

Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus**

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Abstract

Different criteria for the assessment of conversion efficiencies of fishes are briefly reviewed, and some important terms defined. In the euryhaline fishes *Megalops cyprinoides* and *Ophiocephalus striatus*, transformation of food has been studied as a function of body weight, using both protein and energy transfer criteria. The duration of the 28 experiments conducted varied from 15 to 30 days. Rates of food intake, digestion, absorption and conversion decrease with increasing body weight. Absorption efficiencies are about 97% for the protein fraction, and 91% for the total food consumed; they do not vary appreciably among the individuals of different body weights. Conversion efficiencies of the protein fraction and the total food consumed decrease from about 40% in 2 g individuals to about 15% in 150 g ones. In general, the relations show curvilinear trends, but in weight groups between 10 and 150 g, straight lines are obtained. The slopes of these lines differ in the two species tested. Such differences are related to the physiological state of the fishes and their growth potential. The inverse relation between body weight on the one hand, and food intake, absorption and conversion on the other, are attributed to aging. It is suggested that age affects these intermediate steps via the enzyme-complex of the digestive system. The b values obtained for the relation between body weight on the one hand, and metabolism, food intake and absorption on the other, do not correspond to the surface or weight proportion rule, but to an intermediary type of neither surface nor weight proportionality. As the values obtained are similar, it is concluded that there exists a direct and proportionate relation between metabolism, food intake and absorption. The respective values for the relation between body weight and conversion rate are low indicating that there is a direct, but nonproportionate relation between growth and metabolism.

Introduction

Although food and feeding habits of fishes have been studied by a number of workers, little attention has been given to the problem of transformation of food into fish tissue. Since food intake, digestion, absorption and conversion are successive steps involved in the transformation of food into animal tissue, modifying effects of environmental or endogenous factors will eventually be reflected in the efficiency of conversion (BRODY, 1945). In recent years the factors controlling food intake and digestion have been studied by HUNT (1960), and those controlling absorption and conversion by GERKING (1952, 1954, 1955), MENZEL (1959, 1960), KINNE (1960, 1962). The object of the present paper is to study all the successive steps in relation to body weight of the fishes tested.

* Dedicated to Professor C. P. GNANAMUTHU, Madras, on his 66th birthday, April 29, 1967.

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The status of our present knowledge on food intake and its close relation to growth and metabolism has been reviewed by WINBERG (1956), PALOHEIMO and DICKIE (1966). Literature pertaining to digestion has been summarised by VON BUDDENBROCK (1956), BARRINGTON (1957) and DARNELL and MELEROTTO (1962). RICKER (1946) and MENZEL (1959) have collected the available information on absorption. Very little is known on conversion; the authors, who have made contributions to this aspect, have used different criteria and hence their results are hardly comparable. A critical assessment of the criteria used by them is necessary. DAWES (1930 to 1931), SCHOLZ (1932), PENTELOW (1939), MOORE (1941), LAGLER and LATTA (1954), PRATHER (1951) and WILLIAMS (1959) have contributed to our knowledge of the conversion efficiency in *Pleuronectes*, *Esox*, *Salmo*, *Lepomis*, *Ambloplites* and *Micropterus*. They have estimated conversion efficiency by relating the wet weight gained to the wet weight of food consumed. The wide range of values obtained by them may be attributed to one or more of the following factors: Firstly, changes in water and fat content of fish, under different nutritional states, influence their wet weight (addition of 1 g fat is associated with 0.1 g water, whereas about 3 g water are incorporated with the addition of 1 g protein, BRODY, 1945, p 52); therefore the gross measurement of wet weight considered by previous workers may not have yielded valuable results. Secondly, these workers have approached the problem without taking body size into consideration. Lastly, DAWES (1930 to 1931), PENTELOW (1939), MOORE (1941) and BROWN (1946) have introduced the maintenance requirement factor in an attempt to measure the net conversion efficiency. The term net conversion efficiency refers to the increase in body weight of fish divided by the quantity of food consumed exclusive of maintenance requirements (BROWN, 1957). The observation of BROWN (1957) that fishes can adapt to different levels of feeding, obviate the importance of maintenance requirement and net conversion efficiency.

Improved methods of study were introduced by the investigators at the Cortland Hatchery (McCAY et al. 1927, 1931; TUNISON and McCAY, 1935; TUNISON, 1940). These workers have obtained their results by subjecting the experimental fish and their food to chemical analyses. Carbohydrates, fats and proteins consumed as food are finally converted into

body substance; the extent to which the body gains in these items during a period of experimental feeding will throw light on the efficiency with which it digests, absorbs and converts. The percentage of energy transformed from food into fish has been considered as a measure conversion efficiency by IVLEV (1939a, b, c, d); KINNE (1960, 1962) estimated the efficiency of the growth process ("gross efficiency") by relating the increase in weight of fish to the dry weight of food consumed. IVLEV's point of energy transfer has been found satisfactory and followed by a number of workers in the studies on bioenergetics of aquatic organisms (TEAL, 1957; RICHMAN, 1958; JOB, 1960). Later, GERKING (1952, 1954, 1955) stressed the importance of proteins for growth and estimated the nitrogen retained by the fish to measure conversion efficiency.

GERKING (1954) defines growth as synthesis of protoplasm and since the synthesis of protein is the most characteristic feature of growth, protein accumulation should be considered as a measure of conversion efficiency. Such a restriction of the study of "protein transfer" to the exclusion of other constituents, although justified in the light of GERKING's (1954) argument, may not be adequate by itself for two reasons. Firstly, both carbohydrates and fats are known to show protein sparing characteristics by the virtue of their caloric properties. Therefore, the differences in the caloric contents of the food consumed by the animal may determine the efficiency with which protein is converted (SWANSON, 1959). Secondly, in regard to the synthesis of fats and carbohydrates from proteins, the deaminated proteins can be converted into fats and/or carbohydrates (BALDWIN, 1952). Different dietary substances like fats, carbohydrates and proteins are in a labile and dynamic state in the body of an animal (SCHÖNHEIMER, 1942). The sum of the total effects of all these differences in the relative proportions of carbohydrates, fats and proteins converted for growth, will be expressed in caloric estimate. It is, therefore, necessary to supplement the index of "protein transfer" with the "energy transfer" index. Such an approach has been emphasized in conversion efficiency studies of laboratory animals by ALLISON (1959). MENZEL (1959, 1960) was the first to incorporate both indices of protein and energy transfers to estimate conversion efficiency of Bermuda reef fish *Epinephelus guttatus*.

Definitions

A number of terms have been used in different ways by previous workers. "Absorption" is being used here in the sense of GERKING (1952, p 362): "The term 'absorption efficiency' is equivalent to the term 'coefficient of digestibility' which is commonly used in standard physiology and nutrition work. Coefficient of digestibility is objected to on the grounds that it is always expressed in percent (not a coefficient) and that digestion does not necessarily result in absorption". "Conversion" is used by GERKING (1952) and

RICKER (1949) synonymously to "utilization". However, the absorbed food is not simply utilized but it is converted, for substances like protein have to be synthesized. To convey the idea of conversion of food into fish substance, the term "conversion" appears more suitable than "utilization". The term "transformation" is taken here to embrace the successive steps: food intake, digestion, absorption and conversion, through which food is transformed into fish substance (BRODY, 1945).

The terms "net" and "gross efficiencies" are used in the sense of RICHMAN (1958). The efficiency of food conversion may be expressed as percentage of food consumed or percentage of food absorbed. In the former case, it is called "gross efficiency" and the latter "net efficiency". These correspond to the "coefficient of first order or K_1 " and "coefficient of second order or K_2 ", respectively (IVLEV, 1945; RICKER, 1946). These terms are again objected to since K_1 and K_2 are expressed in percent and are not coefficients.

Material and Methods

Experimental fish: For the present study *Megalops cyprinoides* BROUSSONET (Elopidae) and *Ophiocephalus striatus* BLOCH (Ophiocephalidae) were chosen since they are easily procured, hardy, and of economic value. *M. cyprinoides* is a marine fish, occurring in the Indian Ocean; its distribution extends from the east coast of Africa to the Pacific Islands. After reaching a standard length of 3 to 4 cm, the offspring migrate to the back waters (east coast of South India), where they grow to a wet weight of about 400 g. They do not attain sexual maturity in these low salinity back waters but return to the sea (JOB and CHACKO, 1947), where they are said to reach a wet weight of about 600 g. They never return to the estuary, after apparently maturing in the sea.

Ophiocephalus striatus occurs in tropical inland waters. It attains maturity after 1 year at a wet weight of about 100 g and spawns at the beginning of the monsoon in June and July; the parents take care of their offspring.

More information on the bionomics of these two fish species have been reported by ALIKUNHI and RAO (1951) and ALIKUNHI (1953).

Three collections of *M. cyprinoides* of different body sizes were brought to the laboratory from the Cooum back waters of Madras (South India). Fingerlings of *O. striatus* were obtained twice from Chetpet Fish Farm, Madras. They were collected while swimming along with their parents. Five different collections were reared separately in large cement tanks; they were fed on chopped bits of fishes and prawns.

Food: Experimental fishes were fed live food, which is said to contain essential growth factors and organic nutrients (GERKING, 1955). The prawn *Metapenaeus monoceros* was used as live food which is known to form the natural food source of the fishes chosen for the experiment (GANAPATI, 1964; PANDIAN,

1966). Prawns were collected from the Cooum back waters and reared in the laboratory feeding them chopped pieces of small marine fishes. They were kept in dilute sea water of 20‰ salinity as recommended by REDDY (1963).

Temperature: All experiments were performed at a temperature of $28^{\circ} \pm 1.5^{\circ}\text{C}$.

Experiments were conducted in aquaria with a capacity of about 50 l. The aquaria were filled with tap water, which was aerated throughout the experiments. The fish were fed until saturation once a day. Prawns were washed free of sand, and the adhering water removed; they were then cut dorsally between cephalothorax and abdomen in order to immobilize them and weighed subsequently to the nearest 5 mg. The feeding period lasted for about 10 min; thereafter all prawns that had not been consumed were removed, dried and weighed; the weight was subtracted from the total amount offered, thus obtaining the amount of food consumed. At the end of a period of 7 or 10 days, the fishes were transferred into new aquaria containing fresh water which had been aerated previously for at least 8 h. The faecal matter accumulated during the period was collected for chemical analyses. The water in which fish had been kept for 7 or 10 days was transferred to huge cylindrical jars which were left undisturbed for a day. The faecal matter which had settled on the bottom was collected by decanting; the decanted water was then filtered through a glass wool pad fitted into the cup of a Büchner funnel kept under suction. The pad was weighed before and after filtering the water, to give the weight of the particulate matter suspended in the water (GERKING, 1955).

Analyses: Chemical analyses were performed on material dried in an oven at 80°C for 24 h; the temperature was then raised to 105°C until weight constancy. The entire dry fish was minced and ground to fine powder in a porcelain mortar and dried for an hour or longer before being packed in air-tight bottles; it was then stored in a desiccator. From such homogenized, preserved samples, aliquots were taken for the estimation of total nitrogen and caloric contents. All samples used were weighed in an analytical balance with an accuracy of ± 0.1 mg.

The total nitrogen content of the sample was determined by employing the microkjeldahl method, followed by the standard procedure described by STEYERMARK (1951). 30 to 40 mg of the sample were digested with 0.5 ml of N free sulphuric acid and digestion mixture at 360°C for 3 to 4 h. The content was then distilled in a Pregl-Parnus-Wagner design microkjeldahl apparatus, with 5 ml of sodium hydroxide-sodium thiosulphate mixture, and ammonia was collected with 5 ml of 4% boric acid. The quantity of ammonia was estimated by titrating the boric acid against 0.05 N hydrochloric acid. All samples were run in duplicate, and appropriate blank values were obtained.

Caloric content of the sample was determined by the moist combustion method originally described by IVLEV (1935) and later used by TEAL (1957) and SITARAMAIAH (1961). The amount of oxygen required to oxidize the fractions of the sample material was determined using a strong oxidizing agent. The caloric content of the sample was computed by applying the oxy-caloric coefficient which equals 3.38 K. Cal/g of oxygen required. The amount of oxygen required for the oxidation of the sample was estimated as follows: a mixture of N/10 potassium dichromate and N/10 silver dichromate was prepared in concentrated sulphuric acid in the ratio of 3:1. The solution was heated in an oven at 140° to 150°C for 1 h and then cooled. From this stock solution, 40 to 50 ml was taken in a round bottomed flask and 20 to 30 mg of the sample added. The flask was heated in a water bath for 2 h. Then the content of the flask was transferred to an Erlenmeyer flask and diluted 3 or 4 times with distilled water, cooled and, after adding 5 ml orthophosphoric acid, titrated against N/10 aqueous potassium dichromate solution according to KNOP (1924). Since it is known that 1 ml of N/10 potassium dichromate solution is equivalent to 0.8 mg of oxygen, from the titre value of N/10 potassium dichromate, the amount of oxygen required to oxidize the sample can be calculated. In such a calculation, a correction has been applied for the amount of protein not oxidized (IVLEV, 1935).

Experimental Design

The experimental design adopted in the present study was the "sacrifice method" of MAXNARD and LOOSLI (1962). This procedure was first applied to fishes by GERKING (1952, 1955) and later also by MENZEL (1960). The fishes chosen for the experiment were starved for 3 days in order to empty their alimentary canals. They were kept in separate aquaria and fed for a definite period as described previously. If the test individuals weighed less than 2 g, 5 specimens were kept together in order to secure sufficient amount of faeces for subsequent nitrogen and caloric determinations. The quantity of nitrogen retained during the period of feeding was estimated by measuring the dry weight and nitrogen content of the fish at the beginning and at the end of the experiment. A group of sample fish of similar weight and nutritional state represented the experimental group at the commencement of feeding. Conversion efficiency of protein was calculated by relating the quantity of nitrogen retained to the quantity of nitrogen absorbed. For the estimation of energy contained in the food converted, the same procedure was followed as described above for nitrogen.

The same individuals were used to collect data on food intake, absorption and conversion. For the estimation of digestion, a different set of individuals was used; the respective experimental procedure is described in the relevant section.

Results

Food intake

In general, *M. cyprinoides* immediately consumed the food offered, showing a distinct change in behaviour when satisfied. Its behaviour was very similar to the one of *Cyprinodon macularius* observed by KINNE (1960). *O. striatus* reacted more slowly; the food had to be left in the aquaria for a period of 10 min in order to satisfy their daily requirements. *M. cyprinoides* of less than 2 g body weight did not feed on whole prawn; they were fed pieces of prawn flesh. The quantity of food consumed varied considerably in both species, the range of variation being wider in *O. striatus* than in *M. cyprinoides*. However, a certain rhythm could be observed: frequently a day of intensive feeding was followed by a day of low feeding. Such day-to-day fluctuations in food intake have also been observed in *Apomotis* and *Heliperca* (MOORE, 1941). On averaging the quantity of food consumed during a definite period, a certain general trend became apparent. The average daily ration was expressed in percentage of body weight of fish, following RICKER (1946).

Feeding rate was fastest in fish weighing less than 2 g. It was 9.2% body weight per day in *M. cyprinoides* of 1.3 g body weight and 7.2% body weight per day in *O. striatus* of 1.9 g body weight. It fell rapidly to about 5.8% body weight per day in the former and to 3.1% body weight per day in one of the latter weighing about 13 g; it decreased thereafter gradually to less than 1.8% body weight per day in individuals of 149.6 g body weight and 123.8 g body weight respectively. When plotting the data, it appeared that the inverse relation was linear for individuals of 10 to 150 g; this straight line relation is altered below 10 g body weight (Fig. 1). Hence the regression lines for the feeding rate-weight relationship have been worked out from the basic data obtained for the 10 to 150 g weight range. The formula $Y = a + bx$ has been applied (FISHER, 1948); where Y is feeding rate, x body weight, b regression coefficient, and a the point where the regression intercepts Y (at 10 g). The regression coefficients were $Y = 3.949 - 0.0158x$ for *M. cyprinoides* and $Y = 2.897 - 0.0098x$ for *O. striatus*, i. e. they showed that for 1 g increase in body weight, the decrease in feeding rate was 0.0158% body weight per day for the former, and 0.0098% body weight per day for the latter.

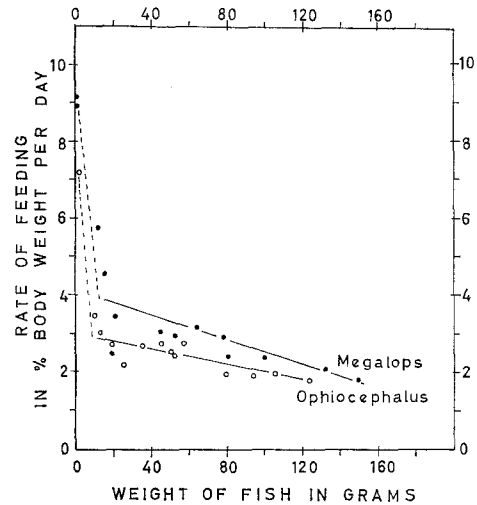


Fig. 1. Relation between feeding rate and body weight in *Megalops cyprinoides* and *Ophiocephalus striatus*. Regressions were calculated for fishes of 10 to 150 g; lines for the data obtained on individuals of less than 10 g were eye-fitted

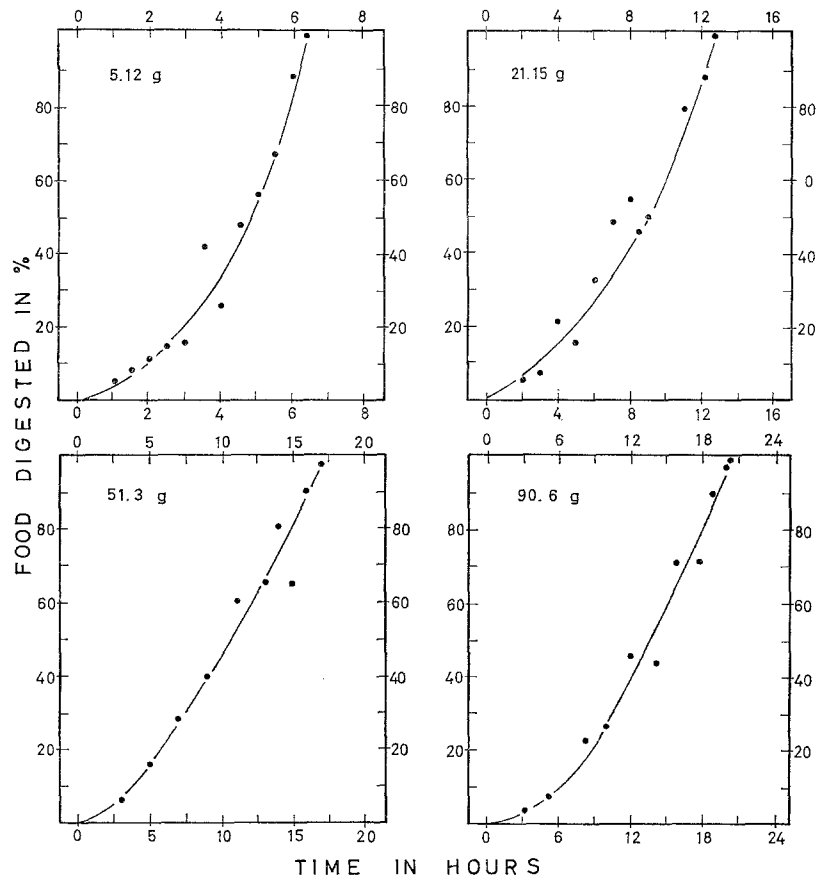


Fig. 2. Percentage of food digested by *Megalops cyprinoides* as a function of time

Digestion

In order to study the relation between weight and digestion rate, four weight groups of *M. cyprinoides* were chosen, namely 5.1 g, 21.2 g, 51.3 g, and 90.6 g.

Each group consisted of 10 to 12 individuals. The fishes were starved for a period of two days in order to clear their stomachs. They were kept in individual aquaria and fed at the same time, each fish receiving a ration equivalent to 2% of its body weight. At intervals of 1 to 3 h of feeding, one fish was killed and the amount of food digested estimated. Complete stomach clearance was used as criterion for the completion of digestion (HUNT, 1960).

In the four weight groups, the amount of food digested during the different intervals varying from

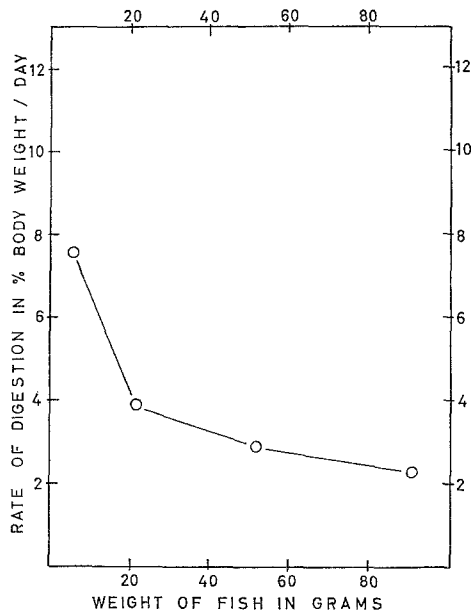


Fig. 3. Relation between body weight of *Megalops cyprinoides* and digestion rate

1 to 20.5 h is expressed as a percentage of food consumed. At the beginning digestion was slow; later on, it became faster, the percentage of food digested being a direct function of time. The same has been observed in *Ocyurus* and *Haemulon* by PIECE (1936). Among the four weight groups, duration of gastric digestion varied from 6.5 to 20.5 h (Fig. 2). The average amount of food digested during 1 h was calculated and expressed as a percentage of body weight. Digestion rate was very high (0.317% body weight/h) in the 5.1 g individual. It fell rapidly to 0.161% body weight per hour in those of 21.5 g and then more gradually to 0.095% body weight per hour in those of 90.6 g. From these values, digestion rates per day have been calculated and plotted against weight (Fig. 3). The trend obtained is curvilinear and parallel to the one obtained for the weight-feeding rate relation (Fig. 4). A faster digestion rate among smaller individuals results in higher feeding rates, while slower digestion rates of larger fish, delaying gastric clearance, decrease the appetite.

Absorption

Absorption efficiency

Absorption efficiency of protein was estimated for each fish relating the quantity of total nitrogen absorbed to the quantity of total nitrogen consumed (GERKING, 1952). The total nitrogen absorbed was determined by subtracting the total nitrogen content of the faeces evacuated from that contained in the food consumed. The values obtained varied from 92.04% to 98.28% for *M. cyprinoides* and from 92.79% to 96.74% for *O. striatus*. These values include a fraction of nonprotein nitrogen. There are two main sources of such nonprotein: (1) amino acids, amides and ammonium salts and (2) chitin. The former made up as much as 3.6% to 4.1% of nitrogen. Nonprotein nitrogen compounds occurring in food are important in nutrition, either as intermediary and/or final products of protein metabolism, or as essential and active constituents of various tissues and secretions (MAYNARD and LOOSLI, 1962). In view of the above mentioned considerations, this fraction of nonprotein nitrogen is considered along with protein nitrogen. Chitin of arthropods is a nonprotein material containing nitrogen (RICHARDS, 1951). As test fishes were fed with the prawn *Metapenaeus monoceros*, chitin formed a fraction of the food consumed. The faeces of the fishes, on inspection, showed flakes of cuticle, indicating that the chitin was not digestible. MANN (1948), and GERKING (1952) reported that the chitin was neither digested by the carp nor by *Lepomis*.

The chitin content of the prawn *M. monoceros* was estimated according to the methods used by FRAENKEL and RUDALL (1940), and HACKMANN (1960). The cuticle was decalcified overnight with 10% acetic acid; fats and pigments were removed via extraction with ether and ethanol. Finally, the cuticular protein was removed by a 4 day extraction with 5% potassium hydroxide at 105 °C. The chitin bits were collected and washed repeatedly in distilled water and ethanol, 3 times with ether and, finally, dried in a vacuum desiccator. The chitin content was expressed as percentage of the dry weight of the prawn. The average chitinous portion of the integument was 5.06% ($\pm 0.72\%$) of the dry weight of the prawn. Chitin is known to contain 6.9% of nitrogen (RICHARDS, 1951).

From the data obtained, the quantity of chitinous nitrogen contained in the food was calculated. As chitin is not digestible, the nitrogen content of the chitin consumed was subtracted from the total nitrogen consumed. Similarly, to estimate the protein nitrogen evacuated, the nitrogen content of chitin was subtracted from the faecal nitrogen content, as has been done by GERKING (1952). The nitrogen contained in the faeces, considered here as true protein nitrogen, may arise from two sources, namely, (1) undigested and unabsorbed protein and (2) metabolic faecal nitrogen. The latter is known to consist of substances such as residues of the bile duct and digestive enzymes,

epithelial cells abraded from the alimentary canal by food passing through it, and bacterial residues. This fraction of metabolic faecal protein is usually small—about 0.1 g for 100 g dry weight of food consumed in rats, pigs and men, and 0.5 g 100 g dry weight of food in ruminants—and it is difficult to estimate accurately (MAYNARD and LOOSLI, 1962). Therefore, the entire protein nitrogen content of the faeces is treated under the unabsorbable protein nitrogen, following previous authors such as GERKING (1952); his formula has been used to estimate the efficiency of protein absorption.

The values obtained for protein absorption vary from 94.56% to 99.24% in *M. cyprinoides*, and from

in the chitin of the food as well as of the faeces was estimated and subtracted to obtain the net energy content of food and faeces. Efficiency of food absorption varied from 86.44% to 97.68% for *M. cyprinoides*, and from 86.58% to 93.30% for *O. striatus*. Closely comparable values have been reported for carp (89%) by IVLEV (1939d) and *Epinephelus* (96%) by MENZEL (1960). A reinterpretation of JOB's (1960) data for *Salvelinus fontinalis* gives 90.33% for food absorption efficiency. The present data are closer to those of IVLEV (1939d) and JOB (1960) than to those of MENZEL (1960). It can be seen from Figs. 4 and 5 that the efficiency to absorb food remains more or less

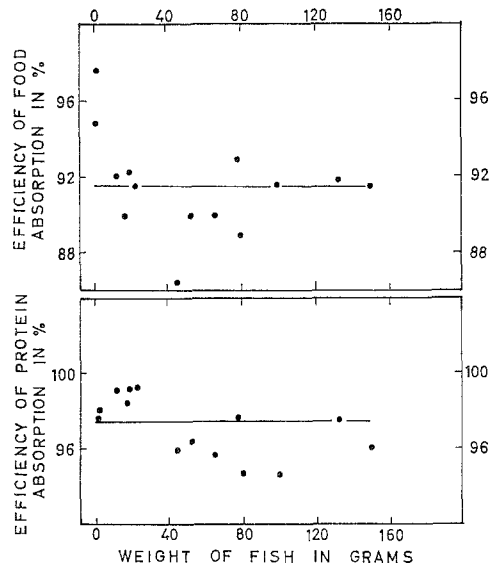


Fig. 4. Food (top) and protein (bottom) absorption efficiencies in *Megalops cyprinoides* of different body weights

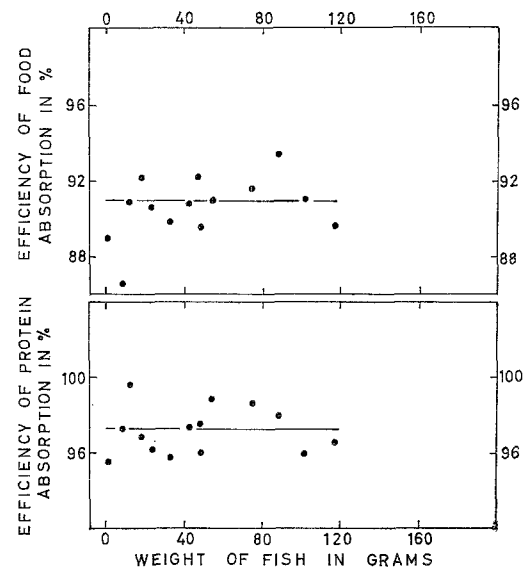


Fig. 5. Food (top) and protein (bottom) absorption efficiencies in *Ophiocephalus striatus* of different body weights

95.57% to 99.63% in *O. striatus*. A few higher values in *M. cyprinoides* were due to subjective error; at that time the technique of filtering water was not perfect and, as the fishes happened to be small, the errors were magnified. In general, the values are in good accordance with those previously reported. TUNISON et al. (1942) have shown, for instance, that trout absorbed 95% of the total protein consumed. It can further be seen from Figs. 4 and 5 that there was no appreciable difference in efficiency among individuals of different weights. This result supports previous findings by GERKING (1952) and MENZEL (1960). GERKING (1952, 1954), using three species of the genus *Lepomis*, and MENZEL (1960), using *Epinephelus guttatus*, reported that efficiency of protein absorption was high (about 96% to 98%) and remained more or less the same in fishes of different weights (ranging from 7 to 600 g).

The foregoing account on absorption is limited to protein. Total food absorption efficiency has also been determined using energy transfer criteria (IVLEV, 1939). As has already been pointed out, prawn chitin is not digestible; therefore, the quantity of energy contained

equal in individuals of different weights. MENZEL (1960) showed that there was no appreciable difference in food absorption efficiency among *Epinephelus guttatus* of 184 g to 600 g. Therefore, it can be said that the efficiency with which nutrient matter is absorbed, does not vary appreciably among individuals of different weights or species.

The average efficiency of absorption was 97.2% ($\pm 1.6\%$) for protein and 91.5% ($\pm 2.6\%$) for total food in *M. cyprinoides* and 97.1% ($\pm 1.3\%$) for protein and 90.6% ($\pm 1.6\%$) for total food in *O. striatus*. These differences between the efficiencies of food and protein absorption suggest that different components of food vary in regard to the efficiency with which they are absorbed. There is some support regarding this suggestion in previous work: absorption efficiency is 80% for fat (TUNISON and McCAY, 1935; MENZEL, 1960) and 63% to 79% for carbohydrate (MENZEL, 1959). It is very likely that such low fat absorption efficiency affects the total food absorption efficiency of *M. cyprinoides* and *O. striatus*. Protein is most easily digested and absorbed; the efficiency of absorption of protein is about 98%.

Absorption rate

Feeding rates in fishes studied in the present investigation were 7 to 9% body weight per day for 2 g individuals; it decreased to about 2% body weight per day for the individuals of about 150 g (Fig. 1). Irrespective of these differences in feeding rate, efficiency of absorption remained constant at about 97% for protein and 91% for food. Relating these

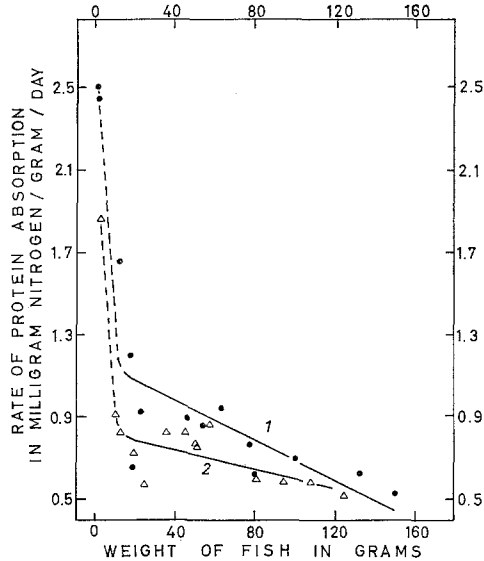


Fig. 6. Relation between protein nitrogen absorption rate and body weight of (1) *Megalops cyprinoides* ($Y = 1.121 - 0.0048x$) and (2) *Ophiocephalus striatus* ($Y = 0.864 - 0.00216x$). Regressions were calculated for fishes of 10 to 150 g

results, one is led to think that the rates at which nutrient matter undergoes digestion and absorption, are faster in smaller individuals than in larger ones. KENNE (1960) touched on this aspect by distinguishing between rates and efficiencies of absorption and conversion. Mammalian physiologists have measured and expressed absorption rate as mg sucrose/sq. cm area of intestine per hour (GREIG, 1955). However, such exact measurements concerning the surface area of the alimentary canal are lacking in fishes. SYAZUKI (1956), in an attempt to assess absorption rates in carp fry fed with food containing different levels of protein, expressed absorption rates in mg protein N per g (body weight of fish) per day. I have followed his procedure in assessing rates of food and protein absorption. From the quantity of protein nitrogen and food absorbed absorption rate was calculated as follows:

$$\left. \begin{array}{l} \text{Rate of protein} \\ \text{absorption} \end{array} \right\} = \frac{\text{Protein N absorbed in mg/day}}{\text{Weight of fish in g}}$$

$$\left. \begin{array}{l} \text{Rate of food} \\ \text{absorption} \end{array} \right\} = \frac{\text{Food absorbed in Cal/day}}{\text{Weight of fish in g}}$$

Protein absorption rate was 2.5 mg N per g per day for 1.38 g *M. cyprinoides*; it fell rapidly to 0.93 mg N per g per day in fish of 22.4 g and thereafter decreased gradually to 0.54 mg N per g per day for a fish of

149.6 g (Fig. 6). Similarly, for *O. striatus* it decreased markedly from 1.86 mg N per g per day to 0.82 mg N per g per day in 35.1 g and then gradually to 0.52 mg N per g per day for 123.8 g (Fig. 6). Similar trends have been obtained for food absorption rates. These decrease from 0.75 Cal per g per day to 0.018 Cal per g per day in *M. cyprinoides* (Fig. 7), and from 0.055 Cal per g per day to 0.015 Cal per g per day in *O. striatus* (Fig. 7).

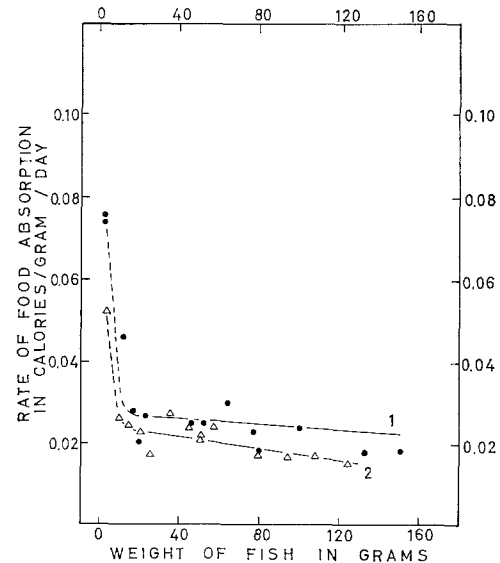


Fig. 7. Relation between food absorption rate and body weight of (1) *Megalops cyprinoides* ($Y = 0.0306 - 0.000103x$) and (2) *Ophiocephalus striatus* ($Y = 0.0234 - 0.0000655x$). Regressions were calculated for individuals of 10 to 150 g.

The quantity of nutrient matter absorbed and made available for conversion decreased with increasing body weight. The trend obtained for weight-absorption rate is similar to the one obtained for the weight-feeding rate relation. It should be noted that the absorption rate of *M. cyprinoides* was slightly higher than that of *O. striatus* of comparable weight. In a fish of 50 g body weight, absorption rate was 0.87 mg N per g per day for protein, and 0.025 Cal per g per day for total food, in the former; it was 0.75 mg N per g per day for protein, and 0.021 Cal per g per day for total food, in the latter. The difference is due to the low feeding potentiality of *O. striatus*. Feeding rates were 2.9 and 2.5% body weight per day respectively for the above mentioned individuals. The absorption rate is then a direct function of feeding rate.

Conversion

Conversion efficiency

It has been shown that as much as 97% protein and 91% energy contained in the food consumed are absorbed. The absorbed protein may be used for (1) the synthesis of new tissue protein and nitrogen containing tissue constituents, (2) the replacement of tissue and products used in the metabolic processes, and (3) for oxidative metabolism (MAYNARD and LOOSLI, 1962). Since the present study is concerned

with the amount of nutrient matter converted for growth, the quantity of protein nitrogen used for the latter has not been directly determined. But this quantity is derived by subtracting the quantity of protein nitrogen converted from that absorbed, and is treated as residual N (Tab. 1 and 2). The total nitrogen retained by the individuals was estimated as described on page 18. From the data obtained, the

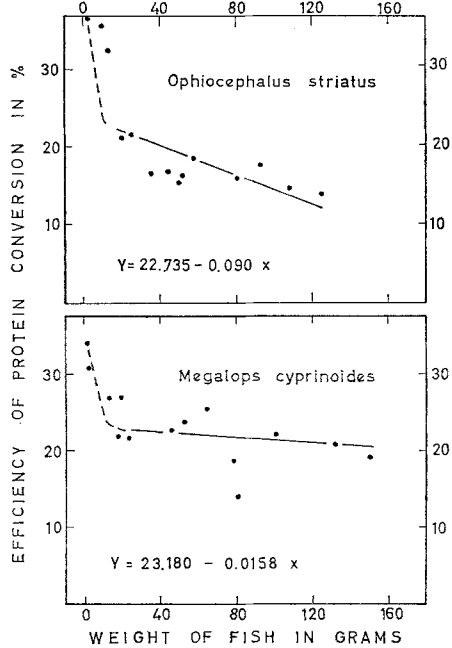


Fig. 8. Relation between protein conversion efficiency and body weight of *Megalops cyprinoides* and *Ophiocephalus striatus*

quantity of protein nitrogen retained per day was calculated and is presented in the Tab. 1 and 2 for *M. cyprinoides* and *O. striatus*, respectively. This amount of protein nitrogen cannot strictly be considered to represent the quantity of nitrogen used for the synthesis of protein; since, of the protein nitrogen retained, a certain quantity is generally said to be pooled in the circulating body fluids, as a nitrogen reservoir (HOUSSAY et al. 1951; BEST and TAYLOR, 1951). A nitrogen reservoir has not directly been demonstrated for fishes. But starvation experiments conducted on trout by MORQUILIS (1919) hinted that there might be a fair quantity of such nitrogen in the blood. Lack of precise information on this aspect may probably be due to the difficulties encountered in the estimation of small quantities. Therefore, the nitrogen retained by the fish is treated as nitrogen used for the synthesis of protein.

Efficiency of protein is calculated relating the quantity of protein nitrogen retained to the quantity of protein nitrogen absorbed. The values obtained are plotted against body weight (Fig. 8). Protein conversion efficiency decreases with increasing body weight. The efficiency was 34.2% for 1.4 g *M. cyprinoides*; it decreased rapidly to 22.4% for a 17.2 g individual,

and, later, gradually to 19.5% for a 149.6 g individual. The curvilinear trend obtained recalls the one obtained for *Lepomis cyanellus* (GERKING, 1952). Similarly, the efficiency decreased from 36.1% for fish of 1.9 g to 21.3% for a 24.6 g individual and then gradually to 14.0% for a 123.8 g *O. striatus*. Regressions were calculated from the basic data obtained for protein conversion efficiency of individuals ranging from 10 to

Table 1. Total nitrogen balance of *Megalops cyprinoides* fed with prawn *Metapenaeus monoceros* during 15 to 30 day-aquarium experiments. Each value represents the result of a single experiment on one individual

Weight (g)	N consumed (mg/day)	N in faeces (mg/day)	N absorbed (mg/day)	N converted (mg/day)	N residual (mg/day)
1.38	3.53	0.08	3.45	1.18	2.27
1.78	4.42	0.08	4.34	1.34	3.00
12.62	19.86	0.17	19.69	5.33	14.36
17.20	21.21	0.34	20.87	4.68	16.19
18.90	12.53	0.10	12.43	3.39	9.04
22.40	20.89	0.17	20.72	4.59	16.13
45.50	42.81	1.78	41.03	9.35	31.69
52.80	47.73	1.71	46.02	11.07	34.96
63.50	63.20	2.70	60.50	15.55	44.95
77.70	61.30	1.44	59.86	11.44	48.42
80.20	52.11	1.70	50.41	7.10	43.31
100.00	74.61	4.03	70.58	15.83	54.75
132.50	86.36	1.84	84.52	18.02	66.50
149.60	83.89	3.26	80.63	15.70	64.93

Table 2. Total nitrogen balance of *Ophiocephalus striatus* fed with prawn *Metapenaeus monoceros* during 15 to 22 day-aquarium experiments. Each value represents the result of a single experiment on one individual

Weight (g)	N consumed (mg/day)	N in faeces (mg/day)	N absorbed (mg/day)	N converted (mg/day)	N residual (mg/day)
1.86	3.62	0.16	3.46	1.25	2.21
9.92	9.29	0.24	9.05	3.20	5.85
13.09	10.80	0.04	10.76	3.48	7.28
19.65	14.52	0.46	14.06	2.96	11.10
24.63	14.45	0.54	13.91	2.96	10.95
35.09	29.92	1.25	28.67	4.75	23.92
45.15	38.68	1.03	37.65	6.24	31.41
50.70	40.22	0.97	39.25	6.10	33.15
51.30	40.02	1.58	38.44	6.25	32.19
57.00	49.92	0.59	49.33	9.16	40.17
79.80	48.32	0.63	47.69	7.68	40.01
93.80	56.07	1.17	54.90	9.70	45.20
107.50	66.02	2.68	63.34	9.36	53.90
123.80	67.56	2.97	64.59	9.06	55.53

150 g body weight used (FISHER 1948). The regression coefficients obtained indicate that, per g weight increase, the decrease in protein conversion efficiency is 0.016% in *M. cyprinoides* and 0.09% in *O. striatus* (Fig. 8).

The values obtained using the "protein transfer" have to be supplemented with that of "energy transfer". The quantity of energy converted was estimated by determining the caloric content of the experimental fish at the beginning and end of the experiment. The caloric values obtained for *M. cyprinoides* and

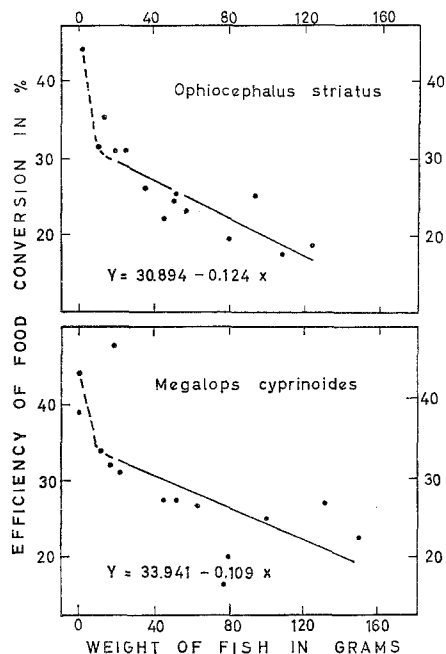


Fig. 9. Relation between food conversion efficiency and body weight of *Megalops cyprinoides* and *Ophiocephalus striatus*

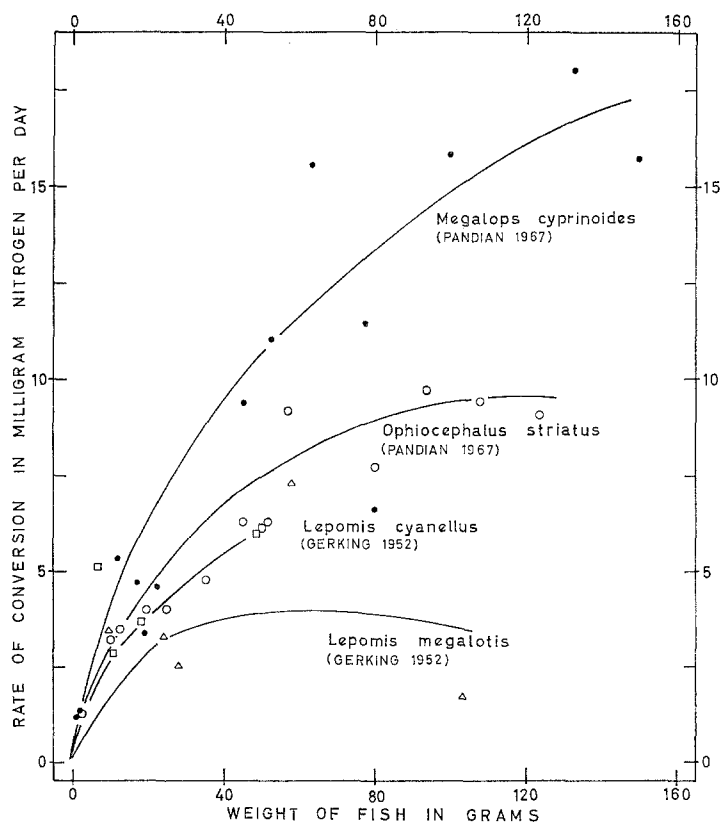


Fig. 10. Relation between protein conversion rate and body weight of the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. The data of GERKING (1952) for the fishes *Lepomis cyanellus* and *L. megalotis* have also been plotted for comparison

O. striatus varied from 4.1 to 4.8 Cal per g dry weight and centered around 4.5 Cal per g dry weight. This value is close to that obtained for minnows by JOB (1960). JOB gives a value of 86.3 Cal per 100 g (wet weight); on the basis of 20% dry weight (VINOGRADOV, 1953) minnows have 4.3 Cal per g dry weight. SCHMITZ (1950) obtained higher values for salmonid fishes; this may be due to their the high percentage of fat. Efficiency to convert food decreased with increasing body weight (Fig. 9). It was 43.7% in a 1.9 g individuals and fell rapidly to 30.8% in a 19.7 g individual, and then gradually to 18.5% in a 123.8 g *O. striatus*. Smaller individuals of *M. cyprinoides* showed more or less similar values; the efficiency was 44.2% and 32.2% for a 1.4 g and a 17.2 g individual, respectively, but larger individuals showed relatively higher efficiencies than in *O. striatus* (e. g., 22.2% efficiency in a 149.6 g *M. cyprinoides* as compared to 18.5% in a 123.8 g *O. striatus*). The regression coefficients show a decrease in food conversion efficiency of 0.109% per g increase in body weight for *M. cyprinoides*; the corresponding value for *O. striatus* is 0.124%.

Conversion rate

The total amount of protein nitrogen and energy converted per day by individuals of *M. cyprinoides* and *O. striatus* is given in Tab. 1, 2, 3 and 4 (5th column) respectively. In addition to the differences observed in conversion efficiency among the two species, it can be seen that there are differences in the rates at which they convert protein or energy for growth. For instance, considering a 13 g individual, the rate of conversion is 5.3 mg N per day for protein and 0.20 Cal per day for food in *M. cyprinoides* and 3.5 mg N per day for protein and 0.11 Cal per day for food in *O. striatus*. This difference is also maintained throughout other body weight ranges (Figs. 10 and 11). These differences and their bearing on growth will be considered in the light of previous work in the discussion.

Quantitative relation of nutritive metabolism to body weight

Both in physiological and ecological studies, the relation between nutritive metabolism and body weight is of considerable importance. It is usually treated in terms of the surface rule established for mammals by RUBNER. VON BERTALANFFY (1941, 1951) distinguishes three major types of animal. The relation between rates of animal metabolism and body

weight can be expressed by the equation, $y = bx^a$, where y is metabolic rate or body surface area, x body weight, and a and b are the constants. This is a special case of the so-called allometric formula (HUXLEY, 1932). If metabolic rate is plotted against body weight double logarithmically, we obtain a straight line, the slope of which indicates the constant b . If b equals $2/3$ or 0.67, metabolism follows the surface law. If b equals 1 or the slope is 45° , metabolism is proportional to weight, and if b equals > 0.67 and is < 1 , metabolic rate represents an intermediary case (VON BERTALANFFY, 1951).

To evaluate my data in the light of this hypothesis, the quantities of food consumed, absorbed and converted, as well as the total amount of food (energy) expended on metabolism (all expressed in energy units; see Tab. 3 and 4, column 6) were related to the body weight of the fishes studied. The data of Figs. 12 and 13 are presented in a double logarithmic grid, illustrating the relation of food consumption, absorption,

has not been estimated directly, but derived by subtracting the quantity of energy converted for growth from that absorbed. This energy is composed of the energy loss through excretion plus that spent on metabolism (JOB, 1960). The energy expended for these two processes has not been estimated separately,

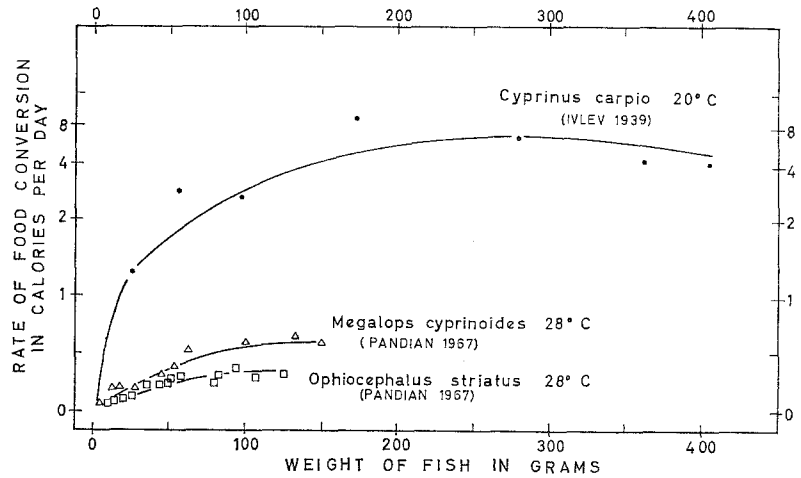


Fig. 11. Food conversion rate in relation to body weight of the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. The data of IVLEV (1939d) for the carp *Cyprinus carpio* have also been plotted for comparison

Table 3. Total energy balance of *Megalops cyprinoides* fed with prawn *Metapenaeus monoceros* during 15 to 30 day-aquarium experiments. Each value represents the result of a single experiment on one individual

Weight (g)	Energy consumed (Cal/day)	Energy in faeces (Cal/day)	Energy absorbed (Cal/day)	Energy converted (Cal/day)	Energy residual (Cal/day)
1.38	0.110	0.006	0.104	0.046	0.058
1.78	0.138	0.003	0.135	0.053	0.082
12.62	0.633	0.049	0.584	0.196	0.388
17.20	0.675	0.070	0.605	0.195	0.410
18.90	0.400	0.031	0.369	0.177	0.192
22.40	0.665	0.056	0.609	0.190	0.509
45.50	1.316	0.179	1.137	0.308	0.829
52.80	1.466	0.147	1.319	0.362	0.957
63.50	2.206	0.224	1.982	0.526	1.456
77.70	1.952	0.138	1.814	0.297	1.517
80.20	1.660	0.185	1.475	0.293	1.182
100.00	2.604	0.219	2.385	0.588	1.795
132.50	2.654	0.215	2.438	0.654	1.784
149.60	2.929	0.249	2.680	0.596	2.083

Table 4. Total energy balance of *Ophiocephalus striatus* fed with prawn *Metapenaeus monoceros* during 15 to 22 day-aquarium experiments. Each value represents the result of a single experiment on one individual

Weight (g)	Energy consumed (Cal/day)	Energy in faeces (Cal/day)	Energy absorbed (Cal/day)	Energy converted (Cal/day)	Energy residual (Cal/day)
1.86	0.115	0.012	0.103	0.045	0.058
9.92	0.296	0.040	0.256	0.081	0.175
13.09	0.344	0.032	0.312	0.110	0.202
19.65	0.462	0.036	0.426	0.131	0.295
24.63	0.460	0.043	0.417	0.128	0.289
35.09	1.044	0.106	0.938	0.244	0.694
45.15	1.189	0.109	1.080	0.237	0.843
50.70	1.237	0.097	1.140	0.281	0.859
51.30	1.230	0.129	1.101	0.289	0.812
57.00	1.535	0.139	1.396	0.319	1.077
79.80	1.485	0.125	1.360	0.263	1.097
93.80	1.724	0.155	1.609	0.400	1.209
107.50	2.029	0.184	1.845	0.318	1.527
123.80	2.076	0.241	1.862	0.345	1.517

residual and conversion to body weight. The lines of the best fit were drawn on the principle of least squares (FISHER 1948). The responses of *M. cyprinoides* and *O. striatus* place these fishes into the third group of VON BERTALANFFY; the slopes of the weight food intake relation are 0.71 and 0.76 respectively. The regression coefficients obtained for absorption (in relation to body weight) are 0.70 for *M. cyprinoides* and 0.77 for *O. striatus*. Food residuals shown in Tab. 3 and 4 represent the quantity of energy expended on metabolism. This quantity, as pointed out previously,

but there is some indication that they are both size dependent (BRODY, 1945, p 384). Therefore, the quantity of residual energy was plotted against body weight, and the regression coefficients were calculated to be 0.77 for *M. cyprinoides* and 0.88 for *O. striatus*. Values of 0.54 for the former and 0.55 for the latter have been obtained for the relation between conversion and body weight.

Discussion

It has been shown that with increasing body weight, feeding rate of the fishes *M. cyprinoides* and

O. striatus decreases and the regression coefficients obtained for the relation between body weight and feeding rate differ in the two species. This indicates that per g increase in body weight, the decrease in feeding rate is 0.016% body weight per day in *M. cyprinoides* and 0.010% body weight per day in *O. striatus*. Since both species grow and mature at quite different rates, this difference appears to be

fishes were, therefore, not alike in their physiological age. A sharp fall in feeding rate has been observed in premature individuals of *Epinephelus guttatus*, and with increasing body weight towards approaching sexual maturity, the decrease in feeding rate was not marked (MENZEL, 1960). The relatively faster decrease in the feeding rate of *M. cyprinoides* may support the view of BRODY (1945).

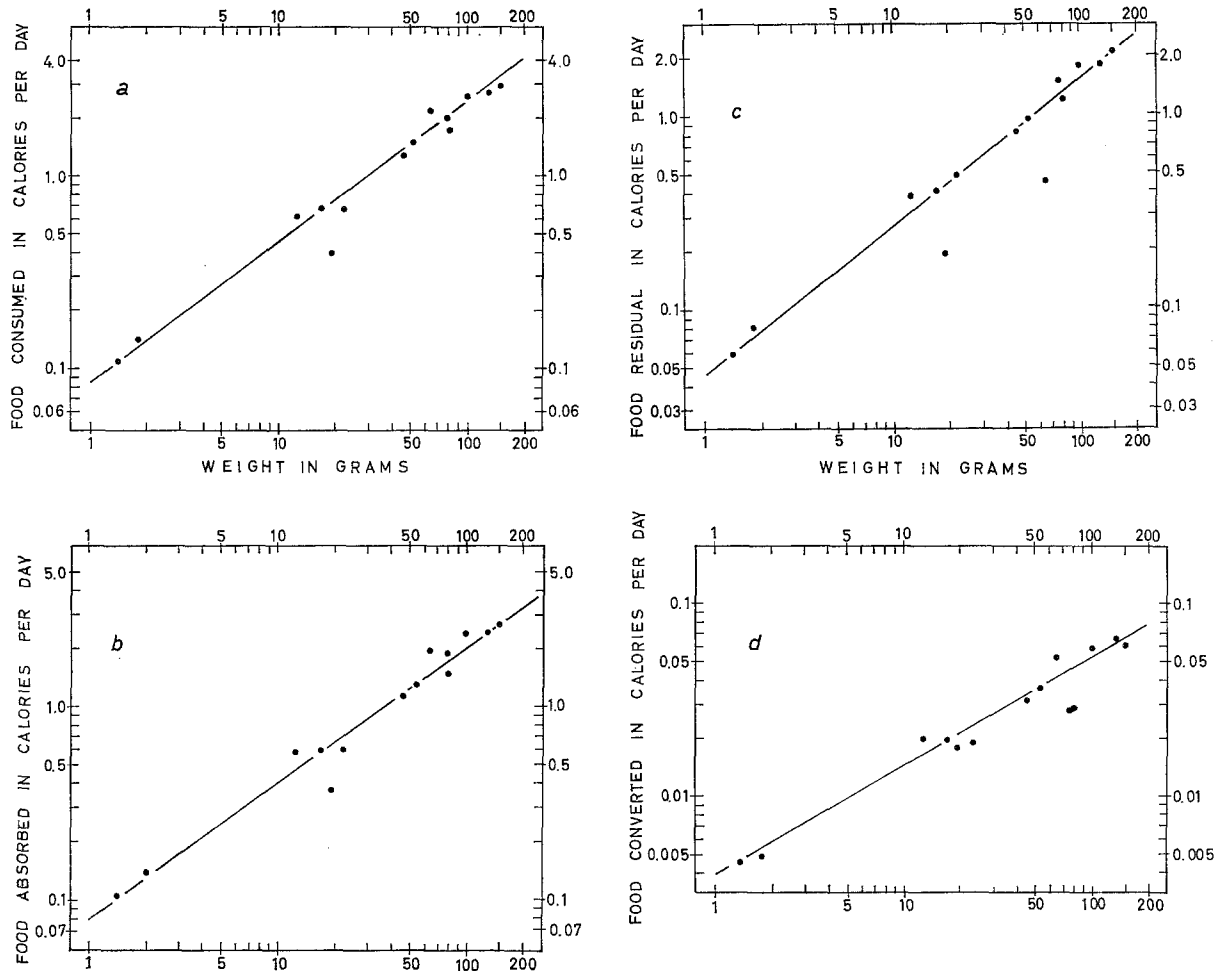


Fig. 12. Quantitative relations between body weight of *Megalops cyprinoides* and (a) food consumption ($Y = 0.0847 + 0.712x$), (b) food absorption ($Y = 0.0807 + 0.700x$), (c) food residual ($Y = 0.0448 + 0.770x$), and (d) food conversion ($Y = 0.0395 + 0.543x$)

related to what has been termed "physiological age" (BRODY, 1945). According to him, the velocity at which growth rate, or any one of the indices of metabolism, decreases with increasing body weight would be relatively faster during the pre-pubertal equivalence in weight growth than during the post-pubertal equivalence in weight growth. In the present study, *O. striatus* has been found to commence gonad functioning at a body weight of about 60 g; at approximately 100 to 120 g, it has been observed to breed (ALIKUNHI, 1953). On the other hand, *M. cyprinoides* do not attain maturity at 400 g (ALIKUNHI and RAO, 1951). Although equal in body weight, the tested

In 10 to 150 g fish, the trends obtained for the relationship between feeding rate and body weight were linear, resembling that of HATHAWAY (1927) for *Eupomotis gibosus* of 13 to 80 g individuals, maintained at 20 °C. In *Micropterus salmoides* weighing from 4 to 112 g, the relationship obtained by WILLIAMS (1959) is curvilinear and differs from the one reported by HATHAWAY (1927). In the present study, individuals from 1.4 to 149.6 g have been used and the curvilinear relation is similar to that observed by WILLIAMS (1959). It appears then, that it is the restricted weight range of the fish used by HATHAWAY, which may account for his deviating results; the

smaller fish of less than 10 g showed high feeding rates and thus transformed the linear into a curvilinear relationship.

Although the present findings support the general trend obtained for *M. salmoides* by WILLIAMS (1959), there are differences, particularly in regard to the slopes of regression. The regression coefficients indicate

decreases per g weight increase varies from species to species. Such species-specific differences have been already known to exist in regard to growth rates. It has further been shown that a decrease in feeding rate is paralleled by growth rates (MENZEL, 1960; KINNE, 1960, 1962).

Another interesting point is that, although feeding

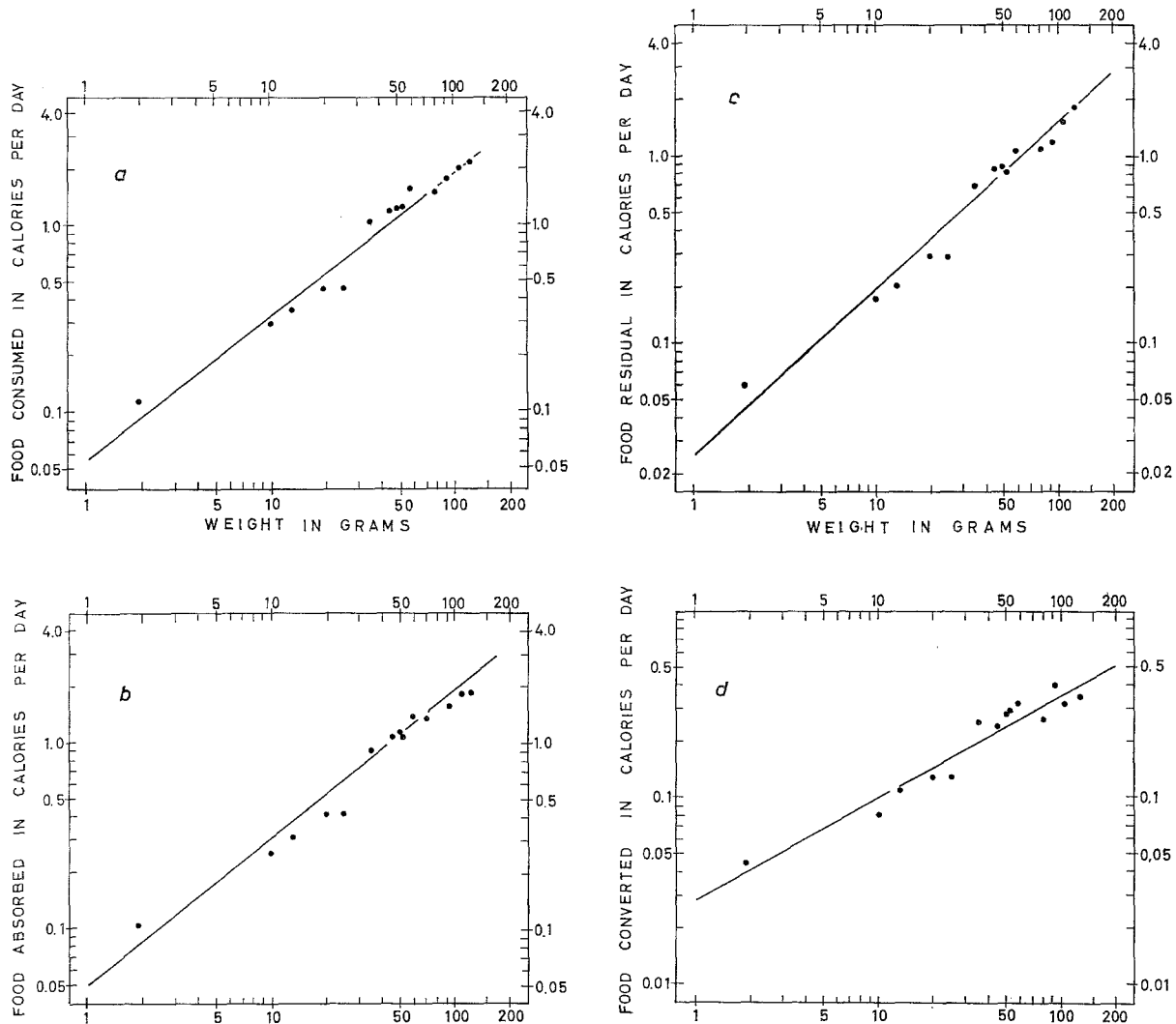


Fig. 13. Quantitative relations between body weight of *Ophiocephalus striatus* and (a) food consumption ($Y = 0.0569 + 0.761 x$), (b) food absorption ($Y = 0.0502 + 0.768 x$), (c) food residual ($Y = 0.0245 + 0.879 x$), and (d) food conversion ($Y = 0.0282 - 0.549 x$)

that per g weight increase, decreases in feeding rates were 0.016% body weight per day in *M. cyprinoides* and 0.010% body weight per day in *O. striatus*. Similar statistical analyses of the data obtained by HATHAWAY (1927), IVLEV (1939d) and WILLIAMS (1959) show that the decrease per g weight increase is 0.059% body weight per day for *E. gibbosus*, 0.026% body weight per day for the carp *Cyprinus carpio* (data from WINBERG, 1956, p 218), 0.008% body weight per day for *M. salmoides*. The gradient at which feeding rate

rate decreases faster with increasing weight in *M. cyprinoides*, the quantity of food consumed per day is greater than in *O. striatus*. Considering a fish weighing 50 g, the former consumes 1.5 g prawn per day, the latter only 1.3 g. Such a difference is maintained throughout the weight-range studied (Fig. 1). In addition to species-specific differences, the general activity of the two species affects their rate of feeding. *O. striatus* is rather a sluggish bottom feeder, whereas *M. cyprinoides* is a fast moving predator. HUNT (1960) working

on *Lepisosteus* and *Micropterus*, has shown that the food intake of these fishes was directly related to their general activity under normal conditions.

Digestion rate has been studied in relation to temperature (RIDDLE, 1909; MARKUS, 1933; BATTLE et al. 1936), quality of food (HESS and RAINWATER, 1939; KARPEVICH, 1941; PANDIAN, 1967b), and quantity of food (HUNT, 1960). KARPEVICH and BOKOFF (1937) have hinted that digestion rate varies as a function of age. But so far no detailed study on the relation between body weight and digestion rate has been made, and the factor responsible for the decrease of digestion rate with increasing body weight is not known. The following explanations may be suggested: digestion rate is a function of the surface area of enzyme secreting digestive organs (RICKER, 1946). The absolute size of the surface area may decrease with increasing body weight; the other possibilities are either the quantity or activity of the enzyme secreted is reduced. Since protein absorption efficiency remains more or less constant among fishes of different weights (GERKING, 1952; MENZEL, 1960; PANDIAN, 1967b), it is suggested that the differences in digestion rate may not be due to the activity or chemical composition but rather to the quantity of enzyme secreted.

In regard to the values obtained on absorption, it is necessary to consider the possibility of bacteria dissipating the energy and protein contents of the faecal matter during its 7 to 10 day stay in the aquarium, particularly at the high test temperature of 28 °C. In a recent paper DAVIES (1964) has assessed the dissipation of energy contained in the three week old faecal matter of the gold fish *Carassius auratus* maintained at 12.5° and 21.5 °C and found only a negligible energy dissipation. It is assumed that energy loss from the faeces was relatively small in the present experiments. The results obtained in regard to absorption efficiency of protein as well as energy are more or less in agreement with those reported by previous workers. There is no previous work on the rate of absorption. I have calculated the data obtained for *Lepomis megalotis* by GERKING (1952) and *Epinephelus guttatus* (MENZEL, 1960) and found that they support the present findings.

As to the reliability of the sacrifice method, the main difficulty is that we do not know the composition of the test individual at the beginning of the experiment. A sample fish of similar weight and nutritional state has been assumed to represent the chemical composition and caloric content of the experimental fish at the beginning of the experiment; however, even a small difference in chemical composition between sample and experimental individuals may introduce considerable errors. In *O. striatus* that were swimming along with their parents and, consequently may be expected to belong to the same brood, individuals were collected, and raised in the laboratory on the same diet. This was not, however, possible in the case of

M. cyprinoides. In fact, this may represent one of the reasons why the data on conversion efficiency are more scattered in *M. cyprinoides* than in *O. striatus* (Figs. 8 and 9). In his experiments on *Cyprinodon macularius*, KINNE (1960) used individuals of the F₁-generation of known parental pairs and reared the offspring under controlled environmental conditions. Such procedure is, of course, ideal. However, it is difficult to apply the same procedure in species with a life span of several years. In these cases, the "sacrifice method"—if used on a large number of individuals—provides the most suitable approach.

Although the present results are in general agreement with the trends obtained by previous workers like GERKING (1952), there are various notable differences. The regression coefficients obtained for the body weight-protein conversion efficiency relations show a decrease of 0.016% per g body weight increase in *M. cyprinoides* and of 0.090% in *O. striatus*. The respective values reported by GERKING (1952) for *Lepomis megalotis* and *L. cyanellus* (and reinterpreted for wet weight-efficiency relationship) are 0.259% for the former and 0.264% for the latter. These two values for *Lepomis* are about 3 times that of *O. striatus* and about 16 times that of *M. cyprinoides*. These differences may be related to the fact that maximum weight attained are 50 g in *L. cyanellus* and 100 g in *L. megalotis*, while corresponding values are 400 g in *O. striatus* and 600 g or more in *M. cyprinoides*. Similar differences can also be noted in the body weight-food conversion efficiency relations. Per g weight increase, the decrease in food conversion efficiency is 0.109% in *M. cyprinoides*, 0.124% in *O. striatus* and 0.123% in the carp *Cyprinus carpio* (IVLEV, 1939d; data from WINBERG, 1956, p 218).

While the relation between conversion efficiency and body weight may serve as indicator for the final attainable maximum size, the relation between conversion rate and body weight appears to be indicative of the time at which the final maximum body weight may be attained. In Fig. 10, the average amounts of protein nitrogen converted per day by *M. cyprinoides* and *O. striatus* are plotted against body weights. GERKING's (1952) data were again used for comparison. From his values showing the amount of nitrogen converted during 50 days, rates of conversion per day have been calculated and are plotted in Fig. 10. It can be seen that conversion rates are much slower in *Lepomis*, as compared to *M. cyprinoides*. This may be associated to the fact that *Lepomis* attain some 50 to 100 g body weight after 6 years (GERKING, 1952), whereas *M. cyprinoides* attains about 380 g body weight after 1 year (ALIKUNHI and RAO, 1951). Similar values obtained for food conversion rates in *M. cyprinoides* and *O. striatus* are shown in Fig. 11. Both, protein and food conversion rates are slower in *O. striatus* than in *M. cyprinoides*. These results are obviously related with the differences in the growth rates of these fishes. It is of interest to note that within

a period of about 1 year, *M. cyprinoides* attains 387 g in the Cooum back waters (ALIKUNHI and RAO, 1951), while *O. striatus* grows to only about 120 g in the Chetpet Fish Farm (ALIKUNHI, 1953).

Although the slope at which conversion efficiency decreases per g weight increase is more or less the same in *O. striatus* (0.124%) and the carp *Cyprinus carpio* (0.123%), the rates of food conversion differ in them widely. I have calculated the data obtained by IVLEV (1939d, as given by WINBERG, 1956, p. 218) for the carp *Cyprinus carpio* and plotted the food conversion rate against body weight in Fig. 11. The food conversion rate of *C. carpio* is considerably faster than the two test species. Considering a fish of about 100 g weight, conversion rate is 0.4 Cal per day in *O. striatus*, 0.6 Cal per day in *M. cyprinoides* and 2.8 Cal per day in *C. carpio*. In other words, conversion rate of *C. carpio* is about 7 times faster than that of *O. striatus* and nearly 5 times faster than that of *M. cyprinoides*. These findings are again related to the fact that IVLEV's carps reach a weight of 400 g in 4 months, while during the same period *O. striatus* hardly attains 40 g and *M. cyprinoides* about 80 g.

The slope at which conversion efficiency decreases, is more or less species-specific; it has been termed "growth potential" by GERKING (1952). I prefer to use the term "growth potential" in relation to conversion rate rather than to conversion efficiency. It has been shown that the pike *Esox lucius* resuming feeding after a period of less than 20 days starvation showed higher efficiency than the controls (IVLEV, 1939b); but when his data were calculated for conversion rate, it became apparent that the individuals resuming feeding after a period of less than 20 days starvation had lower conversion rates than the controls (PANDIAN, 1967a). In Fig. 10, I have also plotted conversion rates of the two species studied by GERKING (1952). The conversion rate is faster in *Lepomis cyanellus* than in *L. megalotis*. GERKING, however, basing his data only on conversion efficiencies, reported that the slope at which conversion efficiency decreased was steeper in the former than in the latter. KINNE (1960) has reported negative relations between rate and efficiency of food conversion in *Cyprinodon macularius* at 20 °C. Therefore, there can be either a positive relation between rate and efficiency of conversion, as in the case of *O. striatus* and *M. cyprinoides*, or a negative one, as in the case of *L. cyanellus* and *L. megalotis*. Growth refers to addition of material in sum of quantity per unit weight per unit time and conversion rate is expressed accordingly. But efficiency refers to a dimensionless percentage. Considering these facts, it is felt, that the term "growth potential" should be restricted to conversion rate rather than to efficiencies.

The inverse relation between body weight and nutritive metabolism is in accordance with that obtained for weight-respiratory metabolism (ZEUTHEN, 1947). Inverse relation obtained in the present study were curvilinear; young individuals showed high

efficiencies and with increasing weight a sharp decrease. There are some indications in literature that small fishes may be very efficient in converting nutrient matter. IVLEV (1939a) found that the larvae of sheet fish *Siluris glanis* were able to convert as much as 67% of the available energy in the yolk. LASKER (1962) studying the rate and efficiency of yolk utilization by developing embryos of Pacific sardine *Sardinops caerulea*, reported about 62% protein conversion efficiency. A sharp decrease is seen up to a weight of about 10 g in the fishes studied and in a few others adequately studied.

The present study of the intermediary steps, intake, digestion, absorption and conversion, involved in the food transformation process shows the importance of the physiological effect of body weight on metabolic rates. Intake of food per unit weight of fish, per unit time decreases with increasing body weight; this relationship is also reflected in the successive steps of transformation. The increase in body weight *per se* appears to reduce feeding rate, and the inverse relations obtained for the rest of the steps vary accordingly. GERKING (1952, 1957), who has studied the efficiencies of absorption and conversion, but not the preliminary steps of feeding, digestion and absorption rates, has suggested that aging slows down protein conversion efficiency. It is seen from the present study that age depresses the rate of feeding and the decrease in conversion efficiency is, thus, primarily due to the decreased quantity of nutrient matter digested, absorbed and made available for conversion. In the fishes like *M. cyprinoides* and *O. striatus*, the way in which age affects all the nutritive metabolism, appears to be through its effect on enzyme complex of the digestive system. By its relation to digestion, it decreases feeding, absorption and ultimately conversion.

The b values obtained for the relation between food intake and body weight are 0.71 for *M. cyprinoides* and 0.76 for *O. striatus* and hence place the fishes in the third group of VON BERTALANFFY (1951). VON BERTALANFFY, based on the findings of MÜLLER (1942), has included the fish in the first group, in which metabolism is proportional to body surface area. Later, in 1957 VON BERTALANFFY pointed out that a relation similar to that stated by him for surface dependence of respiration in *Lebistis reticulatus* was found by YOSHIDA (1956) with respect to food intake. The quantity of plankton consumed by *Sardinops melanosticta* is proportional to the square of the body weight and the same appeared to be true of assimilating organs such as gill rakers and the gut. The b values found in the present study are closer to the 0.91 value obtained by BALDWIN (1956) for *Salvelinus fontinalis*; (if the data for a large individual with tail rod were removed from the calculations, the value was 0.72; see PALOHEIMO and DICKIE, 1966). The values obtained for weight-absorption relations, again, place our two species in the third group of VON BERTALANFFY. No detailed information on this aspect is

available; I have calculated GERKING'S (1952) data on protein nitrogen absorption in relation to body weight in *Lepomis megalotis* and found it to be 0.94, which places *L. megalotis* in the third group of VON BERTALANFFY. Similarly, the values obtained for the relation between weight and residual energy—although not strictly comparable to those obtained for the respiratory metabolism by ZEUTHEN (1947), SCHOLANDER et al. (1953), and JOB (1955)—favourably compare with the values reported by these workers. Thus, there are direct and proportional relations between body weight and food intake, absorption or metabolism. These relations have been discussed in detail in a recent paper by PALOHEIMO and DICKIE (1966).

The b values obtained for the relation between weight and conversion are 0.54 for *M. cyprinoides* and 0.55 for *O. striatus*. These values are low compared to those obtained for the relations between weight and food intake, absorption or metabolism, respectively. I have calculated the data of IVLEV (1939d) for *Cyprinus carpio* and KINNE (1960) for *Cyprinodon macularius*. The b values for *C. carpio* is about 0.55 (28° slope) the corresponding values for *C. macularius* are about 0.60 (31° slope) at 15 °C, 0.57 (30° slope) at 20 °C, 0.34 (19° slope) at 25 °C, 0.42 (23° slope) at 30 °C and 0.45 (24° slope) at 35 °C. While the values calculated for *C. carpio* and *C. macularius* compares well with those obtained for *M. cyprinoides* and *O. striatus*, it is not yet understood why the relation between body weight and conversion alone are so different from the values obtained for the other intermediate steps of food transformation. Further work paying attention to all these steps is urgently needed.

Summary

1. The status of our present knowledge concerning the transformation of food into fish substance is considered. The different approaches and the various criteria employed are critically assessed, and a few important terms defined.

2. In the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*, transformation of food, particularly as a function of body weight, has been studied, using protein and energy transfer as criteria; the four intermediate steps involved—feeding, digestion, absorption, and conversion—are considered with a view to correlate them.

3. In both species, rates of feeding, digestion, absorption and conversion are found to decrease with increasing body weight; the trends obtained are curvilinear. There is no appreciable difference in absorption efficiencies of protein or total food among individuals of different body weights. Efficiencies to convert nutrient matter decreased from about 40% in 2 g individuals to about 15% in 150 g individuals.

4. The inverse relationship between body weight and feeding, digestion, absorption and conversion are attributed to age (senility). It is suggested that age

affects the intermediate steps through changes in digestive enzymes.

5. The quantitative relation between body weight and the four intermediate steps of food transformation are, in general, curvilinear; however, in individuals ranging from 10 to 150 g, straight line relations predominate. In all cases, the resulting slopes differ in both species. These differences have been correlated to the different physiological state ("physiological age") of the test species and their different "growth potential".

6. The b values obtained for the relation between body weight and metabolic rate, food intake or absorption do not correspond to surface or weight proportionality, but to an intermediary type, indicating neither surface nor weight proportionality. It is assumed therefore that there exist a direct and proportional quantitative relation between metabolic rate, food intake and absorption. Additional values from the present work as well as from the literature regarding the relation between body weight and conversion are unexpectedly low, indicating a direct, but non-proportional relation between growth and metabolism.

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