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Reprinted from

THE UGANDA JOURNAL

Vol. 19, No. 1. MARCH 1955

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Introduction

ONE of the more important inland fisheries in East Africa is the *Tilapia* fishery. These fish are not only sold for local consumption but, dried or salted, they are exported in large numbers. Their popularity as a fish easily cultivated in ponds is growing, but the natural population in the inland waters of East Africa produces by far the largest contribution to the industry. The value of these fish to the economy of the country has led to a considerable amount of research being done on them by the East African Fisheries Research Organization and others. Amongst the many factors influencing the growth of the fish, its food is of the greatest importance. Much remains to be done before a complete understanding is reached of the food requirements of the species of *Tilapia*, but the data already collected show some rather unusual features. It is well known that they are herbivorous and, as in all herbivores, relatively large quantities of material have to be eaten because a large proportion of the food is indigestible. It is important to know what part of the ingested material is digested by the fish; this can be determined by comparing, under the microscope, the contents of the stomach with that of the rectum or by making chemical analyses of the gut contents.

The Selective Digestion of Plankton

The best known species of *Tilapia* is the 'ngege', *Tilapia esculenta* Graham which feeds on suspended plankton in the water (Fish, 1952). The mechanism used to collect the suspended material from the water has been described (Greenwood, 1953). The plankton adheres to mucus produced in the mouth and the mucus is then passed into the stomach. Other species of *Tilapia*, e.g. *T. variabilis* Blgr. and *T. nilotica* (L.), feed on the plankton but also on algae growing on rocks and on aquatic plants. The stomach contains a mass of mucus in which the algae are embedded. These algae, in most lakes, consist mainly of diatoms together with members of two other main groups, the green (Chlorophyceae) and blue-green (Cyanophyceae) algae. When the fish have been browsing on the epiphytic flora, filaments of green and blue-green algae, fragments of plant epidermis and epiphytic diatoms are also found in the stomachs. The contents of the rectum are similar to those of the stomach except that the diatoms have been digested (Figs. 1, 2). The other algae pass through the alimentary canal apparently unharmed, unless the cell wall has been damaged, in which case the contents of the cells are digested. Vaas and Hofstede (1952), in Indonesia, have successfully cultured green algae obtained from the faeces of *T. mossambica* Peters, a species with feeding habits similar to those of *T. nilotica*, and thus confirm our observations. Any small crustacea which are occasionally eaten are also digested but, according to the data collected at present, form only a very small proportion of the plankton ingested by the fish.

1746

The conclusion to be drawn from these observations is that these species of *Tilapia* normally depend on diatoms in their food for their nutrition. This conclusion is supported by data collected from certain areas where the water supports an abundant algal population which lacks diatoms. Such areas have been found in the Lake Albert region where there are lagoons, originally forming part of the main lake but now isolated owing to a fall in lake level. The chemical composition of the water in these lagoons has been altered as a result of evaporation, and, although a large algal plankton is found in them, it is made up almost entirely of blue-green algae and contains very few diatoms. Certain dams which have been examined contain plankton composed mainly of green algae. The plankton-feeding fish in these waters show definite signs of malnutrition. On the other hand, certain habitats unusually rich in diatoms have produced unusually high catches of fish. An officer of the Lake Victoria Fishery Service obtained up to 100 *Tilapia variabilis* per 4-inch gill net near Butera Island in the south-west of Lake Victoria; a sample of water taken at the same time was examined and found to contain over 6,000 diatoms per cubic centimetre. These figures of fish caught and of diatom population are both high as compared with other parts of Lake Victoria.

The results of the selective action of the digestive enzymes of these fish can be clearly seen under the microscope, but as yet no adequate explanation can be offered. It is likely that a fundamental difference in cell-wall structure between the diatoms and other algae is the main factor involved. Diatoms have an extremely resistant cell-wall composed of silica. Nevertheless there is direct connexion between the protoplasm and the surrounding water because the cell-wall is pierced by pores or a raphe according to the species. The silica shells remain clearly identifiable after passing through the gut, but are empty. All other algae have a cell-wall of cellulose, or a derivative of cellulose, which is continuous and impervious to the digestive enzymes.

The Digestion of Certain Species of Blue-Green Algae

Fish from Lake Rudolf, one of the very alkaline lakes in Kenya, were exceptional in that they were found to be digesting blue-green algae. *Tilapia nilotica* in the Ferguson Gulf region of this lake grows to an extraordinary size and fish of ten pounds weight are frequently caught. The plankton of the Gulf is very rich, colouring the water green, but it is composed almost entirely of species of *Spirulina* and *Anabaenopsis*. These are both blue-green algae and are freely ingested by the larger *Tilapia*. They are readily digested (Figs. 3, 4) and no doubt the very large size attained by the fish is related to the abundance of this food. These algae, belonging to a group not usually digested by *Tilapia*, are limited in East Africa to the highly alkaline waters of lakes such as Rudolf and Elmenteita. There is no visible difference in cell-wall structure between these and other blue-green algae, but it is possibly significant that water with a high sodium-to-calcium ratio (as found in these alkaline lakes) does seem to affect the cell-walls of some blue-green algae when they are cultured in the laboratory. *Anabaena cylindrica* (Lyngb.) when grown in such a medium develops thick gelatinous walls causing the filaments to clump together.

Nevertheless diatoms may still be important to the nutrition of the *Tilapia* in Lake Rudolf. All specimens below 40 centimetres in length contained large numbers of epiphytic diatoms and only those above this size were feeding on the blue-green algae. A migration of the fish from the inshore to the offshore waters of the gulf at a length of about forty centimetres is indicated by these data, which were collected during a visit in January 1953. The observations need confirmation by further collections at other times of the year.

It is of interest that these blue-green algae which are digested by *Tilapia* in Lake Rudolf also on occasion form an important source of food for the Lesser Flamingo (*Phoeniconaias minor* (Geoffrey)) (Rich, 1931; Ridley and Percy, 1953). Samples of gut contents of these birds from Lakes Elmenteita, Naivasha, Magadi and Hannington have been examined and it is clear that these algae are selectively collected and eaten in large quantities.

The Diet of Weed-eating Fish

Submerged water plants, e.g. *Ceratophyllum* and *Utricularia*, form a major source of food for some species of *Tilapia* such as *T. zillii* (Gervais) and *T. melanopleura* Duméril. In these fish the stomach is usually filled with macerated plant remains together with the associated algal flora of epiphytic diatoms and filamentous and epiphytic members of other groups. An examination of the contents of the rectum shows that when phanerogam cells are ruptured, the contents are digested. However, the maceration is often not sufficiently vigorous to break more than a relatively small proportion of the cells, and, where the cell-wall is undamaged, there appears to be no digestion of the contents. The amount of digestible food that these fish obtain from flowering plants therefore varies according to the degree of maceration prior to passing into the stomach. Apart from these plants, filaments of green and blue-green algae are often present in great numbers and pass through the alimentary canal unchanged. The diatom flora is digested. The fish are somewhat selective in their choice of plants for food and no fragments of water lilies or of other plants growing on or above the water surface have been found in their stomachs.

The Value of Decaying Matter and Bacteria in the Diet of *Tilapia*

On one occasion, *Tilapia zillii* collected from a pond was found to have been feeding on a blue-green alga, *Oscillatoria*, which had previously been growing vigorously in the pond but was then beginning to die off. It was noticed that some of the filaments of these algae had changed colour from green to yellow during their passage through the gut of the fish and therefore were probably partially digested. While it is not likely that senescent filaments of *Oscillatoria* are an important source of food for *Tilapia*, this observation serves to illustrate the inadvisability of drawing hard and fast distinctions between digestible and indigestible matter. In fact, all the material classed above as indigestible may be of value to the fish after a certain amount of autolysis or decay has set in. Bacterial action breaks down the cellulose cell-walls and the contents are decomposed. In addition, bacteria themselves may be digested: high populations of bacteria are found on fertile mud surfaces. In addition there is an associated fauna of protozoa. Data are available showing that *Tilapia nilotica* in Lake Kivu subsist largely on a large planktonic spirillum (Private communication: Chef de Mission des Lacs, Goma, Kivu). The flourishing fishery for *Tilapia* in this lake shows that these are a suitable food for the fish.

Usually it is not possible by ordinary microscopical methods to determine whether there is a significant contribution made by bacteria to the nutrition of the fish, but the habit of eating bottom debris is widespread in the genus and there is no doubt that bottom deposits do often contain a certain amount of food material. An example of the value of bottom debris to the nutrition of the fish was found during a survey of the Malagarasi Swamps in Tanganyika made by the East African Fisheries Research Organization in 1952. These swamps, about 700 square miles in area, are largely covered by water lilies and other water weeds and support a dense population of fish (including *Tilapia nilotica* and *Tilapia karomo* Poll) which forms the basis of an African fishing industry. There is no plankton to be found in the water and the *Tilapia* feed on the soft flocculent bottom deposits. These deposits consist of finely divided plant fragments together with many protozoa and bacteria. The water-lily plants in this region are eaten by two species of fish, *Alestes macrophthalmus* Günther and *Distichodus* sp. and, after passing through their gut, the partially-digested plant-remains form part of the bottom deposits. It has yet to be established whether this material is then directly digestible by the *Tilapia* or whether the rich growths of protozoa and bacteria supported by these remains are the food for the fish.

Crude protein in any material can be estimated by the chemical analysis of organic nitrogen; this method has been used to evaluate bottom deposits as possible fish food in Lake George. The lake supports a large fish population which is exploited by the Uganda Fish Marketing Corporation. The waters of this very shallow lake are bright green owing to the enormous quantities of phytoplankton in them. Although diatoms are present, the greater part of this phytoplankton is composed of green and blue-green algae which are not digested by the fish. The stomach contents of the *Tilapia* species (*T. nilotica* and *T. leucosticta* Trewavas) from this lake show that the very soft bottom deposits are their principal food. This is confirmed by the chemical analyses. The amount of crude protein in these deposits was found to be equal to that found in the plankton itself in Lake Victoria. Samples of the contents of the rectum and stomach of the *Tilapia* from Lake George were analysed in the same way. The figures obtained show that the crude protein in the stomach contents is reduced to 60 per cent of its value by the time it reaches the rectum. These data indicate that bottom deposits are a source of food for *Tilapia*. They do not however show whether the food is mainly in the form of bacteria and protozoa which are decomposing the debris or whether this decomposition renders previously indigestible material available as food. More detailed chemical analysis of the deposits and gut contents of the fish feeding on them are necessary before this problem can be completely solved.

SUMMARY

The study of the food relationships of the *Tilapia* species is of considerable importance, not only in order to help to understand the distribution of these

Fig. 1

Photomicrograph of the stomach contents of *Tilapia esculenta* caught in Lake Victoria at Jinja. This fish was feeding on phytoplankton. The large mass of small round cells is a colony of *Microcystis flos-aquae* (Wittr.) Kirchn. (blue-green alga), the star-shaped colony is *Pediastrum* sp. (green alga) and the long straight filaments are cells of *Melosira* spp. (diatoms).

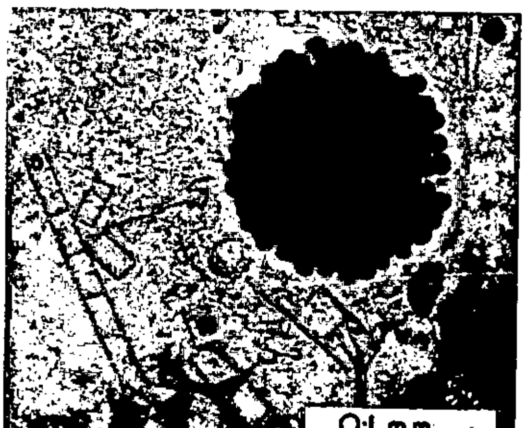

Fig. 2

Photomicrograph of the contents of the rectum of the same fish as in Fig. 1, showing the empty shells of the diatom *Melosira*. *Pediastrum* (green alga) and *Microcystis* (blue-green alga) are not digested.

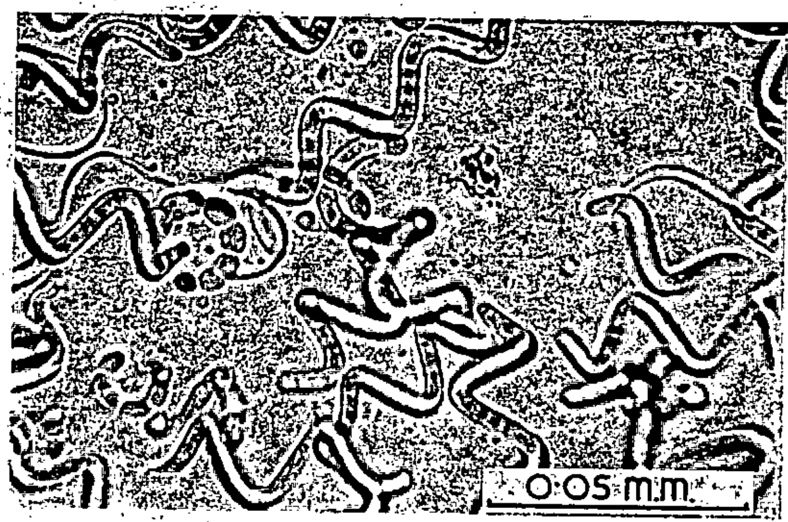

FIG. 3

Photomicrograph of the stomach contents of *Tilapia nilotica* caught in the Ferguson Gulf, Lake Rudolf. This fish was feeding on blue-green algae (*Spirulina* and *Anabaenopsis*).

fish, but also to estimate the productivity of natural waters in East Africa. Recommendations encouraging or limiting *Tilapia* fisheries so that maximum advantage is taken of this valuable natural resource will depend on knowledge of the food available for the fish as well as on other factors. The first step in estimating the food available for the fish is to know what plants the various species digest. The data above shows that these plants are diatoms, blue-green algae in Lake Rudolf, or aquatic weeds in many of the smaller bodies of water. The problem is more complex when bottom deposits, or the organisms associated with their decomposition are utilized as sources of food, but chemical analyses may be of great assistance in such cases.

These data could not have been collected without the assistance of Mrs. R. B. McConnell (née Miss R. H. Lowe) who not only provided all the samples from the Malagarasi Swamps and Lake Rudolf, but also identified the fish examined. Her interest and encouragement, and that of the Director and Staff of the East African Fisheries Research Organization are gratefully acknowledged. Thanks are due also to Lord Richard Percy who sent samples of flamingo gut-contents; to the Game and Fisheries Department of the Uganda Government for the many samples of fish; and to the Agricultural Research Station at Kawanda who performed the nitrogen estimations.

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