in this and later experiments we will discuss are given in Table 1.

Food consumption and scope for growth in calories per fish per day and assimilation efficiency were greatest at 28° C and decreased at lower and higher temperatures (Fig. 2 and Table 2). The energy utilization of the starved fish does not suggest that standard metabolism (Q_s) together with a probably variable cost of activity (Q_a) (Fry, 1964) accounted for a very large portion of the energy of the food consumed.

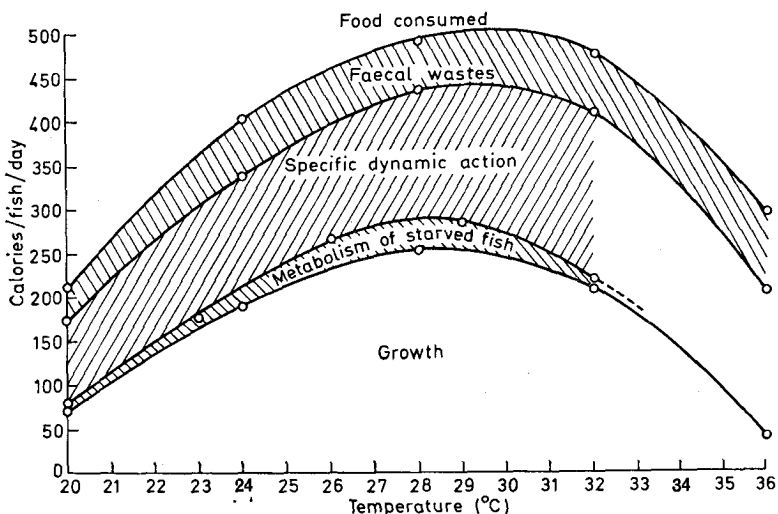


FIG. 2. Influence of temperature on the food consumption, losses and uses of energy of food materials, and scope for growth of young *Cichlasoma bimaculatum* fed *ad libitum* for a period of 14 days, shown as calories per fish per day. Categories of faecal wastes and specific dynamic action include small percentages of nitrogenous wastes. Estimates of metabolism of starved fish were based on experiments with fish larger than those used for other estimates and have been adjusted for size differences (Data of Hari Sethi).

Specific dynamic action (Q_a) accounted for more energy than did faecal losses and starvation metabolism combined at all temperatures where this comparison can be made. Faecal losses represented 30 per cent of the energy of the food consumed at 36° C, but starvation metabolism was not determined at this temperature. The wet combustion method of determining the energy value of faecal wastes may result in the oxidation

TABLE 2. Influence of temperature on the energy utilization in calories per individual cichlid (*Cichlasoma bimaculatum*) held in groups of 7 fish and fed *ad libitum* on *Tubifex* or starved for a 14-day period.

Temp (°C)	Mean energy content of fish	Food consumed	Assimi- lation efficiency %	Food not assimi- lated	Food assimi- lated	Growth	Respiration ¹	Gross efficiency %
				<i>Fed ad libitum</i>				
20	1,812	2,982	82.8	513	2,469	1,006	1,463	33.7
24	3,118	5,670	84.0	907	4,763	2,694	2,069	44.0
28	3,838	6,930	88.6	790	6,140	3,585	2,555	51.7
32	3,833	6,748	85.6	972	5,776	2,926	2,850	43.4
36	1,660	4,200	69.6	1,277	2,923	607	2,316	14.5
				<i>Starved</i>				
20	5,974	—	—	—	—	—319	319	—
23	5,902	—	—	—	—	—368	368	—
26	6,572	—	—	—	—	—960	960	—
29	6,225	—	—	—	—	—753	753	—
32	6,202	—	—	—	—	—607	607	—

¹ Respiration values were calculated by difference between food assimilated and growth, and, as determined, they may include some of energy value of nitrogenous materials lost through gills and kidneys.

of a part but not all of the nitrogenous wastes excreted through the kidneys, gills, and skin. In consequence, small portions of the energy values given for faecal wastes and for SDA, which was determined by difference, properly should be attributed to such nitrogenous wastes. The methods used here do not permit quantitative separation of this waste category, but further separation would not greatly alter the above relationships since the energy value of the nitrogenous wastes of fish, even on a maintenance ration, is only in the order of 7 per cent of the energy value of the food they consume (Winberg, 1956).

The effect of an environmental factor on the bioenergetics of an animal must be considered not only in terms of total energy utilization and loss but also in rate terms. The cichlids at 36° C consumed more food per unit of body material than did those at the other temperatures (Fig. 3). Though starvation data are lacking at this temperature, poor utilization of food for growth probably resulted not only from poor assimilation but also from metabolic failure causing increased SDA. This also occurs at 20° C. Kinne (1960) found the total consumption of food by the desert pupfish (*Cyprinodon macularius*) to be greatly increased at high temperatures and efficiency of food utilization for growth greatly decreased. There were indications that this was at least

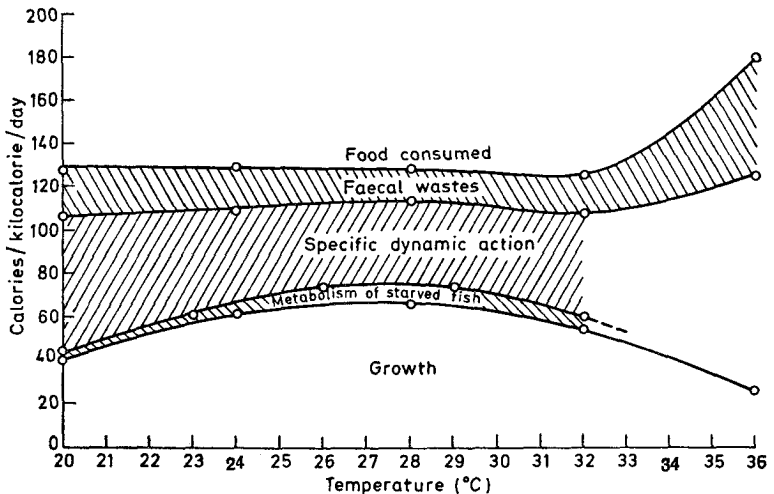


FIG. 3. Influence of temperature on the food consumption, losses and uses of energy of food materials, and scope for growth of young *Cichlasoma bimaculatum* shown as calories per mean kilocalorie of fish biomass per day. See legend for Fig. 2 for other information (data of Hari Sethi).

in part due to very poor assimilation. Anderson (1959) found the percentages of consumed protein retained by bluegill (*Lepomis macrochirus*) at 80, 70, 60, and 50° F to be 42, 35, 35 and 14, respectively, indicating a considerable increase in deamination and SDA at the lowest temperature, since protein assimilation was essentially constant.

Sethi has also determined SDA by taking the difference between the metabolic rates of cichlids swimming at a fixed low velocity when not fed and when fed *ad libitum* at each of the test temperatures. Total SDA for the food consumed was greatest at 36 and 20° C even though the fish consumed much more food at intermediate temperatures. SDA per gram of food consumed was about four times as great at 36° C and about thirteen times as great at 20° C as at 28° C.

The influence of dissolved oxygen concentration on the *ad libitum* food consumption and growth of coho salmon (*Oncorhynchus kisutch*) fed amphipods (Hermann et al, 1962), of those fed *Tubifex* (Fisher, 1963), and of largemouth bass (*Micropterus salmoides*) fed earthworms (Stewart, 1962) has been studied in our laboratories. The food consumption and the growth of these fish declined with any appreciable decreases in oxygen concentration below the air saturation level. Marked changes in gross food conversion efficiency occurred only at concentrations below about 4 mg/l. Moderate decreases in dissolved oxygen result in reductions in scope for growth apparently by limiting the amount of food the fish will consume. Fry (1957) has suggested that the maximum metabolic rate of fish is restricted by respiratory surface and that, in consequence, this 'surface rather than the absorptive surface of the digestive tract may be the limit of the maximum rate of growth of which fish are capable.' Sethi was able to detect little or no difference in the metabolic rates of fed and unfed cichlids when these fish were forced to swim at high velocities. The fish were apparently unable to digest or utilize the consumed food when swimming performance required all of the oxygen they could obtain from their environment.

Ivlev (1961b) has examined food as a factor determining the scope for growth of a fish by relating consumption, respiration, and growth to food density. He determined the growth rate of the plankton-feeding bleak (*Alburnus alburnus*) at one food density in a hatchery pond. By means of a mathematical model, he then attempted to estimate what the consumption, respiration, and growth of this species would be at different food densities. Necessary data on maximum rations and routine and active metabolic rates were obtained from laboratory

studies. His analysis indicated that consumption rates would increase, respiration rates would decline, and growth rates would increase with increases in food density. He assumed that changes in respiration would be due to changes in swimming activity necessary to capture food and did not consider changes in respiration that would result from changes in food consumption rate. For reasons to be discussed below, we believe the latter effect to be the more important, but this does not detract from the imaginative manner in which Ivlev related scope for growth to food density.

EFFICIENCIES OF FOOD UTILIZATION FOR GROWTH AND MAINTENANCE

Discussion of food consumption and growth will lead us to consider the efficiency with which food is utilized for growth or maintenance under different circumstances. There are two general types of efficiencies with which we will be concerned, total efficiencies and partial efficiencies (Kleiber, 1961a). Each type of efficiency may be employed with any of the food energy categories, total, digestible, metabolizable, or net (Fig. 1). It is necessary to specify the type of efficiency and the food energy category when discussing efficiencies. Throughout this paper, the total food energy category will be referred to unless stated otherwise.

Total efficiency, E_t , is the *gross efficiency* of Brody (1945) and Brown (1946, 1957):

$$E_t = \frac{G}{I} \quad (7)$$

where

G = growth, and
 I = food intake.

Ivlev's (1939a, 1945) coefficient of growth of the first order (K_1) is total efficiency on the basis of the total food energy category; his coefficient of the second order (K_2) is total efficiency on the basis of metabolizable food energy.

Partial growth efficiency, E_{pg} , is the *net efficiency* of Brody (1945) and Brown (1946, 1957):

$$E_{pg} = \frac{G}{I - M} \quad (8)$$

where

M = maintenance ration.

This ratio expresses the efficiency with which an animal utilizes for growth that food consumed over and above the amount it would require to just maintain its tissues. Brown (1946) used the digestible food energy category in calculating net efficiency.

Partial maintenance efficiency, E_{pm} , is an expression of the efficiency with which an animal utilizes rations at or below the maintenance ration to maintain its tissues or to prevent them from being catabolized (Kleiber, 1961a):

$$E_{pm} = \frac{L_p}{I_p} \quad (9)$$

where

L_p = tissue loss prevented, and

I_p = part of ration preventing loss.

Partial maintenance efficiencies appear not to have been used by fishery scientists. Considering that many if not most species of freshwater fish in the temperate world grow during only about 6 months of the year, there should be not only theoretical but practical interest in the efficiency with which these fish maintain themselves, avoiding death from starvation or from a combination of starvation and other environmental factors as shown by Ivlev (1961a).

Total efficiencies can be determined with information on growth at one ration. To determine partial growth efficiencies, the maintenance ration also must be known. Partial maintenance efficiency can be determined only when data on weight changes corresponding to two different rations at or below the maintenance ration are available. It is the ratio of the difference between tissue lost at the two rations to the corresponding difference between the two rations.

With increasing ration, gross efficiency increases from zero at the maintenance ration and asymptotically approaches a maximum at the maximum ration if net efficiency is constant. If net efficiency declines with increasing ration, gross efficiency will increase to a maximum with ration increases to some intermediate level and then decline with further increases. Paloheimo & Dickie (1965), after examining literature on the food consumption and growth of fish, conclude that gross efficiency decreases from a maximum value at low feeding levels and is independent of the size of fish. They recognize certain restrictions that must be placed on this generalization, but our experience leads us to believe their statement is not sufficiently restrictive. Unless net efficiency declines drastically with increases in ration from low levels, and this is

not generally the case, gross efficiency will not decline with increasing ration except beyond some intermediate level of feeding. Within any growth stanza (Parker & Larkin, 1959), the gross efficiency of a particular fish must decline with increasing size, as a greater portion of the food the fish can obtain is necessary for maintenance, and its growth rate will approach zero. If the fish crosses some ecological or physiological threshold which permits more efficient procurement or utilization of food, its gross efficiency and growth rate may increase again. Animals of different races or species and of greatly different sizes may exhibit nearly the same absolute growth with the same absolute ration (Kleiber, 1926, 1933, 1936), but this is true only when increases in maintenance costs are compensated by increases in growth rates, which may occur in different races at equivalent physiological ages (Brody, 1945). Faster growing individuals in the same group could have gross efficiencies similar to those of slower growing individuals even though the former were larger.

Net efficiencies tend to decline with increasing ration size because of declining assimilation efficiency and increasing SDA, but under some conditions they can be remarkably constant over a wide range of ration sizes, as we will show later. Unless very precise data are available, net efficiencies (partial growth efficiencies) should probably not be computed for animals that are barely growing, since most of the energy of the food consumed is being used for maintenance requirements. Difficulty in precisely measuring small amounts of growth and the differences between maintenance rations and rations little above these can lead to unreasonable values for net efficiencies such as those near and over 100 per cent found by Brown (1946, 1957), unreasonable even for the digestible food energy category.

FOOD CONSUMPTION, ACTIVITY, RESPIRATION, AND GROWTH

In nature fish obtain and utilize food for maintenance and growth under various environmental conditions. Not only food availability and quality but other environmental factors determine how much food is available for growth and how much is lost or utilized in other ways. Laboratory studies of growth will be most useful if they permit the examination of the different uses fish make of food when consuming widely different amounts of foods of different quality under a variety of conditions.

We have studied the food consumption and growth of individual sculpins (*Cottus perplexus*) which were held separately in aquaria at seasonal temperatures and fed midge larvae. Some individuals received rations near or below the maintenance level, others were fed well above this level, and some were given all the food they would consume. Wet weights were determined at the beginning of an experiment, and wet and dry weights at its conclusion. Dry weights of typical individuals were also determined at the beginning. Heats of combustion of samples of fish and of food organisms were used for converting dry weight data to caloric values (Table 1). Percentages of food consumed that were assimilated were determined by the wet combustion method described by Davis & Warren (1965), and mean values were used (Table 3).

TABLE 3. Percentages of food consumed that were assimilated by cutthroat trout and sculpins

Species	Number of determinations	Percentages of food assimilated	
		Range	Mean
Trout (<i>Salmo clarki</i>)	6	84.9-86.1	85.5
Sculpins (<i>Cottus perplexus</i>)	10	78.4-84.4	81.9

The use of mean values for assimilation efficiency in this and later experiments does not take into account differences in assimilation with differences in ration size or season. The means are for fish held at 10° C during the winter and fed somewhat less than a maximum ration, and they may approximate minimum assimilation efficiencies. This will result in some error in the respiration values, determined by difference, but this error is probably not sufficient under the conditions of these experiments to alter appreciably our general findings.

Maximum food consumption and food utilization for growth in a fall experiment differed strikingly from those observed in a winter experiment (Fig. 4). Similar differences have occurred in other experiments conducted during different seasons (Davis & Warren, 1965; Brocksen, 1966). In the fall experiment, net efficiencies declined moderately with increases of ration size over the wide range of rations the fish would consume; consequently, the maximum gross efficiencies were achieved at two-thirds the maximum ration and declined beyond this level (Table 4). Energy losses and utilizations in the respiration category

(Q_r) were about four times as great at maximum rations as at rations near the maintenance level. This can be attributed almost entirely to increased SDA (Q_d). Fry (1957) states that 'Job (1954) in a single preliminary experiment found that the consumption of minnows by two yearling *S. fontinalis* fed to repletion required a rate of oxygen consumption for the assimilation of this food equivalent to their active oxygen consumption as determined in the rotating chamber.' Paloheimo & Dickie (1966), making use of Winberg's (1956) balanced equation, found on examining the data of Dawes (1930-31a, b), Pentelow (1939) and Gerking (1955) that the level of metabolism of the experimental fish increased 4 to 5 times with an increase in ration level from maintenance to maximum. Not only increases in total daily ration but also increases in individual meal size will increase SDA. The same total ration given in a greater number of feedings will result in a reduction in SDA (Brody, 1945; Cohn, 1963) and in more efficient utilization of food for growth.

Sculpins consumed much less food in the winter experiment than in the fall experiment. At rations slightly above the maintenance level, their gross efficiencies in winter were about the same as those observed in the fall, but gross efficiencies in winter remained nearly constant with

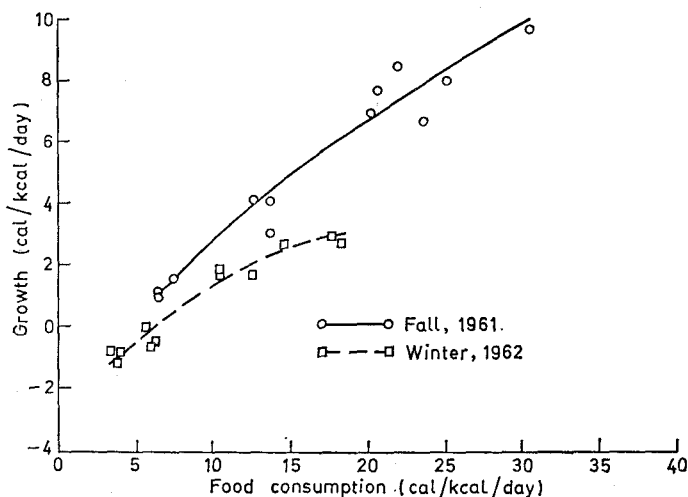


FIG. 4. Relationships between yearling sculpin (*Cottus perplexus*) food consumption rate and growth rate determined in aquarium experiments conducted during the fall, 1961, and the winter, 1962 (from Davis & Warren, 1965).

increases in ration size (Table 5). Net efficiencies at rations somewhat above the maintenance level were similar in the two experiments, but only in the winter experiment did slightly higher rations result in marked decreases in net efficiency (Fig. 5). Respiration accounted for about as much energy at consumptions near 1,600 calories in the winter experiment as at consumptions near 2,000 calories in the fall experiment (Tables 4 and 5). The decline of net efficiencies over such a narrow range of rations was probably primarily due to increases in SDA.

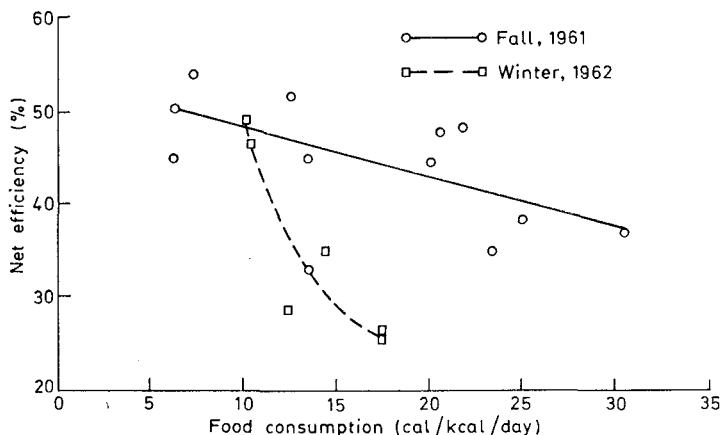


FIG. 5. Relationships between food consumption rate and net efficiency of food utilization for growth of yearling sculpins (*Cottus perplexus*) in aquarium experiments conducted during the fall, 1961 and the winter, 1962 (data from Davis & Warren, 1965).

Such increases can be expected to occur when animals are unable effectively to utilize food for growth either because of nutrient imbalances (Brody, 1945) or because of the metabolic state of the animal. Under some circumstances, metabolic processes may limit food utilization for growth to rates below those possible under other circumstances. If an animal is unable to synthesize protein from the amino acids available in its food, deamination will increase SDA. Sculpins and other fish may be metabolically unable to utilize food for growth effectively during periods of the year when they do not normally grow, though they must be able to obtain and utilize enough food to maintain themselves during these periods. In the winter experiment, partial maintenance efficiencies also declined with increases in ration size; at the lowest rations these efficiencies approximated the highest net

TABLE 4. Energy values in calories per individual for yearling sculpins (*Cottus perplexus*) held separately in aquaria and fed measured amounts of midge larvae during the fall, 1961, from 13 September to 8 November at temperatures ranging from 8.3 to 15.0° C (mean 11.6° C)

Fish number	Mean energy content of fish	Food consumed	Food not assimilated	Food assimilated	Growth	Respiration ¹	Gross efficiency %	Net efficiency %
1	1,346	467	84	383	60	323	12.8	45.1
2	1,246	505	91	414	106	308	21.0	50.5
3	1,451	511	92	419	77	342	15.1	54.0
4	1,440	993	179	814	327	487	32.9	51.4
5	1,352	1,011	182	829	225	604	22.3	44.8
6	1,372	1,024	184	840	307	533	30.0	33.2
7	1,587	1,754	316	1,438	607	831	34.6	44.6
8	1,490	1,795	323	1,472	692	780	38.6	47.9
9	1,591	1,800	324	1,476	674	802	37.4	48.5
10	1,554	2,005	361	1,644	568	1,076	28.3	35.0
11	1,507	2,078	374	1,704	656	1,048	31.6	38.4
12	1,559	2,618	471	2,147	822	1,325	31.4	36.8

¹ See footnote to Table 2.

TABLE 5. Energy values in calories per individual for yearling sculpins (*Cottus perplexus*) held separately in aquaria and fed measured amounts of midge larvae during the winter, 1962, from 18 January to 15 March, at temperatures ranging from 3.9 to 8.9° C (mean 6.9° C)

Fish number	Mean energy content of fish consumed	Food assimilated	Food not assimilated	Food assimilated	Growth	Respiration ¹	Gross efficiency %	Partial maintenance efficiency %	Net efficiency %
1	1,650	317	57	260	-75	335	—	53.4	—
2	1,504	321	58	263	-109	372	—	35.2	—
3	1,497	332	60	272	-72	344	—	45.0	—
4	1,481	467	84	383	0	383	—	47.0	—
5	1,448	486	87	399	-57	456	—	32.4	—
6	1,442	509	92	417	-51	468	—	32.0	—
7	1,565	915	165	750	165	585	18.0	—	49.2
8	1,338	954	172	782	131	651	13.7	—	46.1
9	1,708	1,002	180	822	170	652	17.0	—	28.5
10	1,800	1,490	268	1,222	288	934	19.3	—	35.0
11	1,610	1,593	287	1,306	247	1,059	15.5	—	24.8
12	1,690	1,678	302	1,376	279	1,097	16.6	—	26.5

¹ See footnote to Table 2.

efficiencies occurring at rations slightly above the maintenance ration (Table 5). Anderson (1959) found bluegill and Brown (1946) found brown trout (*Salmo trutta*) to have reduced rates of food consumption and growth during late summer, fall, and winter even though these fish were held at constant temperatures. These workers suggest that seasonal changes in growth may be hormonally controlled.

Figure 6 (unpublished data of Brocksen) suggests that cutthroat trout (*Salmo clarki*) may utilize food for growth under some conditions in late winter with higher gross efficiency than in the spring, at least over the narrow range of rations the fish will consume in the winter.

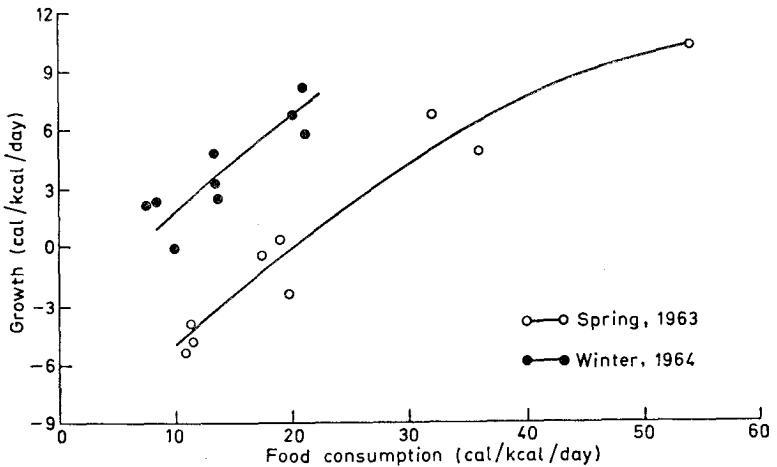


FIG. 6. Relationships between food consumption rate and growth rate of yearling cutthroat trout (*Salmo clarki*) determined in aquarium experiments conducted during the spring, 1963, and the winter, 1964 (data of Robert Brocksen).

The higher gross efficiencies in winter were primarily due to the lower maintenance costs, probably resulting from lower temperatures. The maximum ration at this time was about equal to the maintenance ration in the spring experiment. The shapes of the two curves indicate that net efficiencies in the winter declined very little but in the spring they declined considerably with increases in ration size. These data suggest that there are seasons and temperatures at which maintenance costs may be low but at which the fish are still metabolically able to utilize food effectively for growth. Under these circumstances, the gross efficiencies will be high. The trout were fed *Tubifex* and the experiments

performed in much the same way as described above for the sculpins.

Experiments like the ones we have discussed were conducted to make it possible to estimate the food consumption of fish in laboratory stream communities on the basis of their growth. The validity of any estimates of food consumption based on growth in the laboratory streams depends on whether or not the energy expenditures for swimming activity (Q_a) in the aquaria were similar to such expenditures in the streams. Brocksen (1966) compared the food consumption and growth of trout in aquaria to those of trout held at two water velocities in laboratory streams in which no food was available other than housefly adults and larvae which he intermittently introduced into the current. Water velocities of 24 and 39 cm/s were provided in different streams. The trout occupied positions near large rocks and moved into faster current usually only in search of food. Some of the stream fish and some of the aquarium fish were starved, while others were fed a range of rations extending to the maximum the fish would consume.

The trout in the streams had higher gross efficiencies of food utilization for growth than did those in the aquaria, but there was no significant difference between the efficiencies of fish in the streams having different water velocities (Fig. 7). The maintenance costs of the fish in the streams

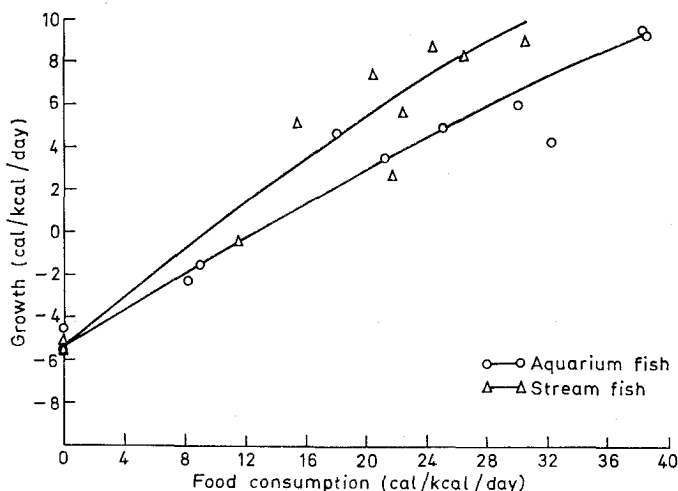


Fig. 7. Relationships between food consumption rate and growth rate of underyearling cutthroat trout (*Salmo clarki*) held in aquaria and in laboratory streams in an experiment conducted during winter, 1966 (data of Robert Brocksen).

appear to have been less than those of the fish in the aquaria. Observation of the fish in the streams and in the aquaria suggested that the random activity of the fish in the aquaria was as great or greater than the activity of the fish in the streams. Even the starved fish in the streams entered the faster current, apparently in search of food.

We can estimate the SDA (Q_a) at different consumption rates in the laboratory streams (Table 6) by assuming that other metabolic costs were the same in fish receiving food as in the starved individuals. SDA increased markedly as the maximum ration was approached and became more than double all other respiratory costs, resulting in a decline in net efficiencies. Thus, gross efficiency reached a maximum at slightly more than two-thirds the maximum ration and then declined.

Allen (1951) and Horton (1961) have used Pentelow's (1939) data on the food consumption and growth of brown trout in the laboratory to estimate the food consumption of trout in streams. Gerking (1962) used similar laboratory data on bluegill (Gerking, 1955) to estimate the food consumption of this species in a lake. Hatanaka & Takahashi (1960), on the basis of laboratory experiments on growth, estimated the food consumption of Pacific mackerel (*Pneumatophorus japonicus*) in nature; and in a series of papers they and their co-workers estimated the food consumption of other marine fish by the same method. Warren et al (1964) estimated the food consumption of cutthroat trout on the basis of food consumption-growth relationships established in laboratory experiments conducted during the growth season under natural temperature and light conditions.

Allen and Horton both assumed that net efficiency of food utilization for growth was constant over a wide range of ration sizes, though analysis of Pentelow's data does not suggest net efficiencies to have been constant (Pentelow, 1939; Horton, 1961). As shown above, not only gross but also net efficiencies can vary widely under different conditions. If laboratory studies on the food consumption and growth of fish are to be used for estimating food consumption in nature, the experiments should be conducted during the season for which the estimates are to be made and they should duplicate natural conditions as nearly as possible with regard to type of food, temperature, and light. It seems unlikely that swimming activity for feeding accounts for a large part of the total metabolic rate (Q_r) of growing fish, if one considers that the energy utilization and loss through SDA (Q_a) in feeding and growing fish is relatively large, and that the energetic costs of moderate levels of swimming activity (Q_a) are relatively low (Brett, 1964; Brett &

TABLE 6. Energy values in calories per individual for under-yearling cutthroat trout (*Salmo clarki*) held separately in laboratory streams and fed measured amounts of housefly larvae and adults during the winter, 1966, from 18 January to 7 February at temperatures ranging from 6.1 to 11.1° C (mean 8.5° C)

Fish number	Mean energy content of fish	Food consumed	Food not assimilated	Food assimilated	Growth	Respiration			Net efficiency %
						Total	SDA ¹	Activity and other costs ²	
1	3,590	0	0	0	-432	432	0	432	—
2	4,027	960	139	821	-54	875	443	432	—
3	3,546	1,144	166	978	387	591	159	432	33.8
4	3,282	1,542	224	1,318	402	916	484	432	26.1
5	3,665	1,637	237	1,400	208	1,192	760	432	12.7
6	5,037	2,142	311	1,831	792	1,039	607	432	37.0
7	4,468	2,271	329	1,942	837	1,105	673	432	36.9
8	4,960	2,745	398	2,347	878	1,469	1,037	432	32.0
9	4,560	2,897	420	2,477	870	1,607	1,175	432	30.0

¹ SDA value is derived by subtracting the calories of respiration of the starved fish from the calories of respiration of the individual fish fed different rations.

² Taken from the respiration value of the unfed fish.

Sutherland, 1965; Brocksen, 1966). Brocksen's (1966) experiment tends to support this viewpoint, which leads to the conclusion that perhaps laboratory studies on food consumption and growth can provide reliable estimates of food consumption in nature.

Mann (1965) has used Winberg's (1956) balanced equation for estimating food consumption by fish. He assumed the metabolic rate (Q_r) of fish in nature to be twice the routine metabolic rate, as Winberg suggested. When one considers how dependent the metabolic rate of fish is on the SDA (Q_d), and how much SDA is influenced by food consumption rate and environmental conditions, there remains doubt as to how reliable estimates of the food consumption of fish in nature may be when based on growth and on routine metabolic rate multiplied by any constant.

STOCK BIOMASS, FOOD CONSUMPTION, GROWTH, AND PRODUCTION

Ivlev (1947) describes the relationship between stock density, growth and production as one in which growth rate declines with increasing density, while production increases to some intermediate density and then declines with further density increases. Beverton & Holt (1957) have also examined some of the possible relationships between stock density, food supply, food consumption, and growth, for use in their theoretical models of exploited fish populations.

We have investigated the relationships between food consumption and growth of fish in aquaria for the purpose of estimating food consumption on the basis of growth of fish in laboratory stream communities (Davis & Warren, 1965; Brocksen, 1966) and in an experimental trout stream, Berry Creek (Warren et al, 1964). The aquarium experiments have been performed concurrently with the stream experiments or during appropriate seasons in different years with fish of similar ages and sizes and with temperature and light conditions varying seasonally and daily as in the streams. Mean growth rates found in the streams have been used to estimate mean consumption rates from curves like those presented earlier in this paper.

Communities of algae and herbivorous midge larvae were allowed to develop in 6 laboratory streams which were then stocked with different amounts and combinations of herbivorous snails, carnivorous stonefly naiads, sculpins, and trout. The midge larvae produced in the streams were the principal food resource of the carnivores. The growth and

production rates of the stocked animals have been estimated directly by recovering and weighing the animals.

Sculpin growth rate declines as their biomass increases (Fig. 8), unless the biomasses of other carnivores are sufficient to alter this relationship. Food consumption rate has also been found to decline with any considerable increase in biomass. Total food consumption increases with increasing sculpin biomass to a level at which depletion of the food resource results in a decline in total consumption. Production, being a function of both growth rate and biomass, increases with increasing biomass to a point at which the decline in food resource and increased utilization of food for maintaining the sculpins reduce the growth rate sufficiently for production to decline. In an experiment in which both sculpins and stonefly naiads were used (Table 7), the sculpins lost weight when stoneflies were present at both high and low sculpin biomasses. Gross efficiencies of food utilization for growth were low at high sculpin biomasses and were high at low sculpin biomasses when stoneflies were absent.

Brocksen (1966) showed that growth rates of cutthroat trout in

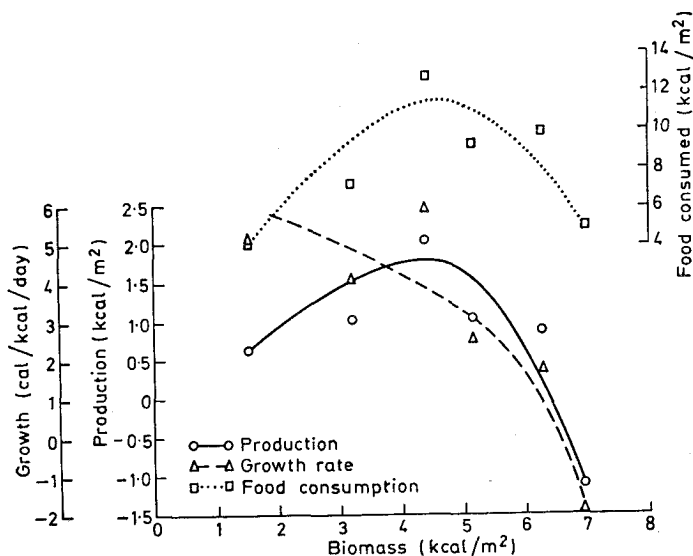


FIG. 8. Relationships between the biomass of yearling sculpins (*Cottus perplexus*) and their food consumption, growth, and production in a laboratory stream experiment conducted during the spring, 1961 (from Davis & Warren, 1965).

TABLE 7. Energy values in calories per square meter for groups of yearling sculpins, (*Cottus perplexus*) as influenced by intraspecific and interspecific competition for food organisms in laboratory streams during the fall, 1961, from 8 September to 8 November at temperatures ranging from 8.3 to 15.0° C (mean 11.6° C)

Stream number	Mean sculpin biomass	Mean stonefly biomass	Food consumed	Food not assimilated	Food assimilated	Growth	Respiration ¹	Gross efficiency %	Partial maintenance efficiency %	
									Net efficiency %	
1	4,230	6,480	1,080	194	886	-70	956	—	71.3	—
2	7,490	—	2,650	477	2,173	310	1,863	11.7	—	52.5
3	4,300	—	2,040	367	1,673	450	1,223	22.1	—	52.5
4	7,460	6,530	820	148	672	-89	761	—	70.4	-5
5	8,500	—	3,320	598	2,722	510	2,212	15.4	—	53.0
6	4,020	—	2,500	450	2,050	670	1,380	26.8	—	50.8

¹ See footnote to Table 2.

laboratory stream communities declined at high trout biomasses (Fig. 9), but that total food consumption increased to a high level and remained high with increasing biomass. Thus, the decline in production from the maximum in the case of the trout was due to increased maintenance costs and not to decline in the food resource. The trout in the laboratory streams feed almost entirely on drifting midge larvae, pupae, and adults and do not appear to reduce greatly the benthic populations producing this drift, as do the sculpins.

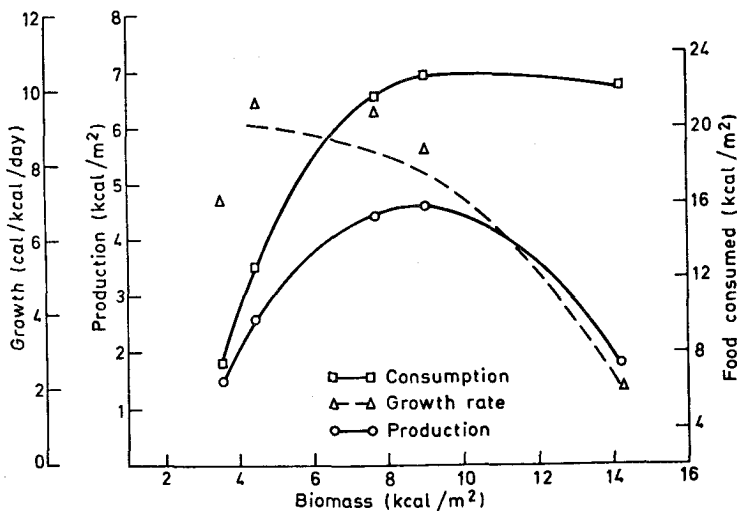


FIG. 9. Relationships between the biomass of yearling cutthroat trout (*Salmo clarki*) and their food consumption, growth, and production in a laboratory stream experiment conducted during the winter, 1964 (From Brocksen, 1966).

Data on the relationships between carnivore biomass, food consumption, and growth are difficult to obtain in nature, but some of the Berry Creek data (Table 8) suggest that the relationships are similar to those found in the laboratory streams. Berry Creek does not support such high trout biomasses as do the laboratory streams, probably because the food organisms in Berry Creek are utilized by many other carnivorous species. The lowest trout biomasses present in two unenriched sections of Berry Creek during 1961, 1962, and 1963 are nearly optimal for production, higher biomasses representing overstocking. Food consumption did not change greatly with increasing biomass, but growth rates declined because of increased utilization of food for

TABLE 8. Energy values in calories per square meter for yearling cutthroat trout (*Salmo clarki*) as influenced by intraspecific competition for food in two sections of Berry Creek during May, June, July, and August, 1961, 1962, and 1963

Stream section	Year	Mean trout biomass	Food consumed	Food not assimilated	Food assimilated	Growth	Respiration	Gross efficiency %	Net efficiency %
1	1961	5,120	8,380	1,215	7,165	-210	7,375	—	—
1	1962	4,630	9,460	1,372	8,088	490	7,598	5.2	35.3
1	1963	3,080	7,450	1,080	6,370	580	5,790	7.8	27.9
2	1961	3,720	6,060	879	5,181	10	5,171	0.2	—
2	1962	4,740	8,090	1,173	6,917	-70	6,987	—	—
2	1963	3,020	8,360	1,212	7,148	990	6,158	11.8	35.4

maintaining the stock. At the highest biomasses, the fish lost weight; gross efficiency of food utilization for growth increased with decreasing biomass.

Biomass level, then, may indicate the extent to which a species will utilize its food resource. The relationships between biomass and food consumption and growth rates may be of use in evaluating the level of intraspecific competition for food. However, these relationships cannot be expected to be the same if there are differences in food production or in the level of interspecific competition. Thus, the biomass of a species generally does not provide us with a measure of the opportunity an individual of that species has to obtain food.

FOOD DENSITY AND SCOPE FOR GROWTH

The idea that fish do not always have unlimited supplies of food in nature is implicit in experiments in which fish are fed restricted rations. The growth occurring at different rations in the laboratory is studied to obtain some insight into how growth might be influenced by food availability in nature. Unfortunately, it is difficult to relate ration levels in the laboratory to food availability in nature, there being no entirely satisfactory solution to the problem of determining the latter. Information on the production of prey species would be of some value, but because of the many different fates of prey, even this information leaves the question of availability unresolved.

One can reasonably conclude that it is the density of food in an animal's immediate surroundings that determines the amount of food the animal can obtain in a short period of time and the energy cost of obtaining this food. Density of a prey species is the outcome of its rate of production and the rates at which it is being consumed, being decomposed, and emigrating. Thus, changes in production, consumption, decomposition, or emigration should be reflected in changes in the density of the prey. Mean prey density over a period of time sufficiently long for measurable weight changes to occur in individual predators would appear to be one useful measure of food as an environmental factor influencing the scope for growth of the predator. Ivlev (1961a) has summarized his research on the effects of prey density as well as prey distribution and predator selectivity on the intensity of feeding of fish. Brocksen (1966) has demonstrated that sculpins and stonefly naiads influence their own food density and that of trout in laboratory streams, but that trout influence their own food density but not that of

the sculpins and stoneflies, apparently because of differences in feeding behaviour.

The food density which must be considered is the density which is appropriate in terms of the structure and feeding behaviour of the fish and the life cycles, structure, and behaviour of their food organisms. The appropriate food density for one life history stage or age group of fish may not be appropriate for another. Seasonal changes in feeding behaviour may necessitate the selection of different groups of food organisms during different seasons for density measurements if these measurements are to be appropriate. Measurements of the total biomass of benthic or planktonic organisms would not always be appropriate. It would depend on what the fish were eating.

Borutsky (1960) distinguishes between the forage resource, 'the total complex of autochthonous and allochthonous animal and vegetable organisms and their decomposition products present,' and the forage base, 'that part of the forage resources utilizable by the existent fish population.' He uses fish population in this context to be all the age groups of all the species present. By restricting the meaning of appropriate food density to the density of food available for a particular life history stage or age group of a particular species, we use this term in a more restricted sense than Borutsky uses forage base.

The absence of an air bladder in the sculpin limits it to a benthic existence, and its mouth is well adapted for removing food organisms from the substrate. In a spring experiment, the food consumption by yearling sculpins appears to have increased almost linearly with increases in the mean density of their food organisms in the benthos of laboratory streams (Fig. 10). The low food density at which the sculpins can just maintain their tissues is of considerable biological interest. It perhaps approximates the density at which sculpins could not be successful if it were the result of low production of food or intensive interspecific competition. Were this low density the result of intensive intraspecific competition, a decline in the stock would presumably occur.

The air bladder, mouth, and behaviour of trout adapt them for feeding in streams on drifting organisms. The extent to which trout remove food organisms from the substrate in natural streams is not known, but in the laboratory streams they feed almost entirely on organisms drifting in the current. In a winter experiment, Brocksen (1966) found that cutthroat trout in laboratory streams required a density of drifting food organisms slightly above 1 cal/m^3 to obtain a maintenance ration

and lost considerable weight at a lower density (Fig. 11). Consumption and growth rates increased most rapidly at densities near 1 cal/m^3 but continued to increase to the highest density of about 10 cal/m^3 .

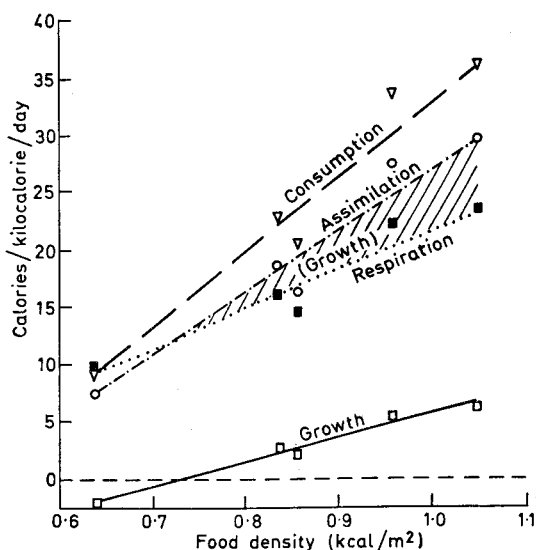


FIG. 10. Relationships between density of food organisms in the benthos and the food consumption, assimilation, respiration, and scope for growth of yearling sculpins (*Cottus perplexus*) determined in a laboratory stream experiment conducted during spring, 1961.

Determining the appropriate food density to measure in nature requires in most instances considerably more knowledge than we have of the feeding behaviour of fish. Detailed food habit information on the species and age groups under consideration is necessary, but the possibility of obtaining this has been demonstrated by many workers (Allen, 1942; Neill, 1938; Maitland, 1965). The growth rates of cutthroat trout in Berry Creek tend to be highest during periods when the densities not only of food organisms drifting in the current but of those in the benthic environment are highest, but the data are too variable to define clearly the relationships. Density of drifting food organisms must be some function of their density in the benthic environment, so relationships between appropriate benthos densities and the food consumption and growth of trout might be expected regardless of the feeding behaviour of the fish.

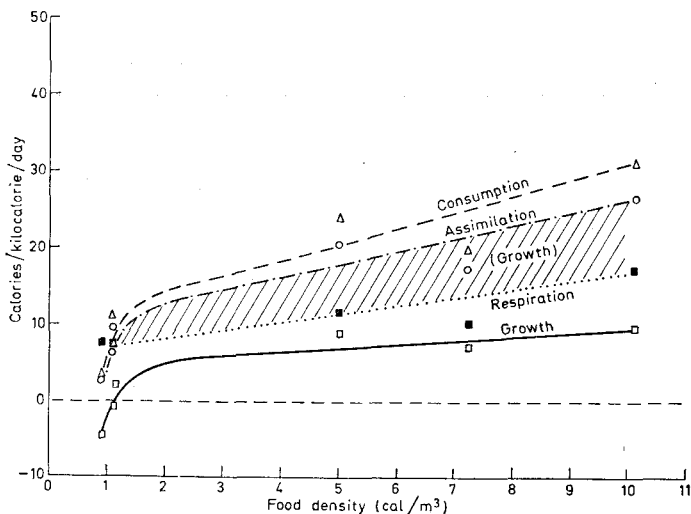


FIG. 11. Relationships between density of drifting food organisms and the food consumption, assimilation, respiration, and scope for growth of yearling cutthroat trout (*Salmo clarki*) determined in a laboratory stream experiment conducted during winter, 1964 (data from Brocksen, 1966).

It is difficult to find data in the literature which make possible examination of the relationships between food density and growth in nature. Most studies apparently have not been directed to such an end. Data of Allen (1951) suggest that a relationship existed between the density of food organisms in the benthos and the growth rate of brown trout, and data of Horton (1961) indicate a similar relationship between benthos density and total food consumption by brown trout (Fig. 12). Johnson (1961) has shown that, in a series of seven basins in the Babine and Nilkitkwa lake system in British Columbia, the mean weight of juvenile sockeye salmon in mid-October exhibits a high positive correlation with the mean dry weight of zooplankton per cubic meter from mid-June to mid-October, the period of the year when nearly all of the growth of age-group 0 occurs. The dry weight of zooplankton during this period exhibited a high negative correlation with the late August density of the fish in numbers. In a later paper, Johnson (1965), using his own data and the data of other workers from three other lakes, demonstrated that the mean weights of juvenile sockeye in mid-October when plotted against the mean density of zooplankton from mid-June to mid-October lie remarkably near the same line. The points from each

lake tend to be grouped, the size of the fish being smallest in the lakes having low plankton densities and largest in lakes having high densities. This suggests that the growth rate the sockeye can maintain at a given plankton density is more a characteristic of this salmon than of the particular lake ecosystem.

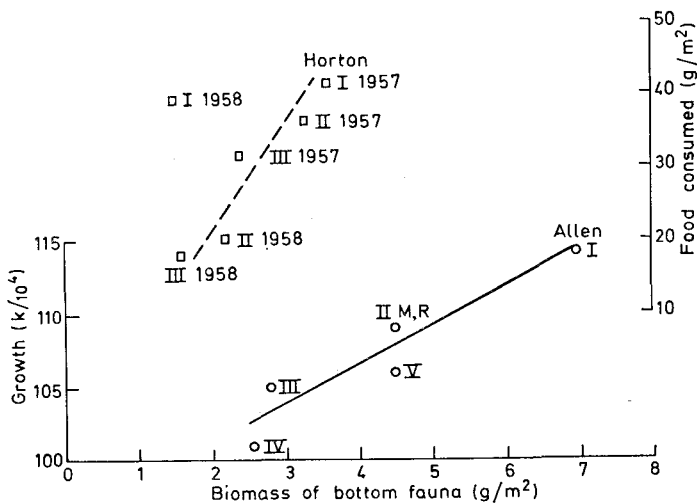


FIG. 12. Relationships between biomass of bottom fauna and growth rate of brown trout (*Salmo trutta*) in the Horokiwi Stream (from Table 66, p. 188, Allen, 1951) and food consumption of brown trout in a Dartmoor stream (from Table 12, p. 333, Horton, 1961).

Since publication of Lindeman's (1942) paper on the trophic dynamic aspect of ecology, the increased interest in the dynamics of production, consumption, and decomposition has resulted in questions of the biological importance of densities of animals being given little attention, except perhaps by the Russians (Ivlev, 1961a, b; Borutsky, 1960). Acknowledging the ultimate importance of these dynamic processes, we must also recognize that we cannot usually hope to measure the rates of production and utilization of more than a few species of prey organisms. Density of prey organisms is an outcome of these dynamic processes, an outcome of considerable importance in determining the scope for growth of the feeding fish.

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