THE DYNAMICS OF FOOD AND FEEDING HABITS OF SOME MARINE FISHES

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Abstract

The study of food and feeding habits of marine fishes can be attempted from the standpoint of transfer of energy from one trophic level to the other. For a proper insight into the problem, it seems desirable to obtain some information on the environment from where the material for the study is taken. Ecologically the food organisms can be divided into seven broad groups. These can further be placed arbitrarily into three main trophic levels. From this type of approach, the trophic spectrum of some of the marine fishes from the Indian waters, on which data are available, can be drawn. These relationships can be interpreted as food chain models showing the groups of organisms which directly form a part of the food chain. A large assemblage of animals with a similar food requirement gives rise to competition within the same trophic level or ecological cannibalism, which makes the food chain long and complex. A suitable approach for the analysis of food seems the determination of organic carbon of the stomach contents. From the carbon content, the caloric value of the food can be determined. The knowledge of the energy contents of food is of much value for making an appraisal of the food conversion efficiency or ecological efficiency. From the ingested food it is possible to work out the the total energy losses and energy utilization.

Introduction

One of the main aspects of the study of the biology of fish is to determine its food and feeding habits, either as a separate investigation, or as a part of the other studies such as breeding and growth. This has, very often, been done without understanding the implications of the study of food, and hence little success has been achieved in developing a predator-prey relationship. The reason for this may be because an investigator faces considerable difficulty in finding a satisfactory method for the analysis of food from the stomach contents. In fact there is not one single method available in the literature which could give sufficient accuracy, cover the qualitative and quantitative aspects of food, and yet be not time-consuming and tedious. However, in most painstaking analyses, with some originality and effort, the study could be made more meaningful and rewarding. The purpose of this communication, therefore, is to provide a critical appraisal of the existing knowledge of the food and feeding habits of some marine fishes from the Indian waters and suggest how best the problem of community nutrition could be attempted in determining the transfer of energy from one trophic level to the other. The fish resources may be regarded as a part of an ecological system in which physical, chemical and biological forces of great complexity operate and fluctuate. These resources are the links in the food chain (energy transmitted through food)—starting with sun's energy and its conversion by plant communities into organic matter and ending up with exploitable fish, crustaceans and molluscs.

Complexity of the Problem

The analysis of the stomach or gut contents poses certain problems. These can briefly be summarized as follows:

(1) The various food items in the gut are very often beyond recognition. They may be in a semi-digested state consisting of a pulpy mass which is difficult to deal with during analysis.

(2) The food may vary with the size of the fish.

(3) The variation may also be associated with seasons, place, environments and depths.

In tropical waters, the rate of digestion, with high temperature, gets accelerated, and although the food may be present throughout the gut, the portion where it is in a recognizable state is the stomach region. For the purpose of analysis, therefore, the rest of the gut could be ignored, unless there are sufficient reasons for not doing so. With the high temperature, the putrefaction of food in the gut is also very quick and hence it is suggested that fishes should be kept immediately after capture in ice and examined in a chilled or refrigerated condition as soon as possible.

The Environment

No clear nutritional picture can emerge from a study without some background information on the environment from which the material is obtained. The fundamental concept of the environmental study in the minds of most fishery biologists of India is largely restricted to the measurements of temperature, salinity and dissolved oxygen; although none of these parameters has any direct bearing on the feeding relationship. A very important factor such as the turbidity of water, which can be determined by a simple device like the Secchi disc, has seldom been measured. The very idea of turbidity gives an index of the material in suspension on which the fish may be dependent. From the Secchi disc readings, the attenuation coefficient (K_{10}) of light can be obtained from the simple equation deduced earlier (Qasim *et al.*, 1968). If the water has been found to be turbid, it would be of immense value to record whether the turbidity is due to living or dead (inert) material. The total seston can be determined by filtering a known volume of water and weighing the filters before and after filtration (see Qasim *et al.,* 1969). The living phytoplankton can be estimated by simple microscopic examination of the settled material and counting the organisms or by pigment analysis (see Qasim and Reddy, 1967). A further examination of 5-minutes zooplankton tows could reveal a better picture of the total zooplankton biomass and the predominance of a particular group of organisms in the environment, which may indicate a strong feeding relationship.

Many studies on the food are based on the material obtained from the fishing boats and thus the investigator refers to his study as "food of fishes from trawl catches" or "...from gill nets" and so on, without referring to the areas in which the gears have been operated, depth of operation, time of operation, distance covered, conditions of the bottom and the condition of the sea and some information on sunshine, wind action etc. Most of these are normally available with the mechanized fishing boats and if collected regularly, could prove to be extremely useful. Similarly, the practice of referring the material as "off Cochin", off Bombay", offshore waters" serves very little purpose ecologically.

Food Groups

As the food association in fishes is generally ecological and seldom taxonomic, it becomes easy to group the various items into the following components: (a) phytoplankton (b) zooplankton (c) suspended detritus (d) pelagic animals (e) demersal animals (f) settled detritus (g) benthic animals and plants.

In these groups, the major difficulty arises in clearly identifying the various categories, as the fishes frequently combine the different components either all the time or with the size, season, place and depth. To counteract this difficulty, it seems desirable to put the different components into trophic levels. Thus, phytoplankton and attached or floating algae come under trophic level I; zooplankton and other filter-feeding animals (pelagic and benthic under trophic level II; detritus, both suspended and settled — being a heterogenous mixture and derived from plants, animals and bacteria—comes almost midway between trophic level I and II. Arbitrarily, and for the sake of convenience, let us put all the other food components, especially of the carnivores, both pelagic and demersal, into trophic level III. From such broad divisions it is evident that despite the great diversity which the food organisms might display in their taxonomic features, their classification into trophic levels is deceptively small.

(a) Phytoplankton

When phytoplankton organisms are seen in the gut, it is important to draw distinction between those which are directly ingested (grazed) and those whose entry into the alimentary canal is accidental. In the former case, it is also essential to make an assessment of the extent to which their contribution in the diet is significant. There are instances when the stomachs of the oil sardine have been found to be full of a particular species of phytoplankton, as if it has been feeding almost exclusively on unialgal cultures (Dhulkhed, 1972). Since the oil sardine is known to feed by straining water (Antony Raja, 1969), in nature such a situation can only arise when the fish is encountering blooms of phytoplankton. Possibly such an intake of *Fragilaria oceanica* led Nair and Subrahmanyan (1955) to postulate that this diatom acts as an indicator species for the oil sardine. A similar situation may arise with the blooms of the blue-green alga, *Trichodesmium* which occur in great profusion in the Arabian Sea. Many fishes have been found to contain *Trichodesmium* in their guts (see Qasim, 1970a), but the entry of this organism seems to be accidental, as no fish negotiating dense patches of bloom can completely avoid *Trichodesmium*. The seasonal blooms of several other blue-green algae, on the contrary, may be readily consumed by the herbivorous species such as mullets.

In April and May 1972, some specimens of the oil sardine were found to have their stomachs full of two species of diatoms (*Nitzschia* sp. and *Pleurosigma* sp.). Of these two, only one organism at a time was ingested to the extent of being gorged. Most of the other fishes in the sample contained the usual dark green plant remains in their stomachs. Except for the blooms of *Trichodesmium*, there is practically no record of the occurrence of blooms of diatoms in the seas around India during the pre-monsoon months (January to April). Most of the recorded blooms of diatoms and dinoflagellates are during the monsoon and post-monsoon months (Brongersma-Sanders, 1957). From the observations on the stomach contents, it follows that probably the blooms which the oil sardine encountered in April and May, were neither massive nor did these occur at the surface in such profusion as to discolour the water; otherwise they could not have remained unnoticed. Presumably these blooms are found below the surface in small isolated patches.

(b) Zooplankton

These organisms form another important food constituent of fishes. In this group also it is important to recognize the extent to which the zooplankton collectively form a major component of the diet of adult fish. It is also necessary to distinguish what group or groups of zooplankton predominate the food. Large quantities of such groups as larvae of a particular fish or of penaeid prawns, if correctly assessed, may have far-reaching ecological implications than their mere identity as food of some fish. Moreover, it is also necessary to indicate if the fish remains a zooplankton feeder throughout life. It is now well established that the young forms of most fishes are largely zooplankton feeders, and therefore, too much significance should not be attached to the zooplankton component of the food of young fishes, unless the relationship happens to be with a particular species or may demand special attention under exceptional conditions. For the calculation of food conversion efficiency, it is important to know at what size the adults change over to food items other than zooplankton, and whether the change is sudden or gradual.

Seasonal occurrence of large quantities of a particular category of zooplankton in the gut of the adult fish is of much importance and may indicate a change over from its normal food as a result of excessive abundance of an organism in the environment or as an adaptation to tide over the shortage of other food items in a particular season. This applies to all the other food components, whose presence or absence in a reasonably large number of fish stomachs in a particular situation may be of immense ecological value.

(c) Suspended detritus

In coastal areas and estuaries, the suspended detritus consists of particles of fine silt and sand, around which organic matter and bacteria adhere and form aggregates of different shapes and sizes. The other constituents of detritus are the faecal pellets, and a variety of recognizable remains of plants and animals. According to Darnell (1967), organic detritus consists of all types of biogenic material in various stages of decomposition. In the open ocean, the source of detritus is only plankton; but in coastal waters and estuaries, in addition to plankton material, benthic plants and animals, and other types of material brought down by the rivers, outfalls and land runoff, form a rich source of detritus. The subject has been reviewed comprehensively by Parsons (1963) and Riley (1970).

In the guts of fishes it is difficult to distinguish the detrital material from the other food items which are in a semi-digested state. However, it should be borne in mind that suspended detritus is generally consumed by those fishes which are able to filter the suspended (dead) material just as they do the living material.

(d) Pelagic animals

These constitute a very large group and include free-swimming crustaceans, molluscs, fishes and other animals. A distinction, very often, between large plankton and pelagic animals seems impossible. Since this group is consumed by the highly carnivorous and predaceous fishes, their occurrence in the gut is a function of availability in the environment and a deliberate effort by the fish to hunt for them. Some species show a peculiar fondness towards a particular animal such as shrimp, squid or fish. However, it is of interest to note that the quantity present in the gut does not signify the degree of predation sought for by the fish because the carnivore may be consuming only a portion of the animal and rejecting the rest. This group is of much significance in relation to pelagic fishery of the open ocean.

(e) Demersal animals

A very large assemblage of animals which live at or near the bottom such as a variety of crustaceans, molluscs, hydroid colonies, bryozoans, polychaetes, fishes etc., are included in this group. These again form a rather difficult component to deal with, for the hard parts and shells may be badly crushed and the soft portions could be in an advanced stage of digestion, often beyond recognition. However, since the demersal group is important in relation to trawl fishery, its assessment as food of fishes is necessary to draw trophic relationship which may be useful in recognising the areas of their occurrence and abundance. In deeper waters, the importance of demersal animals as food of fishes may be even greater, as their occurrence gives a clue of the potentially rich areas for trawling.

(f) Settled detritus

Settled detritus is a heterogenous mixture of animal and plant remains, silt and sand particles coated with decaying (organic) matter and large colonies of bacteria and infusorians. In turbid waters, since the euphotic zone (photosynthetic depth) becomes shallow, a large fall-out of plant and animal material occurs almost continuously. The importance of settled detritus, its rate of sedimentation, its chemical composition and nutritive value in the Cochin Backwater have been described recently (Qasim and Sankaranarayanan, 1972). Detritus occurs at the bottom in coarsely particulate form and is perhaps the most readily available and universally abundant food material in shallow areas of the sea, estuaries, freshwater lakes, ponds etc. In many environments, the importance of settled detritus as food of adult fish is much greater than all the other food groups combined. The presence of chitinous material, plant fibres (undigested cellulose), portion of disintegrated phytoplankton cells, remnants of exoskeleton of zooplankton, spicules of sponges, stems of hydrozoans, foraminiferans, broken shells of clams and gastropods, fish scales and bones and large quantities of silt, sand and clay in the gut signifies nothing else but detritus.

Many investigators, on finding such varieties of animal and plant-remains, get totally confused and draw conclusion that the fish probably feeds on all trophic levels, although in actual fact it is simply a detritus feeder. Normally, these detritus feeders graze upon the floor swallowing larger aggregates of detritus with mud or by scraping adhered material from submerged objects such as rocks, shells, pilings and wooden or metal structures. In an estuarine community, detritus has been found to be consumed, very often, even by the most carnivorous species (Darnell, 1961 & 1967). Rajan (1968), while studying the food spectrum of fishes from the Chilka Lake, states that 36.4% of the fishes examined by him were found to feed on detritus, even when the other food organisms were readily available in the lake. His list of detritus feeders includes some of the well-known carnivores. He further emphasizes that, of the total number of detritus feeders noticed by him, at least 50% were found to feed on other types of food by earlier workers.

(g) Benthic animals and plants

These two groups form important food items in the littoral zone and in special types of ecosystems such as the coral reefs, marshy areas, mangrove swamps, seagrass beds and in areas where luxuriant growth of algae is found. In these environments, all the other food groups described above, except perhaps detritus, play a minor or insignificant role. Sedentary animals, such as barnacles and serpulids have been found to be the main food of blennies (Qasim, 1957 a & b), whereas seagrasses and other macrophyte may provide a source of nutrition of fishes of an atoll (Qasim and Bhattathiri, 1971).

TROPHIC RELATIONSHIP

A survey of the literature on food and feeding habits of fishes from the seas around India gives a picture which is somewhat distorted and often incomplete. Lack of proper considerations of source, character and disposition of food material present in the gut, makes the problem even more complex. The relationship, however, which could be inferred from some of the selected references, is given in Table 1. The limitations in deriving such a relationship are quite apparent, for many species do not restrict themselves to a particular trophic level. From the available data, the present author has attempted to speculate in some cases, but this has been done in a generalized way.

From Table 1 it is clear that very few marine and estuarine fishes are truly phytoplankton feeders. Even in those fishes where information on phytoplankton food is available, it is not certain as to how much is the contribution of suspended detritus in the food. The species which combine phytoplankton with benthic plants in their food are also few; but the reported phytoplankton and zooplankton feeders include the mackerel, several species of clupeoids and other fishes (Table 1). The species which are predominantly zooplankton feeders amount to approximately 17% of the total fishes listed. Here again a distinction between a zooplankton feeder and a carnivorous fish is difficult to make, but those which feed at two trophic levels (II and III) constitute about 7% of the total and have been listed as zooplankton feeders and carnivores (Table 1). The number of typically carnivorous fishes in the population seems to be large (about 50%). Among the carnivores also a distinction between a typically predatory fish and those which subsist on all types of food of animal and plant origin (omnivores) could not be made.

The other fairly large group seems to be of detritus feeders, despite the fact that in many investigations the presence of detritus has been ignored. The fishes which feed on detritus do not conform to any single food habit. From these observations the conclusion seems inevitable, that, as a single factor, detritus is the most predominant material ingested by the fish. Many species remain exclusively detritus feeders while others combine detritus with the other food materials (Table 1).

TABLE 1. *Feeding habits of some marine fishes as deduced from the works of different authors. Only some references have heen given here as it is not the intention to give a comprehensive review of the subject*

Feeding habit	Species	Authors
Phytoplankton feeder	*Sardinella longiceps*	Kagwade, 1967 Antony Raja, 1969
Detritus feeders	*Liza macrolepis*	Luther, 1965
	Mugil speigleri	Sarojini, 1954
	Mugil parsia	Sarojini, 1954
	Mugil cephalus	Rajan, 1968
	Mugil cunnesius	Rajan, 1968
	Mugil seheli	Rajan, 1968
	Therapon puta	Rajan, 1968
	Glossogobius giuris	Rajan, 1968
	Sciaena russelli	Rajan, 1968
Detritus and benthic plant feeder	*Hemirhamphus far*	Talwar, 1964
Phyto- and zooplankton feeders	*Rastrelliger kanagurta*	George, 1964 Narayana Rao, 1964
	Sardinella gibbosa	Ganapati and Srinivasa Rao, 1958
	Sardinella albella	Sekharan, 1971
	Sardinella fimbriata	Venkataraman, 1960
	Kowala coval	Venkataraman, 1960
	Leiognathus splendens	Venkataraman, 1960
Zooplankton feeders	*Sardinella melanura*	Vijayaraghavan, 1953
	Coilia dussumieri	Bal and Joshi, 1956
	Dussumieria hasselti	Venkataraman, 1960
	Anchoviella tri	Venkataraman, 1960
	Anchoviella commersonii	Venkataraman, 1960
	Selaroides leptolepis	Tandon, 1960
	Caranx djedaba	Venkataraman, 1960
	Caranx kalla	Kagwade, 1971
	Ambassis gymnocephalus	Venkataraman, 1960
Zooplankton and detritus feeder	*Leiognathus insidiator*	Venkataraman, 1960
Zooplankton feeders and carnivores	*Opisthopterus tardoore*	Radhakrishnan, 1968
	Leiognathus bindus	Balan, 1967
	Hemirhamphus marginatus	Talwar, 1964
	Hyporhamphus georgii	Talwar, 1964
	Hyporhamphus quoyi	Talwar, 1964

Continued

TABLE 1. *Contd.*

Feeding habit	Species	Authors
Carnivores	*Thrissocles malabaricus*	Venkataraman, 1960
	Thrissocles mystax	Venkataraman, 1956
	Thrissocles hamiltonii	Rajan, 1968
	Harpodon nehereus	Bapat, 1970
	Lepturacanthus savala	James, 1967
	Trichiurus lepturus	James, 1967
	Trichiurus haumela	Prabhu, 1955
	Eupleurogrammus intermedius	James, 1967
	Auxis thazard	Kumaran, 1964
	Auxis thynnoides	Kumaran, 1964
	Sarda orientalis	Kumaran, 1964
	Katsuwonus pelamis	Raju, 1964
	Euthynnus affinis affinis	Kumaran, 1964
	Neothunnus macropterus	Thomas, 1964
	Scomberomorus guttatus	Vijayaraghavan, 1955
	Megalaspis cordyla	Venkataraman, 1960
	Otolithes ruber	Venkataraman, 1960
	Johnius belengeri	Venkataraman, 1960
	Pseudosciaena sina	Venkataraman, 1960
	Pseudosciaena diacanthus	Venkatasubba Rao, 1968
	Pseudosciaena coibor	Rajan, 1968
	Parastromateus niger	Sivaprakasam, 1967
	Pampus argenteus	Kuthalingam 1967
	Polydactylus heptadactylus	Venkataraman, 1960
	Polynemus indicus	Karekar and Bal, 1958
	Polydactylus indicus	Mohamed, 1955
	Saurida tumbil	Kuthalingam, 1959
	Nemipterus japonicus	Kuthalingam, 1969
	Lactarius lactarius	Venkataraman, 1960
	Sillago sihama	Radhakrishnan, 1957
	Lates calcarifer	Rajan, 1968
	Pomadasys hasta	Rajan, 1968
Carnivores and detritus feeders	*Cynoglossus lingua*	Kuthalingam, 1957
	Cynoglossus semifasciatus	Seshappa and Bhimachar, 1955

FOOD CHAIN MODELS

From the broad pattern of feeding relationship given above, it is possible to develop theoretical models of food chains. The simplest and direct models would be:

Phytoplankton $\rightarrow$ fish ...... (1)

or

Algae, rooted plants $\rightarrow$ fish ...... (2)

Similarly, the fishes which subsist on detritus occupy a place almost midway between herbivores and carnivores. Thus the model would be:

Organic detritus → fish ...... (3)

or

Plants,
Animals,
Organic aggregates etc. → detritus → fish ...... (4)

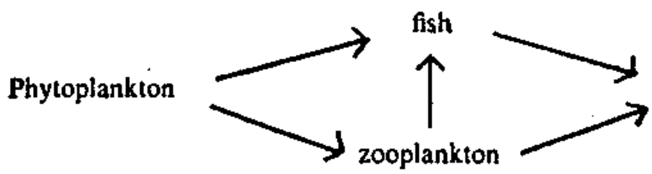
The detritus feeders have a trophic level which is almost intermediate between the first and second.

Fishes which feed on the second trophic level will have models such as:

Phytoplankton → zooplankton (copepods) → fish ...... (5)

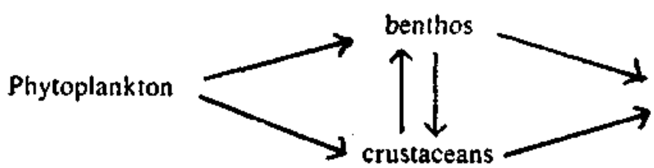
Phytoplankton → bivalves (other invertebrates) → fish ...... (6)

The models for the carnivores which generally feed on the third trophic level but keep on changing the trophic levels, depending upon the availability of food can be illustrated as:



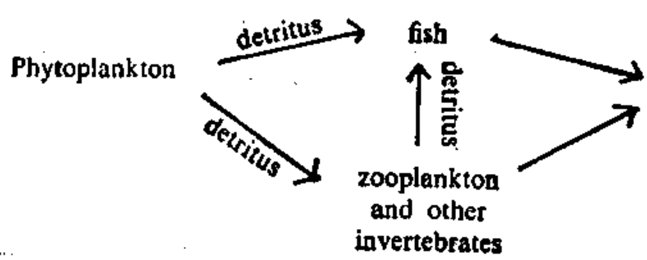
...... (7)

or



...... (8)

or



...... (9)

In nature the food chains are far more complicated than those expressed by the 9 models noted above; but the main purpose of showing these models in a simple way is to enable an investigator to identify the trophic levels at which a fish could possibly feed. A combination of two or more of these models can give rise to all possible trophic relationships in any environment.

From these models it is also possible to recognise (a) short food chains (b) average food chains and (c) long food chains. In the short food chains, the loss of energy from one trophic level to the other is reduced to a minimum, and conversely, in a long food chain, energy is lost at every link.

Ecological Cannibalism

In the models 1-6, the horizontal and diagonal arrows indicate the transfer of food from one trophic level to the other, whereas in the models 7-9, the vertical arrows show the predation or competition for food within the same trophic level. Such a competition has been referred to as "ecological cannibalism" (Steele, 1965). More realistic representations of the food chains have been given in earlier communications (Qasim, 1970b & 1971). As an example, one of the diagrams has been shown in Fig. 1. The vertical and diagonal arrows in Fig. 1 indicate the transfer of food from one trophic level to the other and the horizontal arrows indicate the possible feeding within the

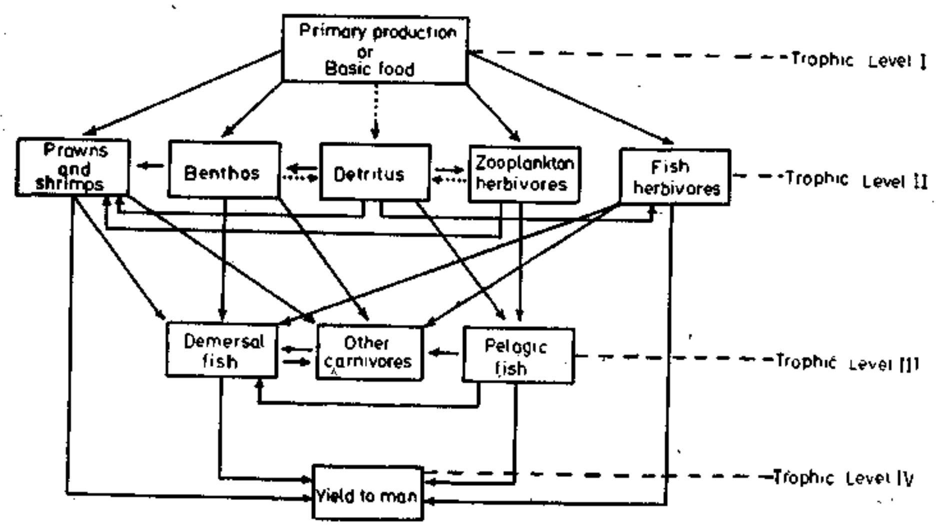


Fig. 1. A diagrammatic representation of the food chain showing an assemblage of animals at the second trophic level which leads to competition for food or ecolocal cannibalism. Broken lines indicate trophic levels I-IV and dotted arrows indicate the pathway of detritus formation and utilization.

same trophic level. As can be seen from Fig. 1, at the trophic level II, there is an assemblage of animals with a maximum degree of ecological cannibalism. In such a complex food model, the exploitable fish stocks have to compete for food with the other animal groups, and their yields determine their success or failure in this competition. When ecological cannibalism increases, the energy gets dispersed within the same trophic level. Thus the food chain becomes long and the losses in the transfer of energy from one trophic level to the other also increase considerably.

A hypothetical representation of the "food web" in an aquatic environment can be found in any text book of ecology. Most of these diagrams are far too complicated and provide no indication of trophic levels and hence are of little practical value. They do not take into consideration a proper nutritional pathway through which energy could be channelled.

Chemical Approach

The various methods commonly used for the analysis of food have been reviewed by several earlier authors (see e.g. Pillay, 1952). The well-known methods applied for the quantitative analysis are (a) numerical (b) volumetric and (c) gravimetric. A combination of numerical and volumetric methods has been found to give a better picture of food than when each of these is applied in isolation (Natarajan and Jhingran, 1962).

However, there is a general lack of the determination of chemical composition of stomach contents. Even a direct chemical analysis of the food into organic and inorganic components has seldom been attempted. Since the whole concept of food consumed is in the form of energy utilization, the validity of a chemical approach is beyond question. The chemical composition can be approximated in a number of ways and in principle the methodology for the gut contents is similar to what is applied for phytoplankton, zooplankton, detritus or fish tissues. However, the present author feels that the simplest approach is to analyse the total organic carbon of the food material, for carbon seems the best single property for determining the caloric value (see Qasim and Sankaranarayanan, 1972).

The total organic carbon can be determined by the wet oxidation method of Wakeel and Riley (1957) in which the sample is digested with chromic acid and then titrated with ferrous ammonium sulphate using ferrous ammonium-phenanthroline as an indicator. The details of this method adapted for the analysis of food of fishes has been given elsewhere (Qasim and Jacob, 1972).

The percentages of organic carbon (average values) in the food of four different species were found to be as follows:

Species	Feeding habit	Organic carbon % dry weight
Sardinella longiceps	Phytoplankton feeder	7.36
Liza macrolepis	Detritus feeder	7.76
Rastrelliger kanagurta	Phyto- and zooplankton feeder	29.86
Nemipterus japonicus	Carnivore	27.42

The degree of precision in the estimation of carbon will depend upon the freshness of the food in the gut. All fishes analysed were kept in ice or frozen. They were thawed and immediately after the qualitative analysis, the food was dried, powdered and stored until the carbon content was determined. The stomach contents of a minimum of 50-60 specimens of *S. longiceps* and 20-30 specimens of each of *L. macrolepis, R. kanagurta* and *N. japonicus* are required for replicate determinations.

ENERGY UNITS OF FOOD CONSUMED

The carbon values of food can be converted into energy units (calories) and for this the following equation given by Platt *et al.* (1969) for zooplankton equivalent seems reliable:

$$\text{cal/g dry wt} = -227 + 152\ (\%\ \text{carbon})$$

However, for obtaining in more precise units, separate conversion factors, specific for the different types of food are necessary.

Thus the calories consumed by the four different species will be:

S. longiceps	89 .72	cal/g dry wt of food
L. macrolepis	952.52	cal/g dry wt of food
R. kanagurta	4311.72	cal/g dry wt of food
N. japonicus	3940.84	cal/g dry wt of food

EFFICIENCIES OF FOOD UTILIZATION

The rate at which food is utilized by the fish in terms of energy units can be expressed as a percentage from the relationship:

$$\frac{\text{calories of food consumed by the predator}}{\text{calories of food supplied}} \times \frac{100}{1}$$

This expression has been termed as "food conversion efficiency" and can be determined by conducting experiments in the laboratory. In a simple food chain such as phytoplankton—zooplankton—fish, if all the phytoplankton which are produced in a day, are consumed by the zooplankton, and all the zooplankton, which are produced per day at the expense of phytoplankton, are consumed by the fish, then the food conversion efficiency will be equal to "gross ecological efficiency".

In a simple *Chlamydomonas-Daphnia* laboratory ecosystem, the gross ecological efficiency has been found to be of the order of 13% (Slobodkin, 1959). In nature, however, such a simple situation seldom exists, as the basic food is transmitted in different pathways (Fig. 1). Much data, therefore, are necessary to develop any generalization, although it has been assumed that gross ecological efficiency is of the order of 10% (Phillipson, 1970). Thus, making the concept of ecological efficiency constant around 10%, it would mean that from 100 calories of plant material consumed by the herbivore, only 10 calories will be passed on to the next trophic level and 1 calorie to the next higher trophic level.

The amount of food intake which is utilized for growth is expressed as "growth efficiency" which is

$$\frac{\text{increase in weight by fish}}{\text{total food consumed}} \times \frac{100}{1}$$

In plaice (*Pleuronectes platessa*), Colman (1970) estimated this efficiency, which he calls "efficiency of food conversion", from 15 to 26%.

However, to get a balance sheet of the energy budget derived from food, it is necessary to take into account both losses and utilization. In order to do this, the following modified version of Ivlev's equation, as given by Warren and Davis (1967), is of much value:

$$C = F + U + \triangle B + R_s + R_d + R_a$$

where C = energy value of food consumed, F = energy value of faeces, U = energy value of material excreted by the kidneys or through the gills and skin, $\triangle B$ = energy utilized for building tissues (growth), R_s = energy utilized by the fish when it is resting, R_d = energy utilized by the fish for digestion, assimilation and other metabolic processes, R_a = energy utilized by the fish for swimming and other activities.

The energy content of the waste product of fish ($F + U$) has been found to be of the order of 20% (Winberg, 1956) of the food consumed (C). Taking a average of 20% (15-26% determined for plaice) as the energy value of the food utilized for growth ($\triangle B$), the remaining 60% seems to be utilized for R_s, R_d and R_a. However, these percentages are only approximations and would vary considerably with the quality and quantity of food consumed.

They are also affected by the metabolic state of the fish. It would be interesting to know how far these values differ in different species depending upon their food habits.

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