Chapitre 11

DETRITIVORY AND HERBIVORY

DETRITIVORES ET HERBIVORES

S.H. Bowen

1 - FISHES AS PRIMARY CONSUMERS IN AFRICAN FRESHWATERS

The majority of African freshwater fishes depend on invertebrates as their link to the photosynthetic food base : fishes that feed directly on living plant matter or detritus are relatively few. Most of these primary consumers are contained in only six genera : *Labeo, Tilapia, Oreochromis, Sarotherodon, Citharinus* and *Distichodus*. Several of the Rift Valley lakes contain haplochromis-derived primary consumers that are either endemic or of limited distribution, but again these represent a small fraction of the total species present. I estimate that of 2,500 freshwater fishes in Africa, only 160 (less that 7%) feed characteristically as primary consumers.

Despite the small number of primary consumer species, their very broad distribution makes them disproportionately well represented in individual aquatic ecosystems. In Lake Barombi Mbo, primary consumers represent 30% of the fish species (4 of 14) (Trewavas, Green & Corbet 1972), in Lake George 30% (3 of 9) (Burgis *et al.*, 1973), in Lake Chad 30% (6 of 21) (Lauzanne, 1981), in Lake Tanganyika about 20 % (22 of 106 studied) (Fryer & Iles, 1972) and in Lake Sibaya 16% (3 of 18) (Bruton, 1979). Furthermore, these primary consumer species commonly comprise a disproportionately great share of the ichthyomass. In Lake George, the three primary consumers comprise 60 % of the ichthyomass (Burgis *et al.*, 1973). In floodplain pools of the Sokota River. Nigeria, primary consumers comprise 74% of the ichthyomass (Holden, cited in Lowe-McConnell, 1975). Even in the River Niger where primary consumers were only 6% of species captured in rivers they comprised 19% of the ichthyomass (Holden, cited in LoweMcConnell, 1975). Thus, the few primary consumers in the African fish fauna are widely distributed and generally develop large populations which are conspicuous components of ecosystem trophic structures.

These observations raise two fundamental questions : Why are there so few primary consumer species?, and Why are primary consumer populations so successful in developing large numbers of individuals? Implicit in these questions is a hypothesis that the relationship between the consumer and its food resource plays the central role. In this chapter I will briefly review studies of the food and feeding of herbivorous and detritivorous African freshwater fishes and discuss the progress that has been made toward answering these two questions.

2 - RELATIONSHIPS BETWEEN PRIMARY CONSUMER FISHES AND THEIR FOOD RESOURCES

2.1 - Ecological fitness of primary consumers.

Ecologists usually interpret ecological relationships as having been favored by natural selection because they increase an organism's fitness - its contribution to the gene pool of the next generation. Since fitness is difficult to measure directly, a variable that is proportional to fitness is often measured instead. In fishes, reproductive output is directly proportional to size, and thus growth is a useful estimator of fitness (Werner and Hall, 1976). Studies of the food and feeding of fishes usually attempt to assess observed feeding behavior in terms of its significance for growth.

Relationships between feeding behavior and growth are likely to be very different when primary and higher level consumers are compared. Animal prey are often in short supply and require considerable consumer investment in search and pursuit. The principal trophic challenge before higher level consumers is obtaining an adequate *quantity* of food at minimal cost in time or energy. In contrast, the food of primary consumers is generally present far in excess of their ability to consume it, but food *quality* is highly variable. Higher plants often contain large quantities of indigestable fiber. Higher plants, bacteria and most algae have cell walls that present obstacles of various types to digestion. Most primary food resources are variable with regard to protein content, a major nutritional variable (Bowen, 1979, 1980b). As a result, we would expect natural selection to have favored adaptations in utilization of primary food resources that increase food quality for the consumer.

2.2 - Adaptations that increase food quality

2.2.1 - Adaptations in diet selection. Selective feeding has been observed in several studies and in some cases the benefit in increased food quality is clear. *Tilapia rendalli* feeding on inundated *Panicum repens* in Lake Kariba selectively ingests leafs and other parts that are low in indigestable fiber relative to the whole plant (Caulton, 1977). *Oreochromis mossambicus* feeding on benthic detrital aggregate in Lake Sibaya (S. Africa) and on periphytic detrital aggregate in Lago de Valencia (Venezuela) selectively ingests food with the highest protein (amino acid) content available (Bowen, 1976b, 1979, 1980b). In Lago de Valencia, high values for percent organic matter were correlated with high protein values, but in Lake Sibaya the fish selected high protein - moderate organic food in preference to moderate protein - high organic food. *Citharinus citharinus* in backwaters and tributaries of the River Niger feeds selectively on benthic detritus rich in both nitrogen (implying protein) and organic matter (Bakare, 1970). The fact that juveniles were considerably more selective than adults may be attributable to the greater requirements of juveniles for protein to support growth (Bowen 1979). Other observations on selective feeding are of unknown significance. For example, *Sarotherodon galilaeus* in Lake Chad selects filamentous bluegreen algae and rejects diatoms as it feeds on benthic deposits (Lauzanne, 1975). This selection would not be expected to increase digestability of the diet (Moriarty, 1973) and thus may be an artifact associated with selection for some other dietary variable.

2.2.2 - Adaptations in digestion and assimilation. To my knowledge, digestion of plant matter or detritus by African freshwater fishes has been studied only for *Tilapia, Oreochromis and Haplochromis* species. These are all cichlids, and have an essentially uniform set of morphological and physiological adaptations which they apply in digestion of a wide variety of primary food resources. All have dorsal and ventral pharyngeal plates which bear teeth used to prepare the food for gastric digestion. The teeth are numerous and fine in species that feed on phytoplankton (e.g.*Oreochromis niloticus, Haplochromis nigripinnis*) and those that feed on fine particulate detritus (e.g. *O. mossambicus, O. leucostictus*). For these fishes the pharyngeal teeth may serve to break up aggregates and thus increase the surface available for enzymic digestion. In species that feed on higher plants (e.g. *Tilapia rendalli, T. zillii*), the pharyngeal teeth are relatively few and robust. These teeth titurate the food, and this step is apparently essential for efficient intestinal digestion (Caulton, 1976).

A second step in digestion by cichlids involves treatment with gastric acid, frequently at pH values below 2.0 and sometimes as low as pH 1.2. This condition has been shown to lyse bluegreen cells (Moriarty, 1973), diatoms (Bowen, 1976b) and bacteria (Bowen, 1976a), to aid in the digestion of macrophytes (Caulton, 1976) and in one case to decompose large quantities of inorganic matter ingested by a detritus feeder in an alkaline lake (Bowen, 1980a).

Gastric processing exposes vulnerable substrates to intestinal enzymic digestion. The intestine in fishes that feed on plants or detritus is generally longer than that in fishes that feed at higher trophic levels (see Fryer & Iles, 1972, Fig. 44). This suggests that one or more essential components of the diet are slow to be digested and both a long residence and extensive exposure to absorbtive surfaces are required. In Lago de Valencia, *O. mossambicus* rapidly digests diatoms and the bulk of the organic detritus in its diet while the food is still in the anterior intestine, but large quantities of detrital amino acids that are essential for the animal's nutrition are digested slowly as the food passes the full length of the intestine (Bowen, 1980a, 1980b). Similar processess doubtless occur in other primary consumer species.

The digestive process is complete when the food has been reduced to low molecular weight compounds that can be assimilated through the gut wall. Assimilation efficiency (amount assimilated expressed as a percentage of amount ingested) is a useful measure of the extent to which a consumer can digest and assimilate its diet. Higher level consumers often assimilate about 85 % of what they ingest. By comparison, values for primary consumers are considerably lower. *Oreochromis niloticus* and *Haplochromis nigripinnis* feeding on phytoplankton, largely *Microcystis* sp., in Lake George assimilate 43 % and 66 % of ingested carbon, respectively (Moriarty and Moriarty, 1973). *O. mossambicus* assimilates about 60 % of a diet of periphytic detrital aggregate (Bowen, 1980a). The macrophyte grazers *T. rendalli* and *T. zilli* assimilate 55 % (Caulton, 1976) and 30 % (Buddington 1979) of their diets, respectively. From these observations it is clear that even though these fishes feed selectively and posses special adaptations for digestion of their diets, the diets they consume are far less digestible than diets utilized by secondary consumers.

3 - WHY ARE THERE SO FEW PRIMARY CONSUMERS AMONG THE AFRICAN FRESHWATER FISHES, AND WHY ARE THEY SO SUCCESSFUL ?

The question of how many species can be supported along a resource gradient has been examined in considerable detail in recent years (see reviews in May, 1981). Virtually all this work considers species numbers to be limited by competition for a limiting resource, usually food, and thus species are expected to be evenly spaced along the resource gradient. The broader the resource spectrum, the greater the number of species that can be supported. For insectivorous birds and lizards, resource gradients such as prey size and perch height are relatively obvious and have provided striking support for a general theory. Regrettably, resource gradients that define relationships among primary consumers are more obscure. Identification of resource gradients is complicated by variation in food quality. For example, we might expect that benthic detrital aggregate could be utilized by several fish species, each well adapted to feed at a different depth (depth as the resource gradient). However, the limited amount of information available suggests that only shallow water detrital aggregate has enough protein to support growth (Bowen, 1976b, 1979). Because we lack an understanding of the resources important to fish that feed on plants or detritus, future attempts to answer this question should perhaps begin with a test of the hypothesis that «Since there are few primary consumers, then the resource spectrum available to them must be narrow.»

The second question, why are these primary consumers so successful?, is similarly difficult to answer. On first examination it may appear that the direct connection of these fishes to the base of the food web would make them 5-10 times more efficient than secondary consumers in conversion of photosynthetically fixed energy to fish biomass. (This is based on a 10-20 % efficiency of energy or material transfer from one trophic level to the next.) However, invertebrate intermediates on which secondary consumer fishes rely appear to be able to utilize many detrital resources that are unsuitable for fishes. Consequently, there is no *a priori* reason why the primary food → primary consumer fish chain should support more ichthyomass than the primary food → invertebrate → secondary consumer fish chain. Again we lack an understanding of the variables that define the food base available to primary consumer fishes, and again we must convert the question into a hypothesis - large populations are supported by an abundant food resource - for further study.

4 - DIRECTION FOR FUTURE RESEARCH

In addition to the innate interest this problem holds for the student of aquatic ecosystems, further study of African freshwater primary consumer fishes is warranted on applied grounds due to their importance in aquaculture and in African fisheries. These fishes produce nearly half of the yield from African freshwaters (Fryer & Iles, 1972, Table 17). In aquaculture, supplementary feeding is potentially much more cost effective with primary consumers since they can utilize vegetable, bacterial and detrital proteins apparently not available to other fishes.

Perhaps the pivotal question on which further progress in this area depends is - What portion of the primary food spectrum is actually available to support primary consumers? This is not to suggest that food limits production in all cases : predation doubtless also plays a role. Nonetheless, in both natural and managed systems, a fish's requirements for specific types of foods that it can identify, gather, digest and assimilate to provide an adequate nutritional balance will determine much of its behavior and greatly influence production. Thus, further study of food selection and its significance for growth in relation to the spectrum of available food resources is likely to yield both interesting and valuable results.

RESUME

Parmi les quelques 2500 poissons d'eau douce africains, 160 seulement se nourrissent de plantes et de détritus. La plupart appartiennent à 5 genres : *Labeo, Tilapia, Sarotherodon, Citharinus* et *Distichodus.* Bien que peu nombreuses, ces espèces ont une vaste répartition et constituent une part proportionnellement importante de la biomasse de beaucoup de peuplements ichtyologiques. Ce chapitre fait le point des connaissances permettant d'expliquer pourquoi si peu de poissons se nourrissent de plantes et de détritus et pourquoi ceux qui le font ont une telle réussite.

Cette source de nourriture primaire est de qualité très variable et souvent mauvaise, ce qui constitue un des principaux obstacles à l'installation des consommateurs primaires. On a observé que les *Tilapia, Sarotherodon* et *Citharinus* se nourrissaient de manière sélective, afin, pense-t-on, de tirer le meilleur profit des ressources disponibles. Il existe chez *Tilapia, Sarotherodon* et *Haplochromis,* des adaptations spéciales au niveau de la digestion gastrique et intestinale qui paraissent augmenter très sensiblement la valeur nutritive de ces sources de nourritures primaires.

Malgré la très grande abondance des plantes et des détritus dans la plupart des milieux, il est possible qu'une petite fraction seulement de ce matériel soit réellement utile en tant que nourriture pour les poissons. Dans l'avenir, il faudrait tenir compte de la variété des ressources disponible et de leur valeur nutritive, afin de mieux comprendre l'origine et les limitations en ce qui concerne la production des poissons consommateurs primaires. Du fait que ces espèces ont un grand intérêt dans les pêches et en aquaculture, une meilleure connaissance du rôle des ressources alimentaires sur leur productivité aurait alors un grand intérêt économique.

REFERENCES

BAKARE O., 1970 - Bottom deposits as food of inland freshwater fish. In (Ed.) VISSER S.A., *Kainji Lake Studies* pp. 65-85. University Press, Ibadan, Nigeria.

BOWEN S. H., 1976a - Mechanism for digestion of detrital bacteria by the cichlid fish *Sarotherodon mossambicus* (Peters). *Nature, Lond.*, 260 : 137-138.

BOWEN S. H., 1976b - Feeding ecology of the cichlid fish *Sarotherodon mossambicus* in Lake Sibaya. KwaZula. Ph.D. dissertation, Rhodes University, Grahamstown, 135 p.

BOWEN S. H., 1979 - A nutritional constraint in detritivory by fishes : the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. *Ecological Monographs*, 49(1) : 17-31.

BOWEN S. H., 1980a - Digestion and assimilation of periphytic detrical aggregate by *Tilapia mossambiCa, Trans. Am. Fish. Soc.*, 110 : 239-245.

BOWEN S. H., 1980b - Detrital non-protein amino acids are the key to rapid growth of tilapia (pisces) in Lake Valencia, Venezuela. *Science*, 207 : 1216-1218.

BOYD C. E. & GOODYEAR, C.P., 1971 - Nutritive quality of food in ecological systems. *Arch. Hydrobiol.*, 69 (2) : 265-270.

BRUTON M. N.. 1979 - The fishes of Lake Sibaya. pp. 172-245. In Allanson B.R., (Ed.). Lake Sibaya. Monographiae Biologicae, 36. Junk, The Hague.

BUDDINGTON R. K., 1979 - Digestion of an aquatic macrophyte by *Tilapia zillii. J. Fish Biol.*, 15 (3) : 449-456.

BURGIS M. J., DARLINGTON J.P.E.C., DUNN I.G., GANF G.G., GWAHABA J.G., McGOWAN L.M., 1973 - The biomass and distribution of organisms in L. George, Uganda. *Proc. R. Soc., Lond.*, B., 184 : 271-298.

CAULTON M. S.. 1977 - A quantitative assessment of the daily ingestion of *Panicum repens* L. by *Tilapia rendalli* Boulenger (Cichlidae) in Lake Kariba. *Trans. Rhod. Sci. Assoc.*, 58 (6) : 38-42.

FRYER G. & Iles T.D., 1972 - *The cichlid fishes of the great lakes of Africa.* Edinburgh, Oliver and Boyd,641p.

LAUZANNE L., 1983 - Trophic relations of fishes in Lake Chad. pp. 489-518. In CARMOUZE J.P., DURAND J.R. & LEVEQUE C. (Eds). Lake Chad. Monographiae Biologicae, 53. Junk, The Hague.

LAUZANNE L. & ILTIS A., 1975. La sélection de la nourriture chez *Tilapia galilaea* (Pisces, Cichlidae) du Lac Tchad. *Cah. O.R.S.T.O.M., sér. Hydrobiol.*, 9 : 193-199.

LOWE-McCONNELL, 1975 - *Fish communities in tropical freshwaters.* Longman, London.

MAY R. M., 1981 - *Theoretical ecology.* Sinauer, Sunderland, Massachusetts, USA.

MORIARTY D. J. W., 1973 - The physiology of digestion of bluegreen algae in the cichlid fish, *Tilapia nilotica. J. Zool.*, 171 (1) : 25-39.

MORIARTY D. J. W. & MORIARTY C.M., 1973 - The assimilation of carbon from phytoplankton by two herbivorous fishes : *Tilapia nilotica* and *Haplochromis nigripinnis. J. Zool.*, 171 (1) 41-55.

TREWAVAS E., GREEN J., CORBET S.A., 1972 - Ecological studies on crater lakes in West Cameroon : fishes of Barombi Mbo. *J. Zool.*, 167 : 41-95.

WERNER E.E. & HALL D.J., 1976 - Niche shifts in sunfishes : experimental evidence and signifiance. *Science* N.Y., 4225 : 404-406.