THE TROPHIC INTERRELATIONSHIPS AND ECOLOGY OF SOME LITTORAL COMMUNITIES OF LAKE NYASA WITH ESPECIAL REFERENCE TO THE FISHES, AND A DISCUSSION OF THE EVOLUTION OF A GROUP OF ROCK-FREQUENTING CICHLIDAE

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GENERAL INTRODUCTION

An essential prerequisite to an understanding of the biological economy of any body of water is a knowledge of the ecology and food requirements of the individual species of animals occupying the various habitats which it provides. The present investigation has been directed towards an elucidation of these aspects of the biology of the animals comprising the littoral zone communities of a selected area of Lake Nyasa, at Nkata Bay (Nyasaland), on the western side of the lake, approximately 150 miles from its northern extremity. The selected area included both a rocky and a sandy shore and also a small, swampy, estuarine region. The data obtained from this area have been supplemented by occasional collections and observations made elsewhere.

The study demanded accuracy in the taxonomy of the fishes and involved the description of some new cichlid species and reconsideration of the validity of others previously recognised. Most of these results have been published elsewhere (Fryer, 1956a, 1956d, 1957a) and, with the earlier work of Regan (1921) and Trewavas (1935), provide the taxonomic basis for this work so far as it concerns the cichlid fishes. The combined study of taxonomy and ecology inevitably leads to the development of views on the evolution of these fishes, and Part II of this paper embodies the conclusions to which I have come on the nature and conditions of speciation within a compact group of endemic rock-frequenting Cichlidae. It is published here because it is more easily followed with the help of the diagrams which illustrate Part I, though it is complete in itself and can be read alone by those who are chiefly interested in evolutionary phenomena.

PART I

THE TROPHIC INTERRELATIONSHIPS AND ECOLOGY OF SOME LITTORAL COMMUNITIES OF LAKE NYASA, WITH ESPECIAL REFERENCE TO THE FISHES

INTRODUCTION

The great depth and tropical setting of L. Nyasa, appear to result in the absence of any seasonal or even intermittent overturn. As a result the waters of the hypolimnion are devoid of oxygen, and a tremendous volume of water and a vast area of bottom are placed out of reach of any save highly specialised anaerobic organisms. Because of this the littoral region is of even greater importance than is the case in many other lakes, both from a biological point of view and from the point of view of fisheries.

In spite of the enormous extent of the shoreline of the lake only two major types of shore are extensively represented, namely those which can be simply described as rocky, and sandy. Between them these two types probably occupy well over 90 per cent of the total shoreline ; rocky shores predominating in the north and sandy shores in the south. Other types of littoral zones do exist and of these swampy regions of relatively small extent, estuarine regions at the point of inflow of certain rivers and streams, and one other type described below, probably embrace all those worthy of inclusion in a broad scheme of classification such as is adopted here.

A few words about the fauna of L. Nyasa are necessary to put the present survey in its correct perspective. Its most outstanding characteristic is the great adaptive radiation shown by the fishes which has resulted in the evolution of large numbers of distinct endemic species, particularly in the family Cichlidae, of which more than 180 species are now known to occur in the lake. Such radiation is shown also, but to a lesser extent, by other families such as the Clariidae. Some groups of invertebrates such as the parasitic Copepoda and the Mollusca exhibit similar though usually much less spectacular speciation, but on the whole the invertebrates do not appear to have produced endemic species to such an extent as is the case in certain other ancient lakes such as Tanganyika and Baikal. It is with some of the many endemic cichlid fishes that this study is largely concerned.

The previous zoological work carried out in Lake Nyasa has been largely of a systematic nature, the only papers containing any real ecological information being those of Worthington (1933), Bertram, Borley & Trewavas (1942) and Lowe (1952, 1953). Of these Worthington's paper, while mainly systematic, includes notes on the gut contents of a few non-cichlid fishes, and certain deductions are made from this information. The report on the fish and fisheries of the lake by Bertram *et al.* gives much more extensive information of a similar nature, but is largely concerned with the fishes of most obvious economic importance. Lowe's work was virtually confined to the genus *Tilapia* and is therefore of somewhat specialised interest. Practically nothing has been written concerning the ecology of the invertebrates of the lake. All in all, therefore, our previous knowledge of the ecology of Lake Nyasa must be regarded as being rather scanty.

Any value attached to the present study is of course, as in all ecological studies, dependent upon sound taxonomy. Even in the well worked temperate lakes, however, the systematics of the larval and nymphal stages of many insects remain to be worked out, so it is inevitable that in a tropical lake such difficulties should be accentuated. In trying to build up a general picture however, little is lost from an ecological point of view by referring to certain groups of animals as " chironomid larvae ", " anisopterid larvae ", etc., when the food of the group as a whole is relatively constant and is assignable to a well defined type. Such a proceeding is at least as valuable and certainly less misleading than a series of erroneous determinations. The number of species of invertebrates involved is, in any case, rather small and this has greatly facilitated certain aspects of the work.

While the quantitative approach has not been entirely ignored it has played a subsidiary role to studies on the natural history of the species concerned. The reasons for this are two-fold. While it would have been comparatively easy to amass numerical data it quickly became obvious that such data, relating as they do to a very complex community organisation, would be of only doubtful value until such times as the part played by the individual members of the community had been accurately determined. Furthermore, the technical difficulties of arriving at an *accurate* estimate of, for instance, the basic production rate of plant protein on the much broken rocky shore were, under prevailing circumstances, so great as to render the effort involved incommensurate with the value of any results obtained.

METHODS

Few specialised techniques have been employed. Fishes have been collected by various means. On the sandy shore a seine net and a 2½ inch mesh gill net have provided most specimens while a few have been taken in traps. In the small estuary a seine net and trap, supplemented by the use of baited hooks proved satisfactory. The rocky shore presented some difficulties for, while a gill net could be used for collecting along the fringes, the major element of the fish fauna of this zone could not be sampled by this method.

Most fish were therefore captured by an ingenious local method. A short, small meshed gill net operated by swimmers is set among the rocks and fishes are chased into it and gilled. Although the method cannot be regarded as being very efficient the dense fish fauna among the rocks and the skill of the boys operating the net resulted in it proving extremely useful.

A special fine-meshed net, here referred to as a " carpet net ", was also constructed for sampling the fish fauna of the rocky shore. It was operated by draping it over the rocks, allowing the fish to swim over it and lifting it, so as to enclose the fishes present. While only moderately successful this net facilitated the capture of some species not readily obtained by other means.

Other rock fishes were collected by stunning them with a bullet fired into the water from a ·303 rifle, while others were angled for by small boys armed with hooks and worms.

Invertebrates were collected by the usual methods.

One item of equipment deserves special mention. This was a glass-fronted mask which, when worn over the eyes, enabled many valuable underwater observations to be made on the fishes. This mask was worn both when swimming and when observations were made from the surface in a boat. Its value was greatly accentuated by the remarkable clarity of the water, especially on the rocky shore, which enabled the fishes to be seen with extreme ease.

Special attention was paid to the detailed composition of the food of the various species studied, particularly as in the case of a few of the fishes only a small number of specimens could be obtained. Even in cases where abundant material was available it was considered advisable to make a very thorough study of the gut contents of a reasonable number of specimens rather than a more casual examination of a large number, especially in cases where the diet is very restricted. Even so well over 1,600 detailed gut analyses were carried out on the fishes alone within the confines of the area under consideration, and many more guts received a cursory examination, while a number from other areas were carefully studied for comparative purposes. The food along the entire length of the gut was studied, except in cases such as *Labeo* and *Varicorhinus* whose gut is of such exceptional length as to render this impracticable.

All references to the length of fishes refer to total length including the caudal fin.

PHYSIOGRAPHIC FEATURES OF THE AREA STUDIED

The area studied is shown in the accompanying map. (Fig. 1). Within this relatively small area fairly typical examples of rocky and sandy shores are represented as is a somewhat swampy miniature river estuary. In addition a fourth type of major habitat with distinctive faunistic peculiarities gradually became recognisable as the study proceeded, this being a very small area between the rocky and sandy shores, which, because of its intermediate character in certain respects, is for convenience henceforth spoken of as the " intermediate zone ". Because of the presence there of crocodiles, the estuary was named " Crocodile Creek " and is referred to by this name throughout the following account. Unless otherwise stated the datum line of water level is that which represented the high water mark during the survey.

The main physiographic features of the four zones are outlined below.

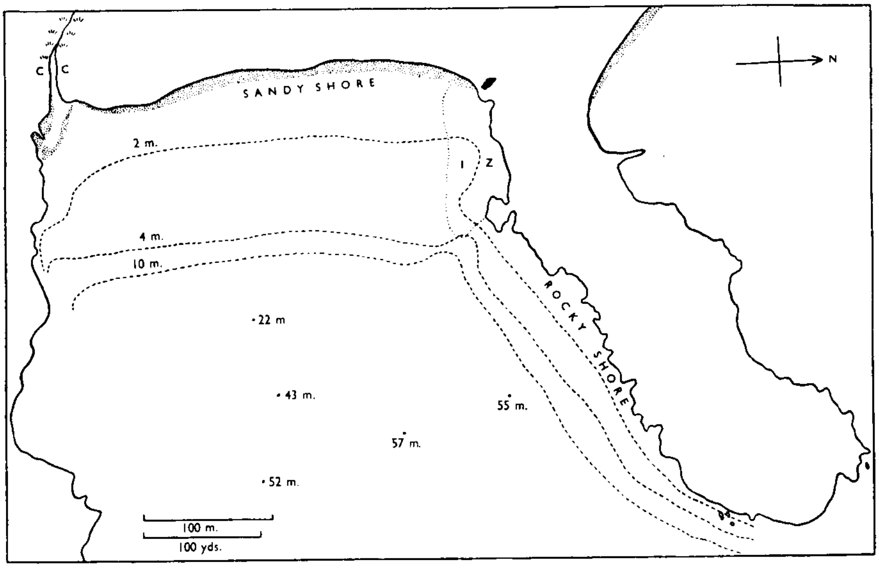

Fig. 1.—Map showing area studied (South Bay, Nkata Bay, Nyasaland) and distribution of major littoral habitats. C.C. =Crocodile Creek. I.Z. =Intermediate Zone.

(a) *The rocky shore*

This zone is admirably described by the word rocky. Rocks of all shapes and sizes, mostly composed of micaceous shists or, less frequently, hard quartzes occur in profusion on a bottom composed in many places of bed rock, coarse gravel or, in rare isolated patches, of coarse sand. Figures 1 and 2 on Plate 1 give a good idea of the general configuration of this zone.

The rocky shore shelves relatively slowly, producing a well marked littoral shelf which extends outwards into the lake for a distance of some 60 metres over most of its length, and whose depth gradually increases from less than one metre to about 10 metres. Beyond this point the bottom plunges suddenly downwards (Fig. 2, B) and even within the small bay shown on the map it descends to a depth of some 150 metres. The present investigations have been almost entirely confined to the littoral shelf.

The water over and among the rocks is exceptionally clear, even after prolonged periods of onshore wind ; and in calm weather the configuration of the bottom can be seen from a boat down to considerable depths. Just off shore a standard 20 cm. diameter Secchi disc is usually visible until it sinks below about 16 metres and it can be seen down to 20 metres when viewed through a glass-fronted mask.

At some time of the day on almost any day of the year the water among the rocks is in a state of turbulence due to wave action and swell. Good testimony to the constancy of this turbulence is the presence on the rocky shore of two species of net spinning caddis larvae of the family Hydropsychidae which require a current for the efficient production and spreading of their nets.

Macrophytic vegetation is entirely lacking, due presumably to the nature of the substratum. The upper surfaces of the rocks, however, are coated with a thick flocculent layer of algae of numerous species among which diatoms are particularly conspicuous. The entire felt is most conveniently described by the comprehensive German term " Aufwuchs " which in its widest sense includes also all the animals living among the algae, but which is here restricted to the plant constituents of the association. Common components of this Aufwuchs community are two species of the bluegreen alga *Calothrix* which are the analogues of trees in a woodland community. Their filaments are firmly attached to the rocks, and between them grow numerous other algae which constitute as it were the undergrowth. Among this algal felt occur also inorganic particles brought there during periods of particularly violent weather.

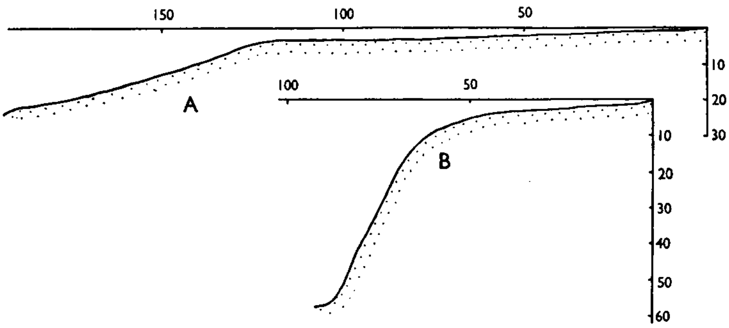

Fig. 2.—Actual sections of A : Sandy shore, B : Rocky shore. Note : The vertical scale is not exaggerated. All figures are in metres.

As the Aufwuchs is of fundamental importance in the biological economy of the rocky shore a few words may be said about its development. The prevailing physical conditions probably approximate closely to those which are optimal for its development and can be listed as follows.

(1) Great transparency of the water : This permits the passage of light of high intensity to the rock surfaces and permits photosynthesis to take place at a great rate.
(2) High light intensity : This is provided by the tropical sun and operates in conjunction with (1).
(3) High temperature : The surface temperature of the lake appears to be always above 20°C. and is sometimes considerably higher. (Maximum recorded at Nkata Bay during two years daily observations 28·6° C. Min. 22·6° C.).
(4) Absence of a winter check in growth : Conditions (2) and (3) persist throughout the year.
(5) Favourably situated for receiving salts swilled in from land.

In addition, the algal Aufwuchs community harbours a very dense microfauna (see below) the products of whose respiration are released in very close proximity to the algae which presumably benefit from this during the process of photosynthesis.

During the dry hot season, when the lake level falls, a fairly thick layer of the filamentous green alga *Cladophora glomerata* (L) Kuetzing develops on many of the rocks around the water line and a few centimetres below it. This layer moves lower down the rocks as the lake level continues to fall, and that which is left high and dry becomes powdery and disintegrates. As the lake level rises with the advent of the rains the alga becomes submerged and during the rainy season, when the lake is at its maximum level, *Cladophora* is virtually absent. Unlike the Aufwuchs, *Cladophora* appears to be of negligible significance in the economy of the rocky shore.

(b) *The sandy shore*

The sandy shore (Pl. 1, fig. 3) consists, in the main, of a sandy slope pitching very gently so as to be only about 4 metres below the surface some 100 to 120 metres from the shore, beyond which point, however, it shelves much more steeply to considerable depths (Fig. 2, A). The sand is fairly fine and somewhat compact along the margin at the northern end due to a considerable admixture of flakes of mica, but is coarser a little way off shore and at the southern end. This monotonous substratum occupies most of the sandy shore but the middle section includes an area in which the bottom is rather soft and humic and contains a number of partly mineralised tree stumps, being in fact a remnant of a once wooded and now innundated shore. A few isolated patches of humic material occur to the north of this area but in general the rest of the shore is sandy.

The water on the sandy shore, while very clear during periods of calm weather, becomes visibly turbid during periods of onshore wind when breakers of considerable size roll onto the beach. It also assumes a red coloration due to the presence of mud particles on those occasions during the rainy season when the stream feeding Crocodile Creek is in spate.

Vegetation is sparse, particularly towards the southern end where its development may be hindered by intermittent deposition of silt from Crocodile Creek during the rainy season. In the main it consists of beds of *Vallisneria*, none of which appear to be more than about 10 sq. metres in extent, the majority being smaller than this. Even towards the northern end of the shore, where they attain their maximum development, these beds occupy no more than about 12 or 15 per cent of the total bottom area. Only two other species of higher plant have been seen on this shore, these being a grass-like species as yet unidentified and *Ceratophyllum* sp. both of which are so rare as to be without importance.

The strap-like leaves of the *Vallisneria* are coated with an Aufwuchs (or periphyton) community whose composition is broadly similar to that found on the rocks of the rocky shore but which does not include the firmly attached species of *Calothrix*.

It may be remarked that the configuration of the sand spits at the mouth of Crocodile Creek varies considerably throughout the year, that shown in the map representing what is approximately the average condition.

During the dry season, when the lake level falls, the more shoreward beds of *Vallisneria*, which had formerly been immune from the major effects of deposition of sand brought into suspension by the breakers, become more exposed to this influence and tend to become buried and disappear or, in some cases, they become exposed to the air and meet a similar fate. Because of the sudden downwards plunge of the sandy shore at a distance of 100 to 120 metres from the high water line the *Vallisneria* is unable to spread outwards to compensate for this destruction so that the total area covered by vegetation becomes progressively reduced as the lake level falls. This seasonal fluctuation in abundance of a primary food source is of considerable ecological and evolutionary importance.

(c) *The intermediate zone*

Between the rocky and sandy shores occurs a zone whose rather restricted limits are roughly indicated on the map. Here conditions are intermediate between those prevailing in the two previously described zones. The margin is rather rocky (Pl. 1, fig. 4) but the rocks tend to be small, while the bottom is composed of sand on which a number of rocks of various sizes are scattered like small islands. Between the rocks there are a number of beds of *Vallisneria* which occupy perhaps 25 per cent of the total bottom area.

Conditions in this zone are more sheltered than they are anywhere along either the rocky or sandy shores. Large waves seldom break on the shore and the bottom is therefore less disturbed than on the sandy shore. The effects of deposition from Crocodile Creek are negligible. Conditions for plant growth are therefore more suitable than they are along most of the sandy shore. Even so, *Vallisneria* is the only higher plant which occurs there in significant amounts.

(d) *Crocodile Creek*

Crocodile Creek is a small lagoon at the mouth of a stream, locally known as the Nkata, which in certain dry seasons at least, dries up completely so that the creek becomes an isolated pool separated from the lake by a spit of sand. By contrast it becomes a swirling muddy torrent during the periods of torrential rain which occur during the rainy season. Throughout most of the year, however, its waters are tranquil and, because it is considerably wider and deeper than the stream feeding it, the water movements are usually barely perceptible.

During the wet season and for some time after, the creek overflows and forms a small, shallow, lateral lagoon on its northern bank which extends some way behind the sandy shore.

The maximum depth of water in the creek seems to be nowhere more than about 3·5 metres.

The bottom, while composed essentially of sand, is covered with flocculent muddy detritus and algal growths, some of which are scoured out during the rainy period.

The water is decidedly "cloudy", so much so that one usually cannot see a Secchi disc at depths of more than 1 metre. This cloudiness persists in jars of water left standing for several days. The water has a peculiar opalescence which seems to be peculiar to sluggish tropical streams but which is not unlike that seen in certain ferruginous waters in Britain and may be due to the presence of ferruginous matter.

Aquatic vegetation is both more plentiful and more varied than that found in any of the lacustrine habitats. The shores of the creek are lined with *Phragmites mauritianus* Kunth, which barely extend into the water, while in the narrower parts the water is overhung by a dense growth of small trees and bushes. In the narrower parts of the creek, and extending some way into the lagoon region, occur dense masses of aquatic grasses, mainly *Vossia cuspidata* (Roxb.) Griff. which, during the dry season when they grow unchecked by floods, become so dense as to make it difficult to force a small boat through them ; the only open " road " usually being that made as a result of the perigrinations of crocodiles. In the more open water of the lagoon region a number of blue water lilies (*Nymphaea* sp.) develop during the dry season, and dense masses of the filamentous green alga *Spirogyra* sp. accumulate.

ZONAL BOUNDARIES

In concluding the description of the area studied a few words must be said about the points at which the various zones meet.

The union of Crocodile Creek and the sandy shore is very clear cut and one can say exactly where one habitat ends and the other begins.

By contrast, the sandy shore and the intermediate zone merge imperceptibly into one another over a zone of some 10 to 20 metres, but on either side of this divide it is very easy to separate the two zones.

The intermediate zone is very well separated from the rocky shore by a large rocky projection which limits the sharply defined zone of contact to a narrow strip.

As shown on the map (Fig. 1) there is a very narrow strip which can be considered as a point of contact between the rocky and sandy shores. While most of this strip lies in rather deeper water than that covering the sandy littoral zone there is a point at which the two meet in only 4 or 5 metres of water even at periods of high lake level.

These notes, together with the map, reveal that there are certainly no obvious barriers to the dispersal of active organisms such as fishes, particularly between the three lacustrine zones.

THE FAUNAL CHARACTERISTICS OF THE FOUR ZONES

In correlation with the physiographic features of the four major habitats outlined above each has its own distinctive animal community. The general composition of each of these communities is briefly outlined below, so providing a background against which to consider the ecology and interrelationships of its various components.

(a) *The rocky shore*

The algal-covered rocks of the rocky shore harbour a surprising wealth of small invertebrates. Among the Aufwuchs occur countless thousands of small chironomid larvae, ostracods and harpacticoid copepods. The chironomid larvae represent several species, some possibly undescribed ; the ostracods are represented almost entirely by two species of *Cypridopsis*, both possibly undescribed, while the dominant copepod is *Schizopera consimilis*

Sars, a species not previously known to occur in the lake. A few specimens of the ostracod *Zonocypris* sp. and of the endemic copepod *Schizopera fimbriata* Sars, also occur but are of negligible importance.

In order to obtain some idea of the approximate abundance of these organisms a rock whose upper, Aufwuchs-covered surface had an area of approximately 510 sq. cm. was carefully scraped and the total fauna was counted. The results can be expressed as follows.

TABLE 1

Invertebrate fauna of upper surface of a stone of area 510 sq. cm. and approximate density per sq. metre deduced from this count.

	Number on stone	Number per sq. metre
Chironomid larvae	3,555	69,700
Cypridopsis spp.	10,102	198,000
Schizopera consimilis	1,000+	20,000+
Other dipterous larvae	22	431
Mites	59	1,158
Eubrianax larvae	3	59
Nymphal bugs	1	19
Afronurus nymphs	1	19
Elmid larvae	1	19

The number of *Schizopera* present was not counted as these minute and delicate organisms tended to be damaged by the scraping process, but it is certain that a number well in excess of 1000 was present. For obvious reasons the tedious count was not repeated. Further information on the total biomass on the rocks has, however, been obtained and is given later.

The most striking feature of the count is the remarkable density of the fauna in what would, on superficial examination, appear to be an uncongenial situation. It is interesting to note that under somewhat similar situations in the sea the existence of similar dense invertebrate faunas has recently been demonstrated, at least in the Azores. (Chapman, 1954).

A few other organisms live among the Aufwuchs as can be seen from Table 1. Of these mites and an unidentified dipterous larva are of fairly frequent occurrence while the other organisms occasionally recorded belong more properly to the under surface fauna of the stones and when recorded from among the Aufwuchs have probably wandered there for feeding purposes. The under surface fauna includes two species of leech, one of which is common, while the other is rare ; a stone-fly nymph *Neoperla spio* (Newman) which is fairly common ; mayfly nymphs belonging to two species of the genus *Afronurus* which are also fairly common ; baëtid nymphs, and nymphs of an anisopterid dragonfly (*Phyllogomphus* sp.) neither being common ; the larvae of two species of hydropsychid caddis flies, one of which is plentiful and the other certainly not rare, a small unidentified caddis larva of negligible importance, the larva of a psephenid beetle (*Eubrianax* sp.) which is fairly common, larvae and adults of a tiny elmid beetle which are seen occasionally, a very rare elmid larva, an occasional bug *Naucoris flavicollis* Sugn., and a few tiny rhabdocoele turbellarians. This list is by no means a long one, and of the under-surface fauna only the mayfly and stonefly nymphs, and the larvae of the hydropsychids and *Eubrianax* have been found to play an important part in the welding together of the community as a whole. An unidentified encrusting sponge with simple monaxonic spicules, and a crab, complete the list of invertebrates other than protozoans and rotifers. Of these the sponge need not be considered further but the crab, *Potamonautes lirrangensis* (Rathbun), until Bott's (1955) recent revision known as *Potamon* (*Potamonautes*) *orbitospinus* Cunnington and believed to be endemic to Lake Nyasa, is of some importance.

Under stones at the water's edge occur occasional tipulid larvae ; and a small collembolan is often present in large numbers on the surface film at the extreme margin.

Most notable among the absentees from the rocky shore are the molluscs which appear to be totally unrepresented here. Possible explanations of this are discussed in a subsequent section.

The density of the larger invertebrates among the rocks is decidedly low. On turning over an easily handled stone one finds perhaps as few as half a dozen specimens of insect nymphs and larvae, and seldom more than about twenty, whereas in many temperate lakes, and certainly some tropical lakes, dozens of similar invertebrates occur under such a stone.

Important from both a biological and an economic point of view are the fishes which abound on the rocky shore. As in most environments in the lake the family Cichlidae predominates, being represented by more than twenty species which can be regarded as permanent residents in this zone. Five non-cichlid fishes belonging to the families Clariidae, Mastacembelidae and Cyprinidae, however, are also important members of this community. In addition several other fishes which must be regarded as either very rare or as being casual in their occurrence have been recorded. These are either unimportant or are visitors to the rocky shore only at certain times of the year, when, however, they may be present in considerable numbers. A list of the more important resident fishes of this zone is given in Table 4 (p. 171) where comparison is made with the fish fauna of the other zones.

While a detailed account of the ecology and interrelationships of these fishes is given in a subsequent section attention may be drawn here to two points concerning their size and abundance. With few exceptions these fishes are small, only a few species exceeding a length of 20 cm. when fully grown. In spite of their small size, however, their biomass is great as they are very numerous. Estimations of abundance using a grid covering an area of one square metre have revealed that on the average at least six or seven fishes occur per square metre of the bottom. Sometimes as many as twelve were observed within the confines of the grid.

A few birds visit the rocky shore. Of these the reed cormorant, *Phalacrocorax africanus* (Gmelin) the South African darter, *Anhinga rufa* (Lacépède & Daudin) and the pied kingfisher, *Ceryle rudis* (L.) are the most important as they all take fish from this zone. Their numbers, however, are not great, and considering the great number of fishes present their depredations are probably inconsequential. Other fish-eating birds such as the fish eagle, *Haliaetus vocifer* (Daudin) and the malachite crested kingfisher, *Corythornis* *cristata* (Pallas) are also seen here occasionally and probably take fishes from time to time.

Torn fishing nets indicate that crocodiles occasionally visit this shore during the course of their nocturnal prowlings though the slight possibility that such damage is sometimes caused by otters cannot be ruled out.

(b) *The sandy shore*

While a few species are common to both the rocky and sandy shores there is, on the whole, a very well marked and clear cut distinction between the two faunas. On the sandy shore there is a more diverse invertebrate fauna and an almost entirely different fish fauna. Among the invertebrates, for example, molluscs, which are unrepresented on the rocky shore, are here represented by four species of gastropods and three lamellibranchs. As shown in Table 3 (p. 169) the crustaceans are more strongly represented than is the case on the rocky shore. Among their number the most striking form is the atyid prawn *Caridina nilotica* Roux.

The weed beds harbour the majority of the sandy shore invertebrates. Here occur all the snails, viz. *Lanistes procerus* (Martens), *Melanoides tuberculata* (O. F. Müller), *Bulinus nyassanus* (E. A. Smith) and *Gabbia stanleyi* (E. A. Smith), a variety of larval and nymphal insects including anisopterid and zygopterid dragonfly nymphs, baëtid nymphs and nymphs of *Caenis* sp., chironomid larvae and a few caddis larvae, numerous mites, and a variety of crustaceans of which the prawn *Caridina nilotica*, the cyclopoid copepods *Microcyclops nyasae* Fryer, and *M. bitaenia* Fryer and the ostracod *Cypridopsis cunningtoni* Sars, are the most abundant. Other invertebrates occur among the weed beds, of which *Schizopera consimilis*, occasional specimens of other copepods and ostracods, and a very occasional leech are worthy of mention, but are probably of scant ecological importance.

While time did not permit the making of detailed quantitative studies of the fauna of the weed beds an attempt was made to collect by the use of nets as many as possible of the larger organisms present in four separate small beds of *Vallisneria*. The technique employed was very crude and some individuals of even the larger species probably evaded capture. Further, such small beds as those sampled probably harboured a less dense fauna than the larger beds which were less amenable to sampling. Bearing these limitations in mind, the figures obtained do serve to give a very rough idea of the minimum number of organisms present per unit area in the weed beds.

TABLE 2

Rough minimum numbers per square metre of larger invertebrates in beds of *Vallisneria*

Species	Average number/sq. metre (4 samples)
Caridina nilotica	178
Baëtid nymphs	28
Caenis nymphs	7
Anisopterid nymphs	8
Caddis larvae	10
Melanoides tuberculata	16
Other invertebrates	see text

In addition chironomid larvae, mites and *Microcyclops nyasae* each had populations running into at least hundreds per sq. metre and the ostracod *Potamocypris cunningtoni* was measurable in thousands per sq. metre.

The areas of bare sand, while giving the impression of being devoid of invertebrate life nevertheless have a distinctive fauna on whose members certain fishes depend entirely or almost entirely for sustenance. The rather important little bivalved mollusc *Corbicula africana* (Krauss) occurs here, as does an unidentified mutelid, and the snail *Melanoides tuberculata* often wanders over the surface ; but of much greater consequence are certain small chironomid larvae which burrow in the sand. These, however, appear to be rather sparsely distributed and the fishes which utilise them as a source of food appear to find it necessary to maintain an almost constant search. Also present in the sand are large numbers of the burrowing harpacticoid copepod *Parastenocaris fossoris* Fryer, whose length is less than 0·5 mm. and whose density has been estimated as being at least 10,000 per sq. metre (Fryer, 1956b).

Several species of burrowing cyclopoid and harpacticoid copepods, a detailed description of which has been given elsewhere (Fryer, 1956b), as well as a number of other minute organisms (ostracods, mites, rotifers, tardigrades, oligochaetes, nematodes, etc.) occur in great numbers in the interstitial spaces of the marginal sand bank of the sandy shore where they constitute a little microcosm of their own which depends basically upon the detritus which becomes trapped among the sand grains, and upon certain minute algae which are able to develop there. Of these, however, one cyclopoid copepod *Microcyclops obscuratus* Fryer, like its harpacticoid relative *Parastenocaris fossoris*, occurs also in the submerged sand and also on its surface and therefore plays some part in the general economy of the sandy shore.

The humic areas do not appear to be very rich faunistically though the endemic copepod *Eucyclops dubius* Sars, is at times to be found there in considerable numbers. A large lamellibranch, *Unio* sp., also occurs here but is very rare.

The fishes of the sandy shore are numerically fewer than among the rocks and the number of species represented by the habitués is less. A comparative list of the fishes is given in Table 4 (p. 171).

The same birds as are seen on the rocky shore also frequent the sandy shore. Casual observations, however, indicate that the pied kingfisher fishes more frequently over the sand than over the rocks, possibly because the juvenile fishes which probably constitute the major part of its diet often belong to shoaling species on the sandy shore and are perhaps more easily obtained here than among the rocks where refuges are abundant.

(c) *The intermediate zone*

Because of the presence of beds of *Vallisneria* the invertebrate fauna of the intermediate zone is very similar to that of the sandy shore, while the rocks, particularly those at the margin, provide conditions which are suitable for certain members of the true rocky shore community. As the marginal area is less in extent than the area dominated by weed beds the invertebrate fauna is, in general more like that of the sandy than the rocky shore. Similarly the fishes of this zone are predominantly those living also on the sandy shore though members of the rocky shore community are also occasionally represented. In addition, however, several fishes of which one, the cichlid *Cyathochromis obliquidens* Trewavas, is the commonest species in this zone, are virtually confined to it, and several other fishes, e.g. *Haplochromis johnstoni* (Günther) and *Hemitilapia oxyrhynchus* Boulenger which frequent the beds of *Vallisneria* are more common here than on the sandy shore, presumably because of the greater extent of the weed beds.

(d) *Crocodile Creek*

The fauna of Crocodile Creek differs as much from that of either the rocky or the sandy shore as do the two latter from one another. Its general characteristics are those of a fauna associated with a weedy lentic environment. Insects are more conspicuous here than in any of the true lake zones. Thus surface-dwelling hemipterans of the family Gerridae, which are unable to establish themselves in the lake zones,* are here very common. Below the surface baëtid nymphs are very common and constitute an important part of the fauna. Living with these nymphs among the vegetation are also several species of nymphal anisopterid and zygopterid dragonflies, adult dytiscid and gyrinid beetles, and bugs of the genera *Ranatra*, *Notonecta* and *Naucoris*, while among the bottom detritus certain chironomid larvae are plentiful. At certain times of the year at least both culicine and anopheline mosquito larvae are also present. Snails are represented by three small species, viz. *Gyraulus costulatus* (Krauss), *Segmentorbis angustus* (Jijkeli) and *Limnaea* sp., while the large *Lanistes procerus* occasionally wanders in from the lake. The crustacean fauna of the creek, when compared with that of the lake zones clearly demonstrates the difference in the environments, being much more diverse (Table 3, p. 169) and including several weed loving and muddy bottom forms which are conspicuous by their absence in the lake. Several of these forms belong to the order Cladocera which appears to be totally unrepresented in the true littoral fauna of this part of the lake. A four-tentacled brown *Hydra*, not recorded from the lake, is also not uncommon among the weeds.

The list of fishes (Table 4, p. 171) is much less impressive than that of any of the lake zones, and the adaptations of many of the species, most of which can be described as " bottom grubbers " are usually less striking.

A few frogs spawn in the creek. Some of the resulting tadpoles attain considerable bodily proportions and must consume as much food as many small fishes per unit of time.

The creek also houses a few crocodiles (*Crocodilus niloticus* L.). Although at least three specimens 3 metres or more in length were destroyed in the early months of 1955 at least two large individuals remained, and a considerable number of young belonging to at least two broods were hatched in this year. Some idea of the abundance of these young can be obtained by noting that no

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* The expression " unable to establish themselves " is used with deliberation as on one occasion during the dry season a number of nymphal gerrids appeared in a sheltered " pool " among the rocks of the rocky shore, thus showing a latent tendency to colonise, but these were quickly exterminated by subsequent wave action and did not survive to maturity.

fewer than seven, each about 30 cm. in length, were on one occasion found imprisoned in a fish trap set by a local African, and several times odd specimens have been caught in this manner. The large crocodiles move into the lake by night, where they presumably feed, and return early in the morning. Part of the day is spent lying in the sun. Thus they enter only indirectly into the economy of the creek by producing manure and keeping open lanes through the vegetation. Young crocodiles feed in the creek and appear to subsist, like the small specimens studied by Cott (1954), on insects. One juvenile contained also the remains of a frog or toad.

Birds are more numerous in the vicinity of this zone than in those previously considered, and while some, such as the numerous weaver birds which build nests overhanging the water, probably contribute nothing more than a rain of faecal matter and an occasional luckless nestling to the food cycle of the creek, others such as the pied kingfisher, the malachite crested kingfisher, and several bitterns and allied forms probably play a much more direct part in the general ecology of the aquatic environment. Of these the pied kingfisher at least has repeatedly been observed fishing here.

Habitat differences reflected by the Crustacea

The faunistic differences in the major habitats are exemplified by the Crustacea, which class, in comparison with certain other groups, is relatively well represented, individually if not specifically, in all the habitats. A comparative table (Table 3) conveniently serves the dual purpose of listing those species which occur and of demonstrating the faunistic reflection of environmental differences.

The crustacean fauna of the intermediate zone is the same as that of the sandy shore and is not listed separately. In order to emphasise its true habitat the crab *Potamonautes lirrangensis*, which frequently wanders into the sandy shore for feeding purposes but which actually spends most of its time among the rocks, is not included in the list of sandy shore species. The true psammophilous copepods living above the water line on the sandy shore are also omitted from the list.

In addition to the dissimilarities shown by the free-living species there are differences between the parasitic crustaceans of the fishes of the lake zones and those of Crocodile Creek. While these not unnaturally largely reflect differences in the host species present, two of the branchiurans infesting members of the genus *Clarias* may be more dependent on certain general characteristics of the environment than on the specific identity of the host. Thus the species of *Clarias* inhabiting the lake proper serve as hosts for *Argulus africanus* Thiele which is very common, and which is not restricted to any one particular species of *Clarias*, nor even to members of the genus. The species has not been recorded in Crocodile Creek. On the other hand, with a single exception, the branchiuran *Dolops ranarum* (Stuhlmann) has not been recorded from the lake proper, yet two of the few specimens of *Clarias mossambicus* Peters, obtained from Crocodile Creek bore specimens of this parasite. It is fairly obvious that conditions in Crocodile Creek will be unsuitable for the larval development of species living in the more open waters of the lake, and the

TABLE 3

Comparative lists of the Crustacea of the rocky and sandy shores and of Crocodile Creek.

ROCKY SHORE	SANDY SHORE	CROCODILE CREEK
Potamonautes lirrangensis (Rathbun)	*Caridina nilotica* Roux	*Caridina nilotica* Roux
Cypridopsis spp.	*Cypridopsis cunningtoni* Sars	*Pseudosida szalayi* Daday
Zonocypris sp.	*Zonocypris* sp.	*Ilyocryptus spinifer* Herrick
Schizopera consimilis Sars	*Microcyclops nyasae* Fryer	*Pseudalona longirostris* (Daday)
Schizopera fimbriata Sars	*Microcyclops bitaenia* Fryer	*Euryalona orientalis* (Daday)
Ectocyclops phaleratus medius Kiefer*	*Microcyclops obscuratus* Fryer	*Pleuroxus denticulatus* Birge
	Eucyclops dubius (Sars)	*Chydorus sphaericus* (O. F. Müller)
	Ergasilus macrodactylus Sars (copepodid)	*Chydorus ventricosus* Daday
	Schizopera consimilis Sars	*Macrocyclops albidus oligolasius* Kiefer
	Parastenocaris fossoris Fryer	*Eucyclops agilis* (Koch)
		Eucyclops euacanthus (Sars)
		Tropocyclops prasinus (Fischer. Schmeil)
		Ectocyclops phaleratus medius Kiefer
		Mesocyclops leuckarti (Claus)
		Microcyclops bicolor breviramus Fryer
		Attheyella bidens (Schmeil)
		Phyllognathopus viguieri (Maupas)
		Stenocypris sp.
		Cypridopsis sp.
		Ostracoda indet.

* A single specimen only encountered.

converse seems to be true for *Dolops ranarum* which has been recorded from swampy lagoons and rivers elsewhere in Nyasaland, and which is by no means restricted to *Clarias mossambicus* as a host.

The crustaceans of the plankton, which often occur in the inshore waters, are not included in the foregoing lists as they do not properly belong to the faunas considered. As they are utilised as food by certain littoral organisms, however, they can be conveniently listed here. They are the copepods *Diaptomus* (*Tropodiaptomus*) *kraepelini* Poppe & Mrazek, *Mesocyclops leuckarti* (Claus), and *Mesocyclops neglectus* Sars, and the cladocerans *Diaphanosoma excisum* var. *stingelini* Jenkin, *Bosmina longirostris* (O. F. Müller) and *Bosminopsis deitersi* Richard. These, together with the larva of the midge *Corethra edulis* Edwards contribute the most important elements of the zooplankton in the northern part of the lake. Of the crustaceans listed *Diaptomus kraepelini* is by far the most important as a source of food for fishes and figures largely in the stomach contents of both inshore and pelagic plankton-feeding species.

THE FISHES : THEIR ECOLOGY AND ADAPTATIONS

A primary object of the present study was to discover something of the habits and ecology of the littoral fishes. A difficulty in presenting the information obtained lies in the fact that, while the majority of the fishes concerned have been named by systematists, in many cases the description necessary to back up the name has not been published, and no illustrations are available to enable the ecologist to gain an idea of the form of the individual species. Partly in order to overcome this difficulty, therefore, and partly to illustrate the discussion on feeding habits, a considerable number of illustrations have been prepared to supplement the following account.

Before discussing the individual species a few words can be said about the salient features of the various fish communities each of which, as the table shows, is remarkably distinct.

The rocky shore is populated by a large number of both species and individuals of small fishes, mostly of the family Cichlidae, which are usually either dark in colour or very brightly coloured, particularly, but not only, when in breeding dress. The most outstanding adaptations of many of them are concerned with the collection of food from hard rock surfaces. Most species, when disturbed, flee only for short distances and then take refuge beneath rocks. These little fishes constitute a rich source of food which has been exploited by a number of rather larger predatory species which take quite a heavy toll of the non-predatory species, and particularly of the juvenile stages. There is some evidence that the predatory fishes from rather deeper water also feed to some extent on the rock fishes. In addition to these forms there are two species which skulk beneath the rocks, being thus quite different in habits from the majority of the rocky shore fishes which spend most of their time hovering around and above the rocks.

It is most interesting to notice that the local Africans, while giving individual names to many of the rock fishes, recognise some of the cichlid members of the community as an ecological unit, refering to them in Chitonga as " Mbuna ".

TABLE 4 List of the fishes of the three littoral communities, and of Crocodile Creek

ROCKY SHORE	SANDY SHORE	INTERMEDIATE ZONE	CROCODILE CREEK
Labeotropheus fuelleborni	*Lethrinops brevis*	*Cyathochromis obliquidens*	*Serranochromis robustus**
Labeotropheus trewavasae	*Lethrinops furcifer*	*Pseudotropheus lucerna*	*Tilapia shirana*
Labidochromis vellicans	*Lethrinops* sp.	*Aulonocara nyassae*	*Tilapia saka-squamipinnis*
Labidochromis caeruleus	*Haplochromis similis*	*Haplochromis compressiceps*	*Haplochromis similis*
Pseudotropheus zebra	*Haplochromis johnstoni*	*Hemitilapia oxyrhynchus*	*Barbus innocens*
Pseudotropheus williamsi	*Haplochromis mola*	*Lethrinops* spp. cf. *praeorbitalis*	*Barbus paludinosus*
Pseudotropheus livingstonii	*Haplochromis rostratus*		*Alestes imberi*
Pseudotropheus auratus	*Haplochromis moorii*	(and most of the sandy shore species).	*Clarias mossambicus*
Pseudotropheus fuscus	*Haplochromis dimidiatus*		*Clarias mellandi*
Pseudotropheus elongatus	*Haplochromis chrysonotus*		
Pseudotropheus minutus	*Haplochromis kiwinge*		
Pseudotropheus fuscoides	*Tilapia saka-squamipinnis*		
Pseudotropheus tropheops	*Tilapia melanopleura*		
Gephyrochromis lawsi	*Tilapia shirana*		
Melanochromis melanopterus	*Hemitilapia oxyrhynchus*		
Getrotilapia tridentiger	*Rhamphochromis* spp.		
Pynotilapia afra	*Alestes imberi*		
Cenyochromis mento	*Barbus johnstonii*		
Haplochromis fenestratus	*Barbus innocens*		
Haplochromis euchilus	*Barbus rhoadesii*		
Haplochromis ornatus	*Labeo mesops*		
Haplochromis pardalis	*Engraulicypris sardella*		
Haplochromis polyodon	*Synodontis zambesensis*		
Haplochromis sp. nov.	*Barilius microcephalus*		
Haplochromis kiwinge			
Haplochromis guentheri			
Rhamphochromis spp.			
Labeo cylindricus			
Varicorhinus nyasensis			
Barilius microcephalus			
Bathyclarias worthingtoni			
Mastacembelus shiranus			

* Recorded as *S. thumbergi* by Trewavas (1935)

NOTE.—This is not a complete list, species having been seen on only rare occasions being omitted. Similarly species which definitely belong to one community but have been found as occasional wanderers (though such cases are remarkably few) have been listed only for the community or communities to which they obviously belong.

Similar recognition of these fishes as an ecological entity is made by the Chinyanja-speaking people of the southern part of the lake who speak of them as " Chindongo ", and a similar name is given to them by the Swahili-speaking people on the north-eastern shore of the lake. This ecological grouping also has taxonomic validity.

In striking contrast to the dark or brightly coloured fishes of the rocky shore those species inhabiting the sandy shore are predominantly silvery or light in colour. The outstanding adaptations of the non-predatory species are concerned largely with the habit of digging in the sand or browsing on the higher aquatic plants or on their covering of Aufwuchs. Their escape reaction is one of precipitous flight rather than refuge seeking. Like the rocky shore the sandy shore has its quota of predators, but these, in the main, belong to different species to those found in the former habitat.

As might be expected there are differences in the breeding habits of the fishes belonging to the rocky and sandy shore communities. The most striking difference in this respect is that some sandy shore species belonging to the family Cichlidae construct sandscrape nests (Lowe, 1952 ; Fryer, 1956c) while the rocky shore species apparently breed among the rocks where many of them occupy definite territories during the breeding periods. Further details of the breeding habits of rocky shore species are given in Part II.

The outstanding features of the fish communities of the intermediate zone and of Crocodile Creek will become apparent during the subsequent account and call for no further comment here.

The very striking adaptations shown by many of these fishes, together with the fact that most of them are rigorously restricted to one habitat and to one kind of food stands in marked contrast to the state of affairs in freshwater fishes in general where, as pointed out recently by Larkin (1956), the tendency is to avoid overspecialisation. The specialisations shown by these Nyasan fishes can be regarded as a reflection of the relatively permanent nature of their environment as opposed to the essentially transient condition of most freshwater situations.

The most important fishes of the various habitats are discussed individually below, each habitat being considered in turn.

(a) *The rocky shore*

A striking feature of the fish fauna of the rocky shore is that a large proportion of its members belong to a group of genera (*Pseudotropheus* and its allies) which are sufficiently distinct from the rest of the Nyasan cichlids to merit them being regarded as at least a tribe (using the term in the sense of a " super-genus "). These fishes, which correspond almost exactly with the " Mbuna " of the local fishermen, are completely unrepresented on the sandy shore. The first eighteen species discussed below belong to this group.

Labeotropheus fuelleborni Ahl. (Figs. 3–7)

This species, which attains a length of about 12 cm., is one of the commonest fishes of the rocky shore. It is seldom to be seen more than a few centimetres from rock surfaces from which it obtains its food, It swims over rocks of all shapes, always keeping its ventral surface approximately parallel to the substratum and can browse with equal facility on vertical and horizontal surfaces.

Examination of the gut contents of forty-eight specimens ranging from 2·7 cm. to 11 cm. in total length collected at Nkata Bay, supplemented by a few such examinations made elsewhere (see p. 233) and by observations on the fish both in nature and in aquaria reveal that the food consists entirely of algal Aufwuchs scraped from rock surfaces. Both the loosely attached algae, henceforth spoken of as " loose Aufwuchs ", and the firmly attached tufts of *Calothrix* are removed from the rocks and swallowed.

The form and position of the mouth, and the dentition are remarkably adapted to this habit. The mouth is ventrally situated so that as the fish swims over the rocks it can be very easily adpressed to their surfaces. It is also exceptionally wide, extending transversely across the full width of the head, thus allowing a wide band of rock surface to be scraped at a single application of the mouth.

Each jaw margin is very straight and is lined with a palisade of teeth whose broadened tips are in contact and form a continuous scraping surface across the jaw (Figs. 3, 4, 5). Each tooth of the palisade is curved so as to allow the broadened spatulate tip to act as a scoop as well as a scraper and, while narrow from side to side at its base, it is broadened and strengthened from back to front in order to give strength along the plane subjected to maximum stress whilst in use (Figs. 6 & 7). The narrowness of each tooth from side to side at the base may possibly permit the passage of water, as through a sieve, between the teeth and thus prevent scraped-up material from being swilled away by currents which may otherwise be set up.

Food is collected by a series of " nibbles ", the mouth being kept adpressed to the rock surfaces throughout the process. A dozen or more " nibbles " usually take place in quick succession during which time the fish moves forwards very slightly. The effect of a forward movement of the lower jaw and a downward (backward) movement of the upper jaw (the latter following as an inevitable consequence of the former during the process of closing the mouth) is to scrape Aufwuchs from the rock surface and pile it up along each palisade of teeth. This piled up food material must then be taken into the buccal cavity, and, although actual observations are most difficult to make, it seems reasonable to suppose that this process is effected by the inflow of water to the mouth as the latter opens.

It is possible that the ability to remove the firmly attached tufts of *Calothrix* from the rocks is only acquired after the juvenile stages have been passed through as while most, but not all, adult specimens obtained at Nkata Bay contained a percentage of *Calothrix* a specimen only 2·7 cm. in length contained only loose Aufwuchs.

While *Calothrix* figures largely in the gut contents of this species it seems to be at most only partially digested and the fish is by no means dependent on this alga as is shown by work carried out at Mbamba Bay (see p. 233).

The general arrangement of the mouth and the method of feeding bear certain striking similarities to those found in the non-cichlid genus *Labeo*, as Ahl obviously realised when he coined the generic name *Labeotropheus*.

This species and members of the genus *Labeo*, when compared, present an interesting example of parallel evolution at both a morphological and an ecological level in fishes belonging to quite different families. (A discussion of the feeding of *Labeo cylindricus* is given on page 189).

Labeotropheus trewavasae Fryer

It was only on making a morphometric study of preserved material after completion of the field work (Fryer, 1956d) that this species, which is very closely related to *L. fuelleborni*, was found to be specifically distinct. While the failure to recognise it as distinct in the field makes it unwise to say much about its ecology there can be no doubt that its requirements are much the same as those of *L. fuelleborni* and that it co-exists with this species in the littoral zone of the rocky shore at Nkata Bay. It is, however, less common than *L. fuelleborni*.

The mouth structure is identical in the two species and the feeding mechanism is therefore presumably the same. The food found in the guts of ten specimens (plus five collected at Ruarwe) ranging from 7·4 to 11·7 cm. in length was inseparable in composition from that found in the guts of *L. fuelleborni*.

Labidochromis vellicans Trewavas. (Figs. 8–11)

This little species, whose total length seldom exceeds 7 cm., is quite common among the rocks close to the shore, but it appears to have a very restricted horizontal range. It has a rather elongate, slender body and large eyes and is very active in its movements, but is rather secretive in habits, always keeping close to the rocks between and under which it hides and seeks its food. Its somewhat sombre coloration is possibly correlated with its general habits.

The gut contents of twenty-six specimens ranging from 4·6 cm. to 6·8 cm. in length reveal that most of the common rocky shore invertebrates are eaten by this species. A list showing their approximate order of importance as food is given in Table 6. (p. 222)

The mouth is very narrow and both upper and lower jaws are armed with exceedingly long, recurved, conical teeth whose apices are opposed and form in effect fine forceps, ideally suited to picking out from among the algae covering the rocks the chironomid larvae and other small invertebrates on which it feeds.

Specimens kept in an aquarium furnished with rocks from the rocky shore were regularly observed to nip food from them with a single quick action. Frequently there is a quick twist of the body as the food is seized, presumably to assist in its dislodgment. Specimens have been seen to take food from the rocks and later to expel from the mouth algal particles presumably picked up inadvertently with the animal food. Thus while there is an original careful visual selection of the food and a deliberate seizure by the teeth, still further selection occurs in the mouth. This explains the relatively insignificant amounts of algal material seen in the guts examined.

Labidochromis caeruleus Fryer

This recently described species is very closely related to *L. vellicans* from which it differs most conspicuously in coloration, both sexes being a beautiful light blue with black bands on the fins (for details see Fryer, 1956a) as opposed to the rather sombre hues of *L. vellicans.* Its oral dentition is practically identical with that of its congeneric associate but it differs somewhat in the pharyngeal dentition, the lower pharyngeal bone having somewhat larger and stouter teeth than its counterpart in *L. vellicans.* This difference might be expected to be correlated with a slight difference in diet, and some evidence that this may indeed be the case is presented in the section dealing with competition among the fishes.

Very little information on the general habits of *L. caeruleus* has been obtained though specimens have been seen swimming about over the rocks on several occasions, sometimes two or three specimens being in company. The impression gained from these casual observations is that it is less of a " skulker " than is *L. vellicans* and is more " sedate " in habits ; facts which may be correlated with its slightly deeper body than that of *L. vellicans.*

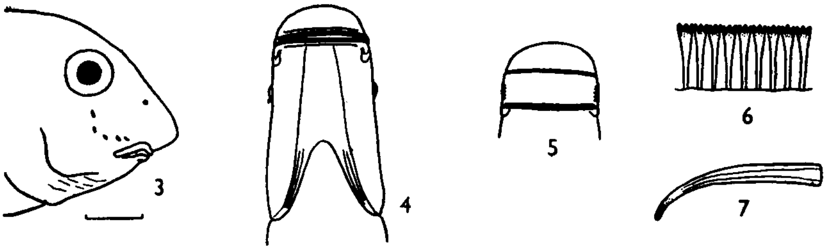
Petrotilapia tridentiger Trewavas. (Figs. 12–15)

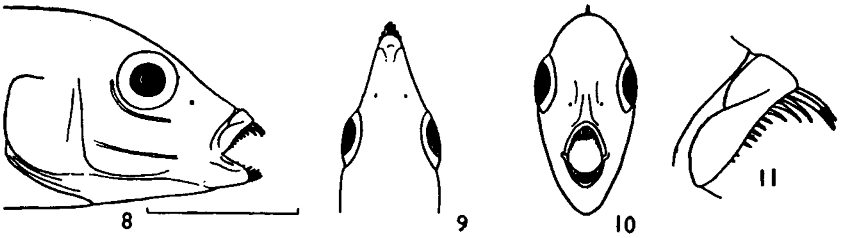
Although one of the largest of the Mbuna the largest specimens of this species do not appear to exceed about 20 cm. in length. It is very common on the rocky shore where it exhibits a bewildering diversity of colour phases. Specimens of this species are rather deep bodied and are very graceful swimmers and, unless disturbed, swim slowly among the rocks from which they obtain their food.

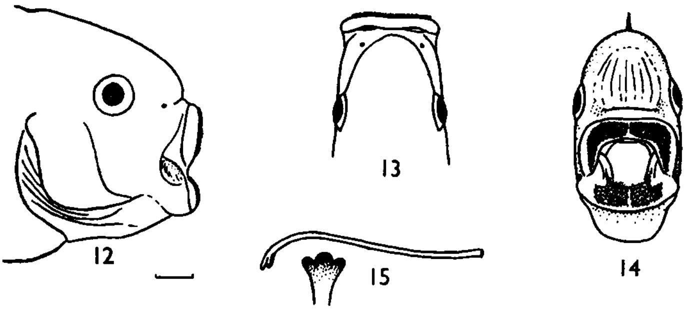
As ascertained from the examination of the gut contents of forty-eight individuals ranging from 3·7 to 19·2 cm. in length, plus several specimens obtained elsewhere, a more casual examination of other specimens, and from underwater observations, its food consists entirely of the algal Aufwuchs growing on rock surfaces. Furthermore, while an occasional tuft of *Calothrix* may be found in the gut of large specimens, such occurrences are exceptional and only the loose Aufwuchs is normally taken.

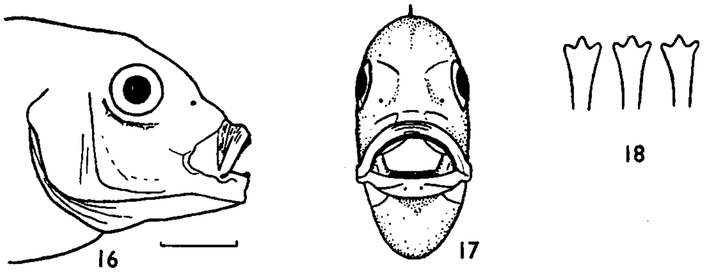
The mouth and dentition are both highly specialised to permit the collection of this material. Both lips are exceedingly mobile and each jaw is provided with a very broad band of numerous slender movable teeth. Each tooth consists of a very long slender shaft, circular in section, which is curved inwards near its tip, where it becomes broadened and flattened to form a spoon-like extremity.

During feeding the mouth is opened widely and pressed against a rock, the mobility of the mouth and the movable nature of the teeth enabling the bands of teeth to accommodate themselves to any irregularities of its surface and thus to form a continuous scraping band. The mouth is then closed. During this process loose Aufwuchs is combed from the rock by the spoon-like tips of the teeth. The entire process is repeated several times in quick succession whilst the fish remains with its mouth adpressed to the rock surface in one very localised area. For convenience the process is henceforth termed









Figs. 3–7.—*Labeotropheus fuelleborni*. 3. Head (lateral). 4. Head (ventral) showing mouth closed. 5. Semi-ventral view showing mouth open. 6. Anterior view of anterior row of teeth. 7. Individual tooth (lateral). (Note : In this and subsequent illustrations of the fishes, some idea of size is given by the line alongside the first figure in a series, which in all cases represents 1 cm. Details of dentition etc., are drawn to various scales.)

Figs. 8–11.—*Labidochromis vellicans*. 8. Head (lateral). 9. Head (dorsal). 10. Anterior view showing mouth. 11. Teeth of upper jaw.

Figs. 12–15.—*Petrotilapia tridentiger*. 12. Head (lateral). 13. Head (dorsal). 14. Anterior view showing mouth. 15. A single tooth as seen from the side, and details of its expanded tip. (Note : These figures were drawn from a particularly large specimen. In smaller individuals the angle between the jaws is not so great as is shown here).

Figs 16–18.—*Pseudotropheus zebra*. 16. Head (lateral). 17. Anterior view showing mouth. 18. Arrangement of teeth in posterior rows.

" sucking ". As in the case of *Labeotropheus fuelleborni* the opening of the mouth in preparation for the next scraping movement probably creates a sufficiently strong current to carry into the mouth the material scraped from the rock by the teeth.

This scraping is carried out both on vertical surfaces, in which case the fish is orientated normally, and on horizontal surfaces, which necessitates the fish standing on its head. This species can therefore exploit all available rock surfaces.

The local (Chitonga) name for *P. tridentiger*, which is recognised as belonging to the Mbuna group, is " Mbunya kumwa " which means " rock hitter ", a name which aptly describes the apparent behaviour of this species when feeding, during which process it appears to be hitting its head against the rock.

Pseudotropheus zebra (Boulenger). (Figs. 16–18 and Pl. 2)

Of all the cichlid fishes of the rocky shore *P. zebra* and *P. tropheops* are the commonest species. *P. zebra* is very common. It shows remarkable colour polymorphism which is discussed in Part II. All the colour forms, however, are structurally identical and all exhibit similar feeding behaviour, and take the same kind of food. For present purposes, therefore, this polymorphism can be ignored.

P. zebra can always be found swimming slowly among the rocks from which it obtains its food. Like *Petrotilapia tridentiger* and *Labeotropheus fuelleborni* it browses equally readily on vertical and horizontal surfaces.

Examination of the gut contents of 114 specimens ranging from 4·4 cm. to 11·0 cm. in length, plus several others collected elsewhere, together with underwater observations and observations made in aquaria, prove that this species subsists entirely on loose Aufwuchs. *Calothrix* is not eaten.

Like *Petrotilapia tridentiger* this species has a very mobile mouth, but it differs markedly from that species in dentition. Each jaw is armed with several rows of teeth. With the exception of a few of the lateral teeth, which are conical, the outermost row consists of close set bicuspid teeth. The inner rows, three or four in number, are composed of tricuspid teeth. These (Fig. 18) are rather long, fairly mobile and widely separated.

The feeding process is, to outward appearances, almost identical with that of *Petrotilapia tridentiger*, for *P. zebra* appears to similarly " suck " the rocks. During the closure of the mouth the inner, tricuspid, teeth scrape up loose material from the rock surface. Because they are widely separated their effect will be similar to that obtained by dragging a coarse-toothed comb through hair. The loose Aufwuchs will be scraped up but the attached filaments of *Calothrix* will pass without hindrance between the teeth. Thus only the loose Aufwuchs is collected.

Pseudotropheus livingstonii Boulenger

Only four specimens of this species have been collected. All were obtained at some distance from the shore, a fact which may indicate that it prefers deeper water than *P. zebra* to which it is closely related.

The gut contents consisted of loose Aufwuchs as in the case of *P. zebra*, but in two specimens sand grains were also present indicating that a somewhat different substratum from that on which *P. zebra* is found might be preferred. One specimen had also swallowed three tiny cichlid fishes, but these had certainly been spat from the mouth of another fish and eaten whilst the net was being brought in and are not regarded as being of much significance in determining the food preferences of this species.

The mouth is very similar to that of *P. zebra* and the dentition is also similar but the number of teeth is fewer and the individual teeth are stouter. No details of the feeding mechanism are known though it may be inferred that the process is similar to that of *P. zebra*.

Pseudotropheus williamsi (Günther)

Although definitely a fish of rocky shores and apparently not uncommon in the Nkata Bay area this species is certainly rare on the shore under consideration, only two specimens having been captured. The reasons for this scarcity have not with certainty been ascertained, but a few notes on its ecology are given in Part II. It feeds both on aquatic insects (particularly mayfly nymphs) and on Aufwuchs. Observations in an aquarium revealed that, as might be expected from its rather similar dentition and mouth structure, this species scrapes rocks in a similar manner to *P. zebra*.

Pseudotropheus fuscus Trewavas. (Figs. 19–22)

In the most inshore waters on the rocky shore *P. fuscus* is one of the commonest fishes but, as observations with a face mask reveal, it becomes much less common as the distance from the shore-line increases and is rare even at distances of 10 or 12 metres from the shore-line. This restricted lateral distribution is one of the outstanding features of its ecology. Its general habits can be summed up by the word skulking, and with these can be correlated its dark and rather sombre coloration.

Examination of the gut contents of thirty-five specimens ranging from 5·9 to 11·0 cm. in length and of several specimens collected elsewhere has revealed that this is another Aufwuchs feeder and that its food is restricted to the loose Aufwuchs.

The mouth is broadly rounded and is very " rigid " as opposed to the soft, mobile mouths of *Petrotilapia tridentiger* and *Pseudotropheus zebra* which take similar food. The dentition consists of several rows of teeth of which the outermost of each jaw is composed of rather stout bicuspid teeth, while the members of the inner rows are smaller and are tricuspid (Fig. 22). The two cusps of each tooth of the outermost row in each jaw are approximately equal in size and are bluntly rounded.

Food is nipped and nibbled from the rocks. Sometimes the fish swims up to a rock, hovers with its snout a few millimetres away from the surface, then moves in to remove food by a single nip of the jaws ; an action which may or may not be accompanied by a distinct twist of the head which presumably helps to loosen attached material and wrench it from its hold, though it is to be noted that, in spite of this, the firmly attached *Calothrix* is not removed. At other times several nibbles follow each other in quick succession.

Pseudotropheus auratus (Boulenger)

This species, although not caught in large numbers, is by no means rare on the rocky shore. Because of the very striking coloration of both sexes it can be very easily picked out during underwater observations.

While structurally very similar to *P. fuscus* it is by no means so skulking in its habits nor is it restricted to a narrow strip of the littoral region as is that species.

Its dentition is very similar to that of *P. fuscus*, and although it has been possible to observe both species feeding under natural conditions and in aquaria, no definable differences in outward behaviour have been detected during the process of food collection. Its food, as revealed by the examination of the gut contents of twelve individuals whose lengths ranged from 4·5 to 8·6 cm., consists entirely of loose Aufwuchs scraped from the rocks.

Pseudotropheus minutus Fryer

Because of its small size this species is difficult to observe in nature and indeed, because of its similarity to the young of other species such as *P. fuscus*, it was never recognised with absolute certainty during underwater swimming operations. Its small size also precluded its capture by the nets used, and most of the specimens seen were caught by small boys angling with worms among the rocks. This showed at least that it occurs very close to the shoreline, but no data on its lateral distribution have been obtained.

In spite of the fact that it will take a worm this species appears to subsist entirely on vegetable matter, for the gut contents of eighteen specimens (length 4·9 to 6·3 cm.) consisted entirely of loose Aufwuchs.

The structure of the mouth and the dentition, while similar in essentials to those of *P. fuscus*, differ in detail. The jaws are rigid and each is armed with four rows of teeth, the inner three of which are composed of tricuspid teeth. With the exception of the last three or four teeth on each side of the upper jaw, which are conical, the teeth of the outermost series are all bicuspid. The median eight or ten of these teeth in each jaw are rather conspicuously enlarged.

Observations in aquaria reveal that, in spite of these differences, this species feeds in a very similar manner to *P. fuscus* and *P. auratus*, taking either single nips or nibbles from rock surfaces. As in these species there is often a sharp twist of the head as if to pull away food clamped between the teeth. A similar function must be assigned to a sudden upward jerk of the head which has been seen on occasion at this point in the feeding process.

Pseudotropheus fuscoides Fryer. (Figs. 23–24)

As its name implies this species is very similar in structure to *P. fuscus*. The similarity superficially extends to the dentition which consists of the same arrangement of a row of bicuspid and several rows of tricuspid teeth in both species. However, the bicuspid teeth of *P. fuscoides* are unequally bicuspid as opposed to the approximately equal cusps of *P. fuscus*, and are distinctly sharper than those of the latter species. This apparently trivial difference is correlated with a marked difference in diet for *P. fuscoides*, while taking a little loose Aufwuchs, appears to subsist mainly on insect nymphs and larvae. In the six guts examined mayfly nymphs predominated, chironomid larvae were fairly plentiful, and a few hydropsychid larvae were seen.

Also correlated with this difference in food preferences is the fact that *P. fuscoides* has a larger eye than has *P. fuscus*. This presumably facilitates detection of the prey.

Pseudotropheus elongatus Fryer

Only a very few specimens of this recently described species have been found and it is not an important member of the rocky shore community at Nkata Bay. It is a feeder on loose Aufwuchs and, judging from its dentition, can be inferred to collect its food in a similar manner to *P. fuscus*.

Pseudotropheus tropheops Regan.* (Figs. 25–27)

This variable species shares with *P. zebra* the distinction of being one of the two commonest fishes on the rocky shore.

The gut contents of 202 specimens ranging from 4·4 to 12·8 cm. in length, as well as specimens collected elsewhere, reveal that it subsists entirely on Aufwuchs and that both loose Aufwuchs and the firmly attached *Calothrix* are eaten. Occasional specimens which had little or no *Calothrix* in the gut were seen, but on the whole this alga comprised a large percentage of the gut contents.

The mouth differs both from that of *P. zebra* and its allies and from that of *P. fuscus* and related species. It is by no means so soft and mobile as is the mouth of *P. zebra* and consequently it does not suck the rock in the manner employed by that species. On the other hand it is not so rigid as is the mouth of *P. fuscus* and is slightly subterminal in position as opposed to the more or less terminal mouth of the latter.

The dentition is similar to that of the other species of the genus in that in both jaws it consists of an outer row of bicuspid teeth and several (usually seven) inner rows of tricuspid teeth. The few outer lateral conical teeth are, however, larger than in the species discussed above and the lower jaw fits between them as the mouth closes, as can be seen from the illustrations.

The feeding process is more similar to that of *P. fuscus* than to that of *P. zebra* in that the fish often takes a single nip from the rock. During this process, however, it would appear that the lower jaw is actually scraped along the rock surface rather than merely closing over the Aufwuchs growing at the point of application as is the case in *P. fuscus*. Because of the close-set arrangement of the rigid tricuspid teeth it seems probable that they will not allow filaments of *Calothrix* to pass easily between them as do the homologous,

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* As recognised here this species embraces the forms previously described as :

P. tropheops tropheops Regan	*P. microstoma* Trewavas
P. tropheops gracilor Trewavas	*P. macrophthalmus* Ahl.

The reasons for uniting these under one specific name will be given elsewhere.

widely spaced, teeth of *P. zebra*. In this case, therefore, the effect will be that of a fine-toothed comb passing through dense hair, and filaments of *Calothrix* will be entangled in the teeth and dislodged. A final loosening of material is probably effected by a sideways or upwards jerk of the head at the completion of closure of the mouth.

Besides taking single nips *P. tropheops* may make a series of such nips ; a process which can be termed nibbling ; moving forwards slightly at the completion of each nip in the nibble and completing about half a dozen nips before withdrawing its mouth from the rocks.

The function of the large, conical, lateral teeth is probably to cut through the edges of the mass of algae accumulated by the lower jaws as the mouth closes. Stouter teeth will be needed for this purpose in species which include the tough *Calothrix* in their diet than in species which collect only loose Aufwuchs.

Gephyrochromis lawsi Fryer

Five specimens of this species have been taken on the rocky shore, all in deeper water than that frequented by most of the rocky shore cichlids. Observations made further north, at Florence Bay, where this species occurred plentifully among coarse shingle and boulders indicate that such conditions rather than truly rocky shores represent the optimal conditions for its occurrence. On rocky shores it can perhaps compete successfully with species typical of this habitat only in deeper water where the population density is low.

The gut contents consisted of loose Aufwuchs with which occurred a considerable admixture of inorganic particles, much as was the case in two of the specimens of *P. livingstonii* which also came from relatively deep water.

Each jaw has five rows of teeth, the outermost of which consists of numerous close-set, long, slender, conical or slightly bicuspid teeth. (See Figs. in Fryer, 1957a). Those of the lower jaw are distinctly protruded. The teeth of the inner rows are shorter and tricuspid. Such a dentition, and particularly the protruded outer row of teeth of the lower jaw, will be suitable for scooping loose material from rock surfaces.

Cynotilapia afra (Günther). (Figs. 28–31)

This species bears a striking superficial resemblance to the blue and black vertical barred form of *P. zebra* from which, however, it can readily be distinguished by its strikingly different dentition. When observed in nature the members of the Nkata Bay race of this species can be readily distinguished from *P. zebra* by the possession of a lemon yellow dorsal fin and, incidentally, by a quite different pattern of behaviour.

Although phylogenetically closely related to *Pseudotropheus* and allied genera which are rigorously confined to the rocks from which they obtain their food, and although its immediate ancestors were obviously rock dwellers, *C. afra* has evolved habits which are emancipating it from the rocks but which have not yet completely done so.

While sometimes occurring fairly close to the shore this species usually frequents deeper water than the other Mbuna. Here it occurs in small shoals, which may, however, exceed a hundred individuals, and feeds largely on plankton. Many of the specimens obtained were captured in nets by fishermen fishing just off shore near rocks for open-water species of *Haplochromis*.

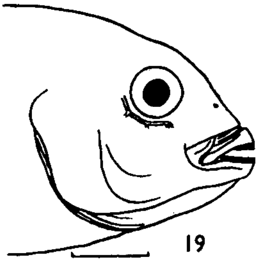
The contents of seventy-five guts of specimens ranging from 5·4 to 9·0 cm. in length, collected at Nkata Bay, were studied in detail, and a considerable number were more casually examined. Of the seventy-five studied in detail forty-five contained only plankton, mainly zooplankton, in which *Diaptomus kraepelini* predominated ; twenty-five contained plankton with the addition of other material, which consisted mainly of algae from the rocks and, in some cases, of chironomid larvae from the same source, and only five contained material derived exclusively from the rocks (chironomid larvae and Aufwuchs). In addition to these, the guts of several small specimens (about 5 cm. in length) were examined and found to contain plankton though, in contradistinction to the larger specimens in which zooplankton predominated, there was a preponderance of phytoplankton and particularly of diatoms (*Melosira*, *Siurella* etc.). This species therefore, at all stages of its life history, occupies quite a different feeding niche from its relatives on the rocky shore.

The mouth is similarly constructed to that of *P. zebra* and is similarly mobile. Here, however, the wide gape which follows as a natural consequence of this mobility, is utilised, not so much for scraping rocks but for the taking in of water from which plankton is sifted. Underwater observations indicate that this species deliberately picks out planktonic organisms for swallowing and is not an indiscriminate filterer.

The dentition is rather striking, consisting of an outer row of rather long, widely spaced, sharp, conical teeth (Figs. 28, 30, 31), and several rather scattered and much smaller inner teeth. The presence of the conical teeth is somewhat enigmatical for, although they are apparently ideal for the removal of chironomid larvae from the rocks, they are not used to any great extent for this purpose, for the fish is now largely a plankton feeder. It is presumed that they are indicative of past rather than of present feeding habits.

Genyochromis mento Trewavas. (Figs. 32–36)

The dentition and feeding mechanism of *G. mento*, whose remarkable diet of fish scales has already been made known (Fryer, Greenwood & Trewavas, 1955), are among the most striking of those shown by any Nyasan fish. While it has not been possible to actually observe this species, collecting its food, the examination of the gut contents of eleven specimens ranging from 6·0 to 12·6 cm. in length has shown conclusively that it subsists mainly on scales scraped from other fishes. One of the fishes examined was a female brooding young in its mouth and, as was expected, its gut was empty ; otherwise, in all save one of the alimentary canals examined, were found numbers of large fish scales identified as those of a *Labeo* and, by inference, as those of *L. cylindricus*, which is the only member of the genus occurring on the rocky shore, and where it is very common. The gut of the one specimen not containing fish scales was only examined after it had spent a night in an aquarium in which it died. In addition to these scales some smaller fish scales of unknown origin occurred in one gut ; fin rays, but no other fish bones, occurred in three guts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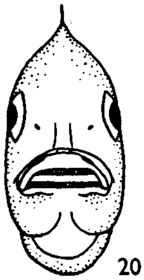
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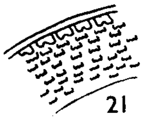
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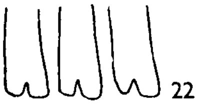
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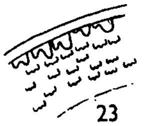
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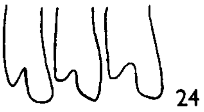
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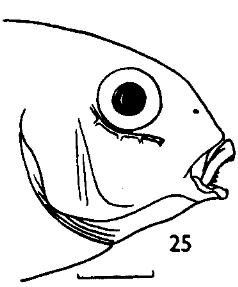
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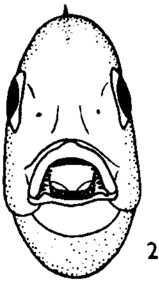
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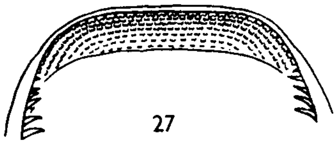
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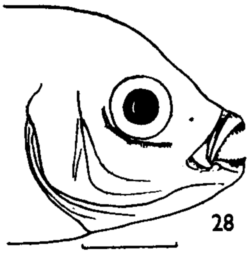
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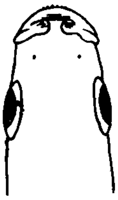
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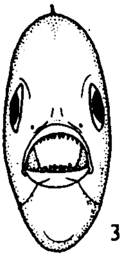
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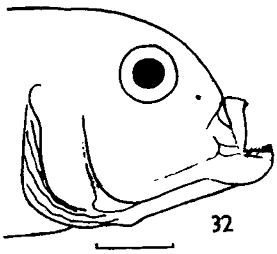
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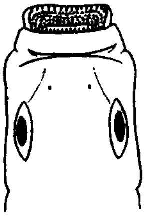
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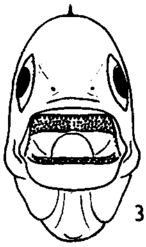
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Figs. 19–22.—*Pseudotropheus fuscus.* 19. Head (lateral). 20. Anterior view showing mouth. 21. Part of dentition of upper jaw. 22. Teeth of outer series of upper jaw.

Figs. 23–24.—*Pseudotropheus fuscoides.* 23. Part of dentition of upper jaw. 24. Teeth of outer series of upper jaw.

Figs. 25–27.—*Pseudotropheus tropheops.* 25. Head (lateral). 26. Anterior view showing mouth. 27. Dentition of upper jaw.

Figs. 28–31.—*Cynotilapia afra.* 28. Head (lateral). 29. Head (dorsal). 30. Anterior view showing mouth. 31. Dentition of upper jaw.

Figs. 32–36.—*Genyochromis mento.* 32. Head (lateral). 33. Head (dorsal). 34. Anterior view showing mouth. 35. Outer tooth of lower jaw. 36. Inner tooth of lower jaw.

including the one in which no scales were found ; small amounts of filamentous algae among which *Calothrix* was recognised occurred in three guts and, most surprisingly as no snails have been found on the rocky shore, one gut contained a tiny gastropod mollusc. It is apparent, therefore, that the diet of *G. mento* consists of scales scraped largely from *Labeo cylindricus* but occasionally from other fishes, supplemented by pieces of fin bitten from other fishes, and by material scraped from rock surfaces.

The appearance of the gut of this species when it contains scales is highly characteristic for, in its median part where its internal diameter is only about 2 mm., it may contain a plate-like pile of scales each about 10 mm. in diameter which bulge the gut considerably.

It is interesting to note that in the Tanganyikan scale-eating fishes of the genera *Perissodus* and *Plecodus* the scales are found piled one above the other in the gut just as they are in *G. mento* (Poll, 1956 a). Incidentally Poll remarks that *Perissodus microlepis* Boulenger probably eats also " les nageoires ou du moins les extrémités des rayons " but presents no evidence to show that this is indeed the case.

It appears that this species can actually digest fish scales for those fairly well down in the gut are very soft and much eroded and only mush can be found at the posterior end of the alimentary canal.

The mouth structure and dentition of *G. mento* are highly specialised. The lower jaw is very rigid and prominent and is lined on its outer margin by a row of sharp teeth which, while actually bicuspid, are functionally unicuspid, for the cusps are very unequal in size (Figs. 35) and the smaller serves largely to strengthen the larger and functional cusp. Internal to the row of bicuspid teeth are five rows of short tricuspid teeth which form a file-like series. The upper jaw, which, when the mouth is open, lies more or less at right angles to the lower jaw, is similarly armed.

If the outer teeth of the lower jaw are inserted under the edge of a scale of *Labeo* the scale is easily removed. It seems probable also that the sharp outer teeth will form a pair of cutting edges to sever the seized pieces of fin which will be firmly held by the inner teeth.

Melanochromis melanopterus Trewavas

The gut contents of only five specimens, three of them less than 8 cm. in length and two exceeding 11 cm., captured on the rocky shore have been examined, together with a few from adjacent rocky shores. These show that this species eats a variety of insects (mayfly nymphs, hydropsychid and chironomid larvae) and, when small, ostracods. One specimen 12·9 cm. in length, had also eaten a crab, another, 7·0 cm. in length, contained the head of a small Mbuna, and a small amount of Aufwuchs was seen in one gut. The dentition is reminiscent of that seen in *Pseudotropheus fuscoides*.

Haplochromis euchilus Trewavas. (Figs. 37–40)

Although captured only in small numbers this distinctive species has been observed on several occasions during the course of underwater observations, and there is no doubt that it is a permanent member of the rocky shore community. It attains a length of at least 22 cm., and the specimens studied ranged from 5·7 to 22 cm. in length. Two of these were taken from rocks on the south side of the bay and their food, which is not included in that listed in Table 6, was very similar to that of specimens from the shore studied except that one contained a few small snails.

The food consists mainly of insect nymphs and larvae (see p. 222 for details) and is picked off from the surface of the rocks. Presumably correlated with the detection of such prey are the remarkably modified lips which are produced into enormous fleshy lobes. During the process of food collection, which has been observed in nature, these lobes are placed against the rock and presumably detect the movements of the prey which is then picked off by the very simple teeth.

Haplochromis ornatus Regan

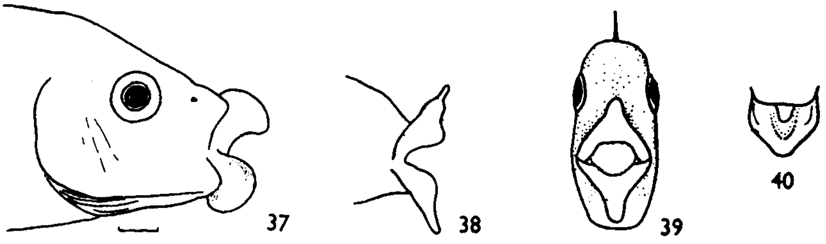
This species, of which six specimens ranging from 7·6 to 12·4 cm. in length have been studied, shows very similar but much less extreme modifications of the lips to *H. euchilus*, both the upper and lower lips being somewhat produced into fleshy outgrowths. The food taken too is similar to that taken by *H. euchilus* and its detailed composition is listed on p. 222.

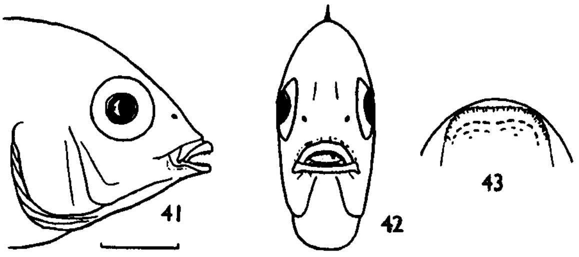
Haplochromis kiwinge Ahl.

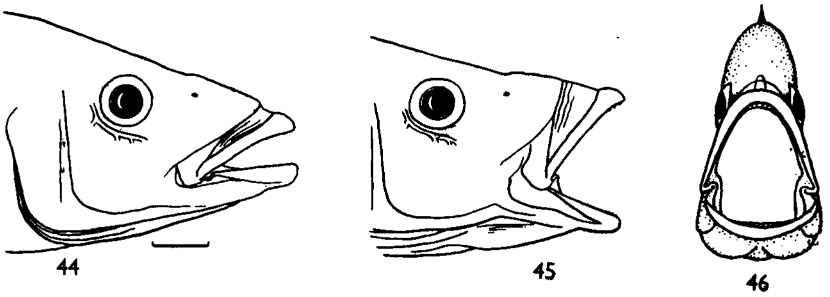
This species, which attains a length of about 30 cm., is by no means confined to rocky shores when adult, but juvenile stages (from 5 to 10 cm. in length) are an important constituent of the rocky shore fauna. The species is a mouth brooder and, although a female with young in the mouth has been captured on the sandy shore studied, an observation made on a rocky shore at Ruarwe when a female was watched " brooding " young about 2·5 cm. in length (Fryer, 1956c), together with the data relating to the occurrence of juvenile specimens among the rocks, indicates that the early stages are spent on rocky shores.

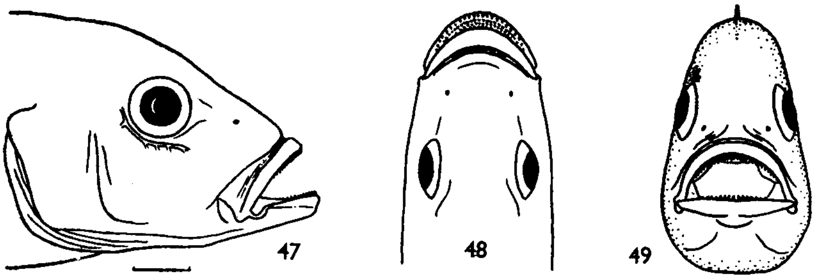
The young guarded by the parent at Ruarwe were seen feeding on particulate matter in the water, presumably plankton, and young of length 2·1 to 2·6 cm from the mouth of the parent captured on the sandy shore contained zooplankton, mainly *Diaptomus kraepelini* and *Mesocyclops leuckarti* with some *Diaphanosoma excisum.* Zooplankton is also the most important single item of diet of specimens up to about 10 cm. in length, though other food in the form of aquatic and blown-in terrestrial insects is also eaten at this stage of the life history. (See p. 222 for more detailed analysis of the food of twenty-six juvenile specimens). Larger specimens become wider ranging and, while partly piscivorous, they appear to be essentially omnivorous. These larger individuals are by no means so intimately integrated into the rocky shore community as are the juvenile stages, and indeed appear to be more frequent on the sandy shore than among the rocks. (See notes on fishes of sandy shore). They also move into deeper water where they make their presence known by appearing around anchored boats in quest of garbage.

Specimens 5 to 10 cm. in length have quite different habits from the true rock fishes (Mbuna), being more active in movements and less concerned with









Figs. 37–40.—*Haplochromis euchilus.* 37. Head (lateral). 38. Fleshy lobes of jaws drawn forward to demonstrate their structure. 39. Anterior view showing mouth. 40. Lower jaw and its dentition.

Figs. 41–43.—*Haplochromis fenestratus.* 41. Head (lateral). 42. Anterior view showing mouth. 43. Dentition of lower jaw.

Figs. 44–46.—*Haplochromis polyodon.* 44. Head (lateral). 45. Head (lateral) showing mouth open to full gape. 46. Anterior view showing mouth open to full gape.

Figs. 47–49.—*Haplochromis pardalis.* 47. Head (lateral). 48. Head (dorsal). 49. Anterior view to show mouth.

the material on rock surfaces. In marked contrast to the Mbuna they quickly congregate when a bait, either animal or vegetable is scattered in the water.

Haplochromis fenestratus Trewavas. (Figs. 41–43)

Of the cichlids not belonging to the Mbuna group this is the commonest species on the rocky shore. It is a very generalised feeder, for examination of the gut contents of seventy-four specimens ranging from 5·3 cm. to 12·7 cm. in length, plus several examined elsewhere, reveals that while it subsists largely on loose Aufwuchs it also includes ostracods, *Schizopera*, and chironomid larvae in its diet. The gut contents sometimes give the impression that it had scooped up whatever material was present on the rock without exerting any selectivity.

It has a rather small and not particularly specialised mouth whose margins are rather sparsely armed with a row of bicuspid teeth, inside which are two or three rows of small tricuspid teeth with only a small number of teeth per row. Food is collected from the rocks by a series of pecks.

Haplochromis polyodon Trewavas. (Figs. 44–46)

This is the commonest and most abundant predatory fish on the rocky shore. The gut contents of twenty-four specimens, 7·5 to 28·9 cm. in length, from the shore studied, plus four obtained just over the boundary of the intermediate zone and three obtained elsewhere, show that it subsists almost entirely on fishes, though a few insects (*Afronurus* and *Neoperla* nymphs and chironomid larvae) were present in three guts. Because of the rapidity of digestion it was usually impossible to identify with certainty the fishes eaten, but, as might be expected, they all appeared to belong to the family Cichlidae, and in one case *Pseudotropheus zebra* was definitely recognised. Juvenile fishes definitely predominated in the guts, but the largest specimen of *H. polyodon* caught had eaten an Mbuna about 10 cm. in length.

The adaptations of this species are obvious—a rather long and slender body, large eyes, a mouth with an enormously wide gape, sharp backwardly-directed teeth, and a similarly armed pharyngeal bone. Most of these features are to be seen in the illustrations.

Haplochromis pardalis Trewavas. (Figs. 47–49)

This is another of the piscivorous rocky shore species, though it is not very common, only three specimens (length 14·4 to 16·4 cm.) having been obtained from the area studied. One had an empty gut but the other two contained fish remains.

Its adaptations are similar to, but less pronounced than those of *H. polyodon* and are illustrated in the figures.

Haplochromis guentheri Regan. (Figs. 50–51)

Underwater observations indicate that, while not very common among the rocks, this species cannot be considered rare.

Thirteen specimens ranging from 5·5 to 12·5 cm. in length have been procured and their gut contents have been examined. While rather catholic in its tastes it definitely shows a marked preference for one kind of food which is apparently not exploited by any other species on the rocky shore, namely filaments of algae, other than *Calothrix*, growing on the rocks. These filamentous algae, whose strands are rather longer than those of *Calothrix* are mostly blue green (*Lyngbya* ?) but the few strands of green algae which occur are also eaten. To see a gut of this species containing these algae after dissecting a large number of specimens of other species from the rocky shore brings home very clearly the fact that a very deliberate selection of food is made at times. Nine of the thirteen guts examined contained such algae ; in five cases to the exclusion of all else. Loose Aufwuchs was present in eight of the guts in varying amounts and comprised the bulk of the food in two cases ; rock-dwelling invertebrates, mostly ostracods, *Schizopera*, and chironomid larvae, were present in two guts ; and the contents of two guts indicated that the fishes concerned had ventured onto the sand for they contained, among other material fragments of *Corbicula*, and one contained a few sand grains.

Scanty underwater observations reveal that this species picks its food from rock surfaces in single nips, but its feeding behaviour has not been observed in detail.

The jaws and teeth are weak, being in this respect " unique in *Haplochromis* " (Trewavas, 1935). The dentition consists of an outer row of small, sharp, rather unequally bicuspid teeth and two inner rows of tiny tricuspid teeth. The arrangement of the teeth on the jaws is shown in Fig. 51. When the mouth is closed what are in effect two spiny ridges come together. These will be suitable for gripping the rather long slender algal filaments for which this species shows a distinct predilection.

" Nguwa "

The above is the local (Chitonga) name for the female of an as yet undescribed species of *Haplochromis* belonging to or closely related to the " Utaka group ". It is *not* however *H. cyaneus*, which name is given by Bertram, Borley & Trewavas (1942) as the scientific equivalent of " Nguwa " at Nkata Bay. The male of this species, while recognised as the mate of the female, is referred to in Chitonga as " Chipali ". A description will be published in due course by Mr T. D. Iles.

This species was caught in considerable numbers in 2½ inch mesh gill nets during the months when these were set on the rocky shore, viz. March, April, May, September and November. Unfortunately no information is available for other months but in all cases the specimens, eighty-seven of which were studied, measured from 18·1 to 21·0 cm. in length and almost all were very ripe or, in a few cases, spent. Of these all save nine had either empty guts or contained traces of indeterminate slime. The food present indicated an omnivorous diet. Three contained zooplankton, one contained fish remains, one was crammed with winged termites, three contained *Calothrix* derived from the rocks, this being accompanied in one case by some mayfly nymphs, and the other contained a few fragmentary insect remains. It seems probable therefore that this species visits the rocky shore, usually at night, for the purpose of laying its eggs, which are then picked up and carried by the female. The indications are that it breeds throughout the year.

While this species appears to require a rocky shore for breeding purposes it is not, however, a regular member of the rocky shore community and it appears to play little part in the trophic interrelationships of the biocoenosis.

Labeo cylindricus Peters. (Figs. 52–55)

This is the commonest and most important non-cichlid fish on the rocky shore. A few specimens have been collected on sandy bottoms but never more than a few yards from rocks. It is a bottom dweller with a ventrally situated mouth which obtains all its food from the rocks among which it lives. Examination of the gut contents of sixty-five specimens ranging from 12 to 34 cm. in length obtained from the rocky shore studied, and of others collected elsewhere, shows that the food consists almost entirely of loose Aufwuchs and such detritus as tends to accumulate on the rocks in the deeper water (10m+) which it frequents as well as the shallower inshore waters. A certain amount of *Calothrix* is eaten but many guts examined appeared to contain only loose Aufwuchs.

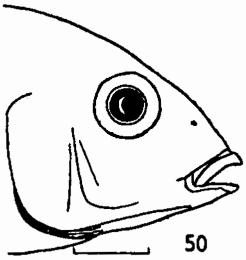
L. cylindricus can very easily be seen feeding in nature though details of the process are difficult to observe. The mouth can be seen moving rapidly as the fish lies over a rock and, as it moves away, a distinct bare area, approximately circular if it remained stationary during the browsing process or more elongate if it moved forward, remains to show where it scraped material from the rock. Material is removed very quickly. Such " bare " patches can be readily picked out during underwater observations and show clearly where *L. cylindricus* has recently fed. One rather important feature of the feeding behaviour of this species is that it has only been observed to feed on approximately horizontal surfaces and has never been seen browsing on vertical surfaces.

The structure of the mouth is very similar to that of *L. horei* (Cuvier) as described by Girgis (1952), and the feeding mechanism appears also to be similar. The protractile mouth is situated ventrally, is crescentic in shape when closed, and is bordered by fleshy mobile lips each of which bears on its inner face numerous rows of sensory papillae (Fig. 55). The rim of the lower lip is also provided with a row of short sensory tentacles. These papillae and tentacles are probably much more important than the eye in food location. Each lip overlies a horny pad whose contours match each other so as to allow the two to come together and form as it were a pair of cutting blades.

During closure of the mouth the horny pads must pass over the rock surface, but often they are apparently not pressed firmly against it or they would always remove the omnipresent tufts of *Calothrix*. It seems probable indeed that much of the loose material eaten is actually sucked into the mouth by expansion of the buccal cavity, and that the horny pads are not always used for the purpose to which they seem so obviously suited and for which the homologous structures in *Varicorhinus nyasensis* (see below) are most certainly used.

The structure of the pharynx and its teeth, and presumably its mode of action, are similar to those of *L. horei* described in considerable detail by Girgis.

Throughout life the snout of this species is covered by horny warts of very hard, almost bony, consistency. During the course of its grubbings about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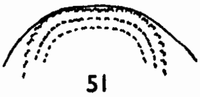
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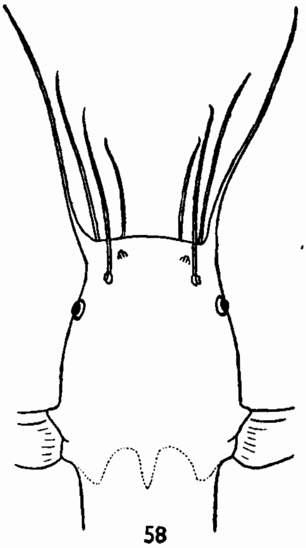
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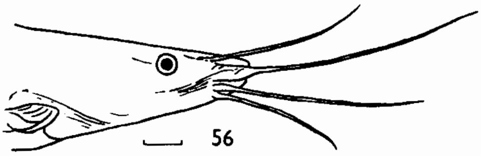
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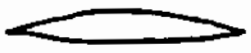
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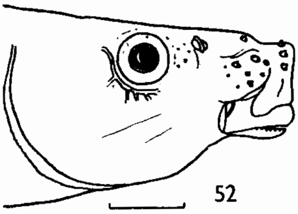
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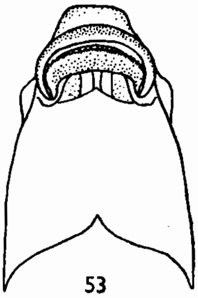
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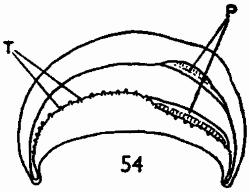

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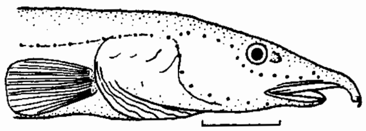
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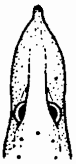
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Figs. 50–51.—*Haplochromis guentheri*. 50. Head (lateral). 51. Dentition of lower jaw.

Figs. 52–55.—*Labeo cylindricus*. 52. Head (lateral). 53. Head (ventral) to show mouth. 54. Details of mouth. P.—Horny pads exposed by folding back fleshy lips. T.—Sensory tentacles. 55. Inner surface of lower lip showing sensory papillae.

Figs. 56–58.—*Bathyclarias worthingtoni*. 56. Head (lateral). 57. Outline of mouth (anterior). 58. Head (dorsal).

Figs. 59–61.—*Mastacembelus shiranus*. 59. Head (lateral). 60. Anterior part of head (ventral). 61. Anterior part of head (dorsal).

among the rocks it is probable that it not infrequently bumps its snout, and it is suggested that the warts may serve as " bumpers " to prevent abrasion of the skin in this region.

Varicorhinus nyasensis Worthington

This fish, which attains a length of more than 29 cm. is not uncommon among the rocks where it occurs in shoals of up to at least fifty individuals. It is a very active species and the shoals can usually be observed only for brief periods before they move away. Paradoxically more specimens have been obtained from the sandy shore during what appear to be migratory movements than from among the rocks.

The gut contents of forty-three specimens ranging from 16·5 to 29·4 cm. in length were examined and, while several of the specimens on the spawning run were empty, sufficient information has been obtained to show that this species takes a mixed diet among which, however, *Calothrix* scraped from the rocks is apparently the main constituent. A few contained fragmentary insect remains and one contained several winged termites, obviously devoured after a hatch, one contained a trace of macerated plankton, and one which had passed over the sandy shore during the spawning run had picked up a few fragments of *Vallisneria*. Some contained ostracods obviously scraped up with the algae from the rocks and two contained *Spirogyra* which had probably been collected in Crocodile Creek or had been swilled down from the creek into the lake by the spate which was running at the time.

The ventrally situated mouth (Fig. in Worthington, 1933) is in many ways similar to that of *Labeo cylindricus* and has similar horny scrapers. These are obviously used for the purpose for which they are so admirably suited—scraping rock surfaces.

The specimens taken on the sandy shore were all collected between February and April when there was considerable flow of water from Crocodile Creek by whose mouth they were captured. Members of both sexes were " ripe " and ready to spawn. The fact that they had come from the rocky shore was shown by the presence of *Calothrix*, sometimes in large quantities, in the guts of some of them. The obvious inference, supported by reports from African fishermen who are very knowledgeable on such matters, is that this species normally lives among the rocks but ascends rivers to spawn during the rainy season. Evidence that it runs up rivers to spawn has also been collected elsewhere, for in mid-February Mr D. Harding brought back from Karonga a specimen of this species which was one of several collected at the mouth of a river.

Barilius microcephalus (Günther)

Although listed as a member of the rocky shore community this species occurs in equal abundance on both the rocky and sandy shores. This ecological euryvalence is a reflection of its feeding habits for it is not bound to any particular kind of substratum but collects most of its food from the open water and water surface. Juvenile specimens (up to about 10 or 12 cm. in length) can always be seen when fish watching on either the rocky or sandy shore. These usually swim, either singly or in shoals of up to about a dozen individuals, just below the surface, thus differing in habits from most of the other fishes of the rocky shore which, with the exception of *Cynotilapia afra*, *Haplochromis kiwinge*, and to some extent *Varicorhinus nyasensis*, live in close contact with the rocks themselves. Larger specimens are very seldom seen and, although gill net captures show that they do come inshore at times, it is presumed that this species moves to deeper water as its size increases. Although small specimens are very common they are not easily caught for, although they can be readily induced to swim over a carpet net, their cylindrical bodies pass easily through even fine meshed nets.

Combining the captures from both rocky and sandy shores gives a total of twenty-six fishes whose guts have been examined. These ranged from 3·1 to 29·8 cm. in length but most did not exceed 10 cm. The predominant food of all these specimens was terrestrial insects (adult midges, termites, ants, beetles, etc.) blown in from the shore, and it was interesting to note that even the very smallest specimens (3 to 5 cm. in length) usually had such material in the gut, though these tended to take a fair proportion of bottom animals such as minute chironomid larvae and, in one case, ostracods, as well as a certain amount of both phyto- and zooplankton, in addition. Only one specimen (length 6·5 cm.) was found to be crammed with zooplankton though a few others had zooplankton, including the larvae of *Corethra*, in the gut in addition to other material. Occasional bottom animals such as chironomid larvae and once a hydropsychid larva were also seen as were chironomid pupae (presumably caught as they rose through the water), and occasional fragments of algae. A specimen 27 cm. in length contained fragmentary fish remains. These gut analyses are very similar to those made on the few ungutted juvenile specimens available to Worthington (1933). It is worthy of note that in addition to the specimens about 3 cm. in length which could be identified as belonging to this species others a little less than 3 cm. and which almost certainly belonged to this species, were also found, and Worthington had for examination specimens only 2 cm. long which had been collected in the lake itself. The presence of such small specimens indicates either that young very quickly come down from the rivers in which some of them at least are born, or that, and more likely, the story told by African fishermen of two " kinds " of " Sanjika ", one of which spawns in rivers and the other in the lake itself, is true. This seems very likely as there is no river up which this species is known to run, within many miles of the point at which these tiny specimens were found. It may even be that these " races ", if they exist, differ in certain morphological characteristics, and this may in part explain the variation encountered by Worthington in his material.

Bathyclarias worthingtoni Jackson (Figs. 56–58)

This is the only species of its genus which occurs regularly among the rocks of the rocky shore. It appears to spend the early part of its life near the shore (though whether the species actually spawns there is not known) and moves to deeper water after attaining a length of about 30 cm. It is a very retiring species which lives under stones and is therefore not to be seen during underwater swimming operations. While a few specimens have been caught in gill nets most have been caught on hooks baited with worms and dangled among the rocks.

The gut contents of sixteen specimens obtained among the rocks, ranging in length from 7·8 to 35·5 cm., have been examined together with two specimens from similar situations at Likoma Island both of which, however, were empty. The food of twelve of these specimens included ostracods (*Cypridopsis*) which often occurred in large numbers and which appear to be a very important article of diet in specimens up to 20 cm. in length, and to be eaten by specimens even larger than this. Aquatic insects, of which chironomid larvae were the most frequent but among which *Neoperla* and *Afronurus* nymphs, anisopterid dragonfly nymphs and hydropsychid larvae were also recognised, also occurred frequently, and mites (four times) and terrestrial insects (once) were also seen. Five of the larger specimens (all of 18 cm. or more in length) also contained remains of the crab *Potamonautes lirrangensis*, these ranging from whole crabs of small size, some of which could not long have been released by the brooding female, to broken carapaces and isolated appendages of rather larger, but not large, specimens. One of the specimens with crabs in the gut had also eaten an unidentifiable fish and one, caught in a gill net, contained many *Labeo* scales possibly scraped from a fish entangled in the net before it was itself captured.

Crabs seem to play an increasingly important role in the diet of this species as it becomes older for they are the most important single article of food taken by the larger individuals of which numerous specimens have been taken in gill nets set in deep water (up to 40 m.) off shore by Mr T. D. Iles. These not unnaturally eat larger crabs than do the smaller individuals living close inshore.

While the long barbels of this species are probably of considerable value in helping it to detect its prey and " feel " its way among the rocks both when young and when older and living in deeper water where light intensities are low, and are probably more important in such situations than are eyes which, not unexpectedly are very small, one is cautioned against attempting to point to adaptations such as this in the Clariidae by the fact that the Nyasan representatives of the family have adopted various modes of life and a variety of diets yet all exhibit the above features and many have a similar type of dentition. The hard palate of the present species, however, will be helpful in the crushing of crabs.

Mastacembelus shiranus Günther. (Figs. 59–61)

This species leads a very secretive existence under rocks and is only seen when these are turned over. It then dashes frantically for a new shelter. Although seldom seen it is apparently not uncommon, and Africans state that in the days when fish poisoning was carried out among the rocks it was caught in large numbers.

Several specimens have been caught on hooks baited with worms and dangled among the rocks, and thirteen guts (of specimens 7·5 to 27 cm. in length) have been examined. These showed that it feeds on aquatic insects—

mayfly (*Afronurus*) and stonefly (*Neoperla*) nymphs, and caddis (hydropsychid) and chironomid larvae. One specimen (24 cm. in length) had eaten a small crab and one contained a piece of woody plant tissue.

Although a specimen of this species has been collected in a somewhat swampy river there is no doubt that its smooth eel-like body is well suited to wriggling underneath rocks and between the narrow spaces encountered there. In such situations touch and taste are likely to be of as great or greater value than sight. The eyes are indeed small and there is at the tip of the snout a remarkable compound tentacle consisting of a median sensory lobe on each side of which are located the nostrils (Fig. 59). This is ideally situated for exploring the physical environment and for the detection of prey.

The lower jaw is exceedingly strong and its somewhat rounded inner (upper) surface is beset with small teeth which, when the mouth is closed, meet with the U-shaped band of teeth on the horny inner (lower) surface of the upper jaw. This arrangement is eminently suitable for the crushing of insects and crabs.

Bagrus meridionalis Günther

This species, which lives in deeper water off-shore, sometimes visits the rocky shore at night as was shown by the capture of twelve specimens ranging from 40 to 62·8 cm. in length caught in 4 inch and 5 inch gill nets. Only two of these contained food which in both cases consisted of fishes, though in neither case was it possible to identify the prey. Mr T. D. Iles has accumulated a large body of data concerning this species and has found occasional rock fishes in the stomachs of specimens captured in deep water off rocky shores, though the importance of this group of fishes as food for *B. meridionalis* appears to be slight.

Besides these large specimens a small individual (length 10·5 cm.) has been collected among the rocks. It contained a mayfly nymph, a chironomid larva, some other unidentified insect fragments and the remains of a prawn ; the latter indicating that it had visited the sandy shore.

By day neither young nor old specimens of this species have been seen among the rocks.

Other fishes of the rocky shore

While the above account covers the most important fishes of the rocky shore it does not include all those which have been found there. A few other species which are to be regarded as rarities or casual visitors have also been seen or collected. These include two clariids (both at least partly predacious) *Rhamphochromis* spp. (predators), *Aristochromis christyi* (predator), an undescribed *Haplochromis* related to *H. pardalis* and *H. livingstoni* (predator), *Serranochromis robustus* (predator), members of the " Utaka group " of *Haplochromis* (plankton feeders), particularly " Mburuli " which sometimes visits the shore in considerable numbers, apparently for the same reason as " Nguwa ", and two unidentified cichlids, both probably new (insect eaters and mild predator), and at least one unidentified species of *Barbus* (browser). They also include a very few specimens of *Cyathochromis obliquidens* and a specimen of *Pseudotropheus lucerna* which had strayed just over the boundary from the intermediate zone and which are mentioned in the section on the fishes of that zone. The species of *Rhamphochromis* tend to occur in rather deeper water than that found in the littoral zone and are thus seen mostly on the fringes of the rocky shore. They appear to prey more upon the open water plankton-eating species of *Haplochromis* than on the littoral fishes.

(b) *The sandy shore*

Lethrinops brevis Boulenger. (Figs. 62—67)

This is a common species on the sandy shore and occurs also in the intermediate zone. The gut contents of thirty specimens from the sandy shore and four from the intermediate zone ranging from 9·2 to 14·5 cm. in length have been examined. These reveal that *Lethrinops brevis* feeds almost exclusively on chironomid larvae dug from the sand, for the gut is usually crammed with a mixture of these organisms and coarse sand grains. The chironomid larvae eaten are small, seldom exceeding 5 mm. in length. Other food in the form of an occasional chironomid pupa and a very occasional ostracod, and once a caddis larva, has been seen in the gut, but there is no doubt that sand dwelling chironomid larvae constitute almost the sole food of this species.

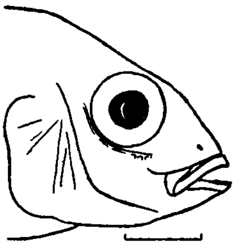
The snout is fairly sharp and the lower jaw is fairly long and pointed and suited to dibbing in the sand when the mouth is protruded as shown in Fig. 63. The teeth are very weak and only those of the outer row are likely to have any functional significance. These are slender and recurved, and it is possible that when the mouth is closed they help to retain its contents. The gill rakers are few in number, there being seven or eight on the lower part of the two anterior arches and no more than ten on the fourth arch. This arrangement of the gill rakers is eminently suited to the process of feeding which takes place in *L. furcifer* (see below) and which probably holds good for this species also, though this remains to be confirmed by actual observations.

Lethrinops furcifer Trewavas. (Figs. 68—71)

This is the commonest fish on the sandy shore where it occurs in considerable numbers. It is not associated with weed beds but occurs in areas of bare sand over which it hovers.

The gut contents of seventy-four specimens ranging from 9·0 to 15·5 cm. in length show that, like *L. brevis*, its food consists almost entirely of chironomid larvae dug from the sand. As in *L. brevis* these chironomid larvae, which are about the same size as those eaten by that species, are mixed with coarse sand grains, and indeed typical gut contents of the two species are indistinguishable. Only two specimens deviated from this very distinct diet. One had eaten six tiny cichlid fishes each about 1 cm. in length which still retained traces of the yolk sac and were still at a stage of development at which they would receive parental care, and one contained several cichlid eggs (perhaps, however, ingested after having been spat out by a brooding female during or immediately after capture).

The mouth structure of this species is very similar to that of *L. brevis* described and figured above, and is similarly protractile. The gill rakers are few in number, there being only eleven or twelve on the most anterior arch. (Fig. 71).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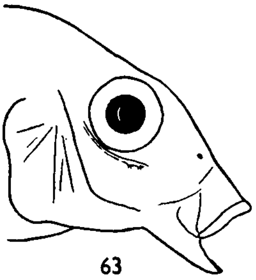
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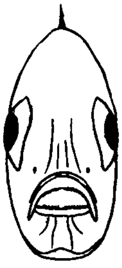
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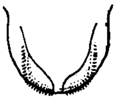
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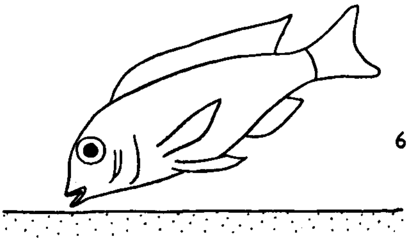
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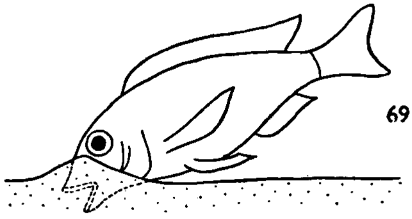
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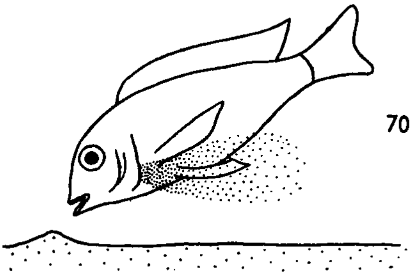
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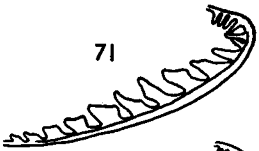
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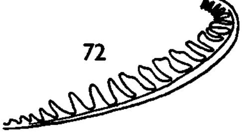
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Figs. 62–67.—*Lethrinops brevis*. 62. Head (lateral). 63. Head (lateral) showing mouth protruded. 64. Anterior view showing mouth. 65. Outline of open mouth. 66 Dentition of lower jaw. 67. Single tooth of outer series viewed from inside.

Figs. 68–70.—Feeding behaviour of *Lethrinops furcifer*, and *Lethrinops* sp.

Figs. 71.—Gill rakers of *Lethrinops furcifer*.

Fig. 72.—Gill rakers of *Lethrinops* sp.

This species is indistinguishable in the field from *Lethrinops* sp. which is discussed below and the feeding behaviour described here may apply to either of the two species but almost certainly applies to both.

Feeding takes place as follows. The fish hovers over the bottom, then, with its body at an angle of between 20° and 35° to the horizontal, it plunges its snout into the sand so deeply that the snout is buried almost to the level of the eye (Fig. 69). The mouth is presumably opened during this process though this cannot of course be seen. After filling its mouth with sand the fish then withdraws its head, moves a short distance from the sand, and discharges the main bulk of its mouthful of sand via the opercular apertures (Fig. 70). The sand is ejected in two dense backwardly directed jets, followed after brief intervals by two or three smaller clouds of sand as the mouth is emptied of its contents. Presumably the chironomid larvae, and the large sand grains, which are found in the alimentary canal of this species are sieved out by the gill rakers as the mouthful of material collected is strained in the manner described.

After the taking of a mouthful of sand in the way described above a distinct pit is left in the sand. Literally thousands of these pits can be seen on the sandy shore after periods of calm weather, and serve to give some measure of the intensity of the feeding activity of the species of *Lethrinops* in this habitat.

Lethrinops sp. (Fig. 72)

This species bears a remarkable similarity to *L. furcifer* with which it co-exists, and indeed can scarcely be separated from it on gross examination. It differs, however, in the number of gill rakers, having sixteen or seventeen on the anterior arch (Fig. 72), and in the pharyngeal bone which is slightly more slender than in *L. furcifer* and has rather more and finer teeth. It also differs markedly in the kind of food taken. Like *L. furcifer* it obtains its food from the sand, presumably by a similar feeding mechanism. The food, however, as shown by the examination of the gut contents of twenty-three specimens ranging from 9·9 to 20·0 cm. in length and one specimen from an adjacent sandy beach for comparative purposes, consists largely of ostracods (*Cypridopsis*) which are always mixed with sand grains whose average size, however, is much smaller than those found in the gut of *L. furcifer*. The harpacticoid copepod *Schizopera consimilis* is also eaten and is sometimes present in considerable numbers in the guts, and occasional chironomid larvae are also eaten though these, when present, are definitely smaller than those eaten by *L. furcifer*. Larger chironomid larvae such as are eaten by *L. furcifer* appear to be definitely avoided. The difference in food from that of *L. furcifer* can be definitely correlated with the finer nature of the sieve formed by the gill rakers, and the more finely-toothed pharyngeal bone is presumably also adaptive.

The fine gill raker sieve would, of course, sift out coarse as well as fine sand grains and it is presumed either that these are never taken in or, more likely, that such grains are spat out via the mouth, but this supposition awaits confirmation by observation.

Haplochromis similis Regan. (Figs. 73–75)

This species occurs commonly on the sandy shore and in the intermediate zone. It has also been found in Crocodile Creek but it does not appear to venture onto the rocky shore.

The gut contents of twenty-three specimens ranging from 6·5 to 17·0 cm. in length taken from the sandy shore and the intermediate zone (where it feeds similarly) show that here it subsists on pieces chopped from the leaves of *Vallisneria*, together with the Aufwuchs growing thereon, and on bottom material which includes diatoms and other algae as well as detritus whose origin is often betrayed by the presence among it of sand grains.

There is no doubt that much of the chopped *Vallisneria* is digested, presumably because the cell walls are ruptured during the process of trituition between the toothed pharyngeal bones.

The oral dentition consists of an outer row of stout bicuspid teeth and four or five rows of smaller tricuspid teeth (Fig. 74). Because of its shape (Fig. 75) each outer tooth forms a small cutting blade. Each jaw therefore has a sharp-edged margin and a roughened inner band. Such a dentition is well suited to the seizing and cutting of water weeds, and it is interesting to compare it with the very similar dentition of *Tilapia melanopleura* which takes similar food.

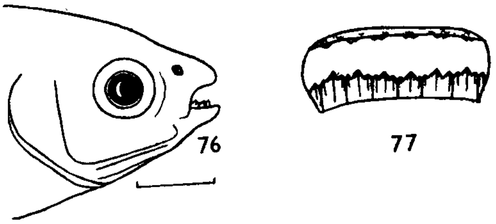
Haplochromis johnstoni (Günther)

This species occurs both on the sandy shore and in the intermediate zone, attaining its greatest numerical density in the latter ; this being correlated with its preferences for beds of *Vallisneria* which are more abundant in the intermediate zone than on the rather bare sandy shore. It is usually to be found among beds of *Vallisneria* where it is fairly well camouflaged by its colour pattern of dark vertical bars on a golden ground which, particularly in small individuals, harmonises fairly well with the strap-like leaves of the plant. (The Chitonga name for both *Vallisneria* and *H. johnstoni* is the same—“ Masimbe ”) It picks its food both from the plants themselves and from the sand at their bases.

The gut contents of eighteen specimens ranging from 9·0 to 16·0 cm. in length collected both on the sandy shore and in the intermediate zone, as well as of three specimens from sandy shores elsewhere and some young from the mouth of a mother, have been examined. These showed *H. johnstoni* to be essentially carnivorous and to have catholic tastes. In the eighteen specimens from the shore under consideration the most frequently occurring item of food was mayfly nymphs (baëtids) which occurred in eight guts. The next in order of frequency were ostracods (seven guts) and fish (six guts). The fish were practically always unrecognisable but included young cichlids. Other foods and their number of occurrences were, fragments of *Vallisneria* (five), gelatinous colonies of algae (five), prawns (two), chironomid larvae, terrestrial insects, mites, lamellibranchs (*Corbicula*), gastropods, and cyclopoid copepods (once each). While some fragments of *Vallisneria* may have been accidentally ingested when snapping at animals, the amount present in some cases indicated deliberate ingestion.

Haplochromis mola Trewavas

This is a mollusc feeder and as such one would expect it to be confined to the sandy shore and intermediate zone, so it is rather surprising that two of the seven specimens captured came from just over the boundary of the rocky shore. Their food, however, had come from the sandy shore so perhaps this is a wandering species. *H. mola* does not appear to be very common on the shore studied, possibly because the area of sand is small and would hardly be expected to support a large population of mollusc-feeding fishes.



Figs. 73–75.—*Haplochromis similis*. 73. Head (lateral). 74. Section of dentition of upper jaw. 75. Teeth of outer series. (Both jaws similar.)
Figs. 76–77.—*Alestes imberi*. 76. Head (lateral). 77. Anterior view of teeth.

The food of all seven specimens (length 9·5 to 14·0 cm.) consisted essentially of molluscs. All contained gastropods among which *Melanoides tuberculata*, small specimens of *Lanistes procerus*, and *Gabbia* sp. were recognised, and four contained also remains of the lamellibranch *Corbicula*. Four also contained insect remains (chironomid larvae and mayfly nymphs) but in contrast to the molluscs their importance was small. One had also eaten a prawn.

The most outstanding adaptation of this species is undoubtedly the structure of both the upper and lower pharyngeal bones which, as in mollusc-feeding cichlids found elsewhere, are armed with a few very large flattened crushing teeth. The lower bone is also much thickened for strength. The teeth in each jaw are small but strong and form small areas in each jaw well adapted for picking up objects of small but not minute, size.

Haplochromis dimidiatus (Günther)

This species is fairly common on the sandy shore and also frequents the intermediate zone. It is an active species and attains a length of more than 25 cm.

The food of twenty-one specimens (two from the intermediate zone and two from the edge of the rocky shore) was examined. These ranged from 8·0 to

25·6 cm. in length. Although definitely carnivorous and with a dentition suited to this diet eight specimens contained the remains of higher plants, identified in seven cases as *Vallisneria.* The indications are, therefore, that some plant material is deliberately ingested. The rest of the food was animal in origin. Terrestrial insects occurred in eight guts and fishes in six. In one case the fish eaten was definitely recognised as being *Engraulicypris sardella,* and other prey included young cichlids. Termites were well represented among the terrestrial insects, in one case the gut being crammed with them. Other foods were mayfly nymphs (baëtids) (three times), chironomid larvae, ostracods, cyclopoid copepods and a prawn (once each). A few fragments of filamentous algae and a gelatinous colony of algae which were also found may have been ingested with the *Vallisneria.*

Most of the food is, therefore, collected in the open water and only a small amount is picked up from the bottom.

Specimens believed to be the young of this species are often common among the beds of *Vallisneria.* Ten of these 1·7 to 1·8 cm. in length, had fed largely on the ostracod *Cypridopsis.* Between them they had in their guts 268 ostracods and a very few other animal remains.

Haplochromis rostratus (Boulenger)

Although individuals of this species can usually be seen cruising about on the sandy shore and in the intermediate zone, usually in groups of five or six, it is not so common as on certain sandy shores examined elsewhere. It is seldom caught, partly because it is an active swimmer, and partly because it has the habit of burying itself in the sand when enclosed by a seine net. (Fryer, 1956 c).

The single specimen caught on the sandy shore contained five young fishes, some cassava washings and sand grains.

Haplochromis moorii (Boulenger)

This species, whose peculiar appearance is well shown in the figure given by Boulenger (1915) is caught from time to time on the sandy shore but is not very common there. The gut contents of four specimens 7·6 to 14·7 cm. in length, consisted of fragments of *Vallisneria* plus sand grains and bottom detritus, and an even larger specimen from an adjacent sandy shore had eaten similar material.

Haplochromis chrysonotus (Boulenger)

Although a member of the " Utaka group " of *Haplochromis,* which includes open water plankton-feeding fishes, this species tends to occur closer inshore than most of its near relatives,* and is occasionally to be found on the sandy shore. One such adult had supplemented its diet of plankton with mayfly nymphs. One specimen caught in a seine net had fifty young in the mouth. The gut contents of ten of these, each 16 or 17 mm. in length, included bottom detritus, centric and naviculoid diatoms, fine threads of filamentous algae, a few ostracods, and, in one case each, a tiny chironomid larva and

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*Information from Mr T. D. Iles who is studying this group of the genus.

some small fragments of *Vallisneria*. All this food had been collected from the bottom so it may be that this species moves onto sandy shores for the purpose of brooding its young.

Tilapia of the *saka-squamipinnis* group

Juvenile members of the *saka-squamipinnis* group of *Tilapia* constitute quite an important element of the fauna of the sandy shore but adults have not been seen there. These juvenile specimens, which seldom exceed 16 cm. in length (the length below which Lowe (1952) says it is impossible to discriminate between the species) seem to be most common during the early months of the year, and a few specimens have even been met with on the rocky shore during April and May, possibly indicating local movements at this time.

As to the identity of these fishes, all that can be said is that while other members of the organisation at Nkata Bay have identified *T. squamipinnis* (Günther) from adults collected elsewhere in the area, a few specimens from the sandy shore which exceed 16 cm. in length had the morphological characteristics of *T. saka* Lowe and even a specimen 14·6 cm. in length had to be identified as *T. saka* on Lowe's criteria. Such information as was obtained on the breeding habits of this species also accords better with what Lowe found out about *T. saka* than about *T. squamipinnis.*

The gut contents of fifty-three specimens, 6·0 to 17·5 cm. in length, from both the sandy shore and the intermediate zone, showed that, without exception, they had fed on the bottom. Typically the gut was crammed from end to end with grit and detritus, being greenish anteriorly due to the presence of fresh plant matter and grey over most of its length where this material had been broken down. Careful scrutiny of the debris showed the green tinge to be due to the presence of occasional diatoms and even fewer fragments of filamentous algae among a mass of inorganic particles. Variety was provided only by three specimens which included fragments of *Vallisneria* among their food. Specimens from an adjoining sandy beach and the few from the rocks had fed likewise. Specimens from Crocodile Creek had similar gut contents but the presence of a more muddy bottom was reflected by their rather different consistency.

Lowe (1952) found that *T. saka* and *T. squamipinnis* tend to feed on open water phytoplankton when this is plentiful but turn to bottom browsing in times of phytoplankton scarcity. The fact that at Nkata Bay they seem always to browse on the bottom may not be unconnected with the fact that the phytoplankton in this part of the lake is extremely sparse ; much sparser for instance than in the more eutrophic South East arm of the lake where most of Lowe's work was carried out. It is possible that the food may include organisms such as protozoans which will not be easily detected, for Ross (1954) states that in L. Victoria he found heavy populations of these organisms in the bottom deposits which " were no doubt ingested and digested by *Tilapia* ".

Tilapia shirana Boulenger

Occasional specimens of this species are found on the sandy shore. It is much less common than the *saka-squamipinnis* group of the genus. The gut contents of four specimens ranging from 13·8 to 25 cm. in length were indistinguishable from those of the previous species. One contained also a few fragments of *Vallisneria.*

Tilapia melanopleura Duméril

This species is definitely rare on the sandy shore. When present it feeds on *Vallisneria.* Bertram *et al.* (1942) record similar food from the stomachs of six Nyasan specimens of this species and Lowe (1952) records it as eating *Ceratophyllum* in the southern part of the lake. As Bertram *et al.* point out its jaws have a strong dentition. They are well suited to seizing a plant and pulling fragments from it as can be seen by putting a leaf between them, closing them, and pulling. The leaf breaks along the line of outer, bicuspid teeth and the seized piece remains clamped firmly between the pads of posterior tricuspid teeth. This dentition is very similar to that of *Haplochromis similis* which takes similar food.

Alestes imberi Peters. (Figs. 76–77)

Specimens of this characin up to about 16 cm., but seldom less than 8 cm., in length often occur in considerable numbers on the sandy shore, but it is without doubt a roving species and is not always present. No specimen has been seen or collected on the rocky shore so it is presumed that shoals move from one sandy shore to another or, on occasion, move up rivers, for it sometimes occurs in Crocodile Creek and has been found in nearby rivers.

Gut contents of thirty-four specimens 7·6 to 16·5 cm. in length, were examined. As in the case of Nyasan examples of this species examined by Worthington (1933) and Betram *et al.* (1942) these showed it to be omnivorous, including as they did insects (mainly terrestrial—termites, beetles, ants—but also a number of mayfly nymphs), plant fragments and seeds, maize and cassava washings, and, in one case, fish remains. Many contained maize and cassava washings resulting from the washing of these materials on the beach by African women.

The striking dentition of this species (Figs. 76–77) is suited to seizing relatively large objects either in the open water or from the bottom.

Barbus johnstonii Boulenger

This species is encountered from time to time on the sandy shore and is, like most members of its genus, a bottom feeder. Nine guts, of specimens 7·5 to 19·9 cm. in length contained a preponderance of vegetable matter, six of them containing fragments of *Vallisneria.* Filamentous algae and diatoms were also present and may have been deliberately scraped from the *Vallisneria.* A single chironomid larva, a single mayfly nymph and a few cyclopoid copepods were also seen.

Barbus rhoadesii Boulenger.

While the data relating to the movements of this species are few the indications are that it moves onto the sandy shore in March, April and May. The only suggestion towards explaining these movements that will be made is that they may be not unconnected with the abundance of young *Tilapia* here during these months.

The guts of thirteen specimens, 23·5 to 30·7 cm. in length were examined. One was empty but all the rest contained fish remains. In one gut two specimens of a *Tilapia* of the *saka-squamipinnis* group each more than 5 cm. in length were recognised but otherwise, beyond being able to identify the prey as cichlids, determinations were not possible.

Worthington (1933) found that five juveniles of this species contained fish remains, insects and " chewed weed "; Bertram *et al.* (1942) found that while it eats an occasional insect or plant it is essentially piscivorous, and Mr T. D. Iles has also found it to be piscivorous.

It differs adaptively from the non-predacious species of the genus in having a very large and more or less terminal mouth.

Barbus innocens Pfeffer

A few specimens of this species, which appears to grub about on the bottom, have been found on the sandy shore. The gut contents of seven specimens, 6·2 to 8·6 cm. in length, were similar to those of four specimens examined by Worthington (1933), and contained plant fragments, debris, ostracods and, in one case a terrestrial beetle.

Barbus eurystomus (Keilhack)

Although rare on the sandy shore this species is mentioned because a specimen of 17·4 cm. in length had its gut crammed with molluscs (*Melanoides* and other gastropods, and *Corbicula*). Three other specimens, almost certainly of this species, included crabs in their diet.

Worthington (1933), who gives figures of the head of this species, found molluscs in the guts of four young specimens. Very large specimens seem to live in the more open waters of the lake.

Labeo mesops Günther

On the sandy shore this species occupies a similar feeding niche to that occupied by *L. cylindricus* on the rocky shore. While *L. cylindricus* is always present among the rocks, however, *L. mesops* is not invariably present on the sandy shore, but seems to occur mainly from about March to May during which period it is present in considerable numbers. At such times it comes inshore from deeper water early each morning often making its presence known by leaping out of the water. Such behaviour has never been seen in *L. cylindricus*.

It feeds, as shown by the contents of nineteen guts plus others examined elsewhere, by sucking up the sand from the bottom which it then passes in large amounts through its enormously elongated alimentary canal presumably extracting from it such organic matter as is present. The mouth structure is similar in essentials to that of *L. cylindricus* (q.v.).

Engraulicypris sardella (Günther)

At times large shoals of this tiny pelagic fish move into the shallow water of the sandy shore, but the factors governing its occurrence are quite unknown and it was not seen at all during 1955.

The gut contents of more than forty specimens, 5·0 to 9·9 cm. in length, some taken on the sandy shore and some from open water outside the bay, showed that in both situations it feeds on plankton. It takes both zooplankton and phytoplankton as was observed by Worthington (1933). While not directly connected with its influence on the sandy shore it can be noted that several specimens from the open lake contained large numbers of chaoborid pupae (as many as ninety in a single fish), obviously captured during their ascent from the depths. The only bottom material observed in any gut of specimens from shallow water was a couple of ostracods.

The part played by *E. sardella* in the economy of the sandy shore is, therefore, to provide an occasional source of food for the predatory species living there, for it has been seen in the gut of *Haplochromis dimidiatus.*

Synodontis zambesensis Peters

This is a wide-ranging species occurring not only in shallow water on sandy shores but also at great depths where oxygen concentrations are low as is evidenced by captures in African traps. It seems, however, to frequent mainly sandy bottomed areas and has not been seen on the rocky shore.

The food taken by ten specimens, 7·5 to 15·5 cm. in length, was very diverse and included chironomid larvae, ostracods, fragmentary fish remains, baëtid nymphs and fragments of *Vallisneria.*

Other fishes of the sandy shore

Quite a few other fishes have been collected from time to time on the sandy shore but are less important than those considered above. These include *Haplochromis kiwinge* and *Barilius microcephalus,* mentioned in the previous section, *Haplochromis compressiceps,* mentioned below, *H. orthognathus H. prostoma* (?) *Haplochromis* of the *tetrastigma* group, *Mormyrus longirostris* and *Rhamphochromis* spp. As on the rocky shore the species of *Rhamphochromis* tend to occur in deeper water than that studied here.

(c) *The intermediate zone*

As noted already many of the sandy shore fishes occur also in the intermediate zone and *Haplochromis johnstoni,* whose habits have already been described, is actually commoner in the intermediate zone than on the sandy shore. Some of the species now mentioned occur also on the sandy shore but are more common in the intermediate zone, and the first three are rigorously confined to it.

Cyathochromis obliquidens Trewavas. (Figs. 78–81)

This is the commonest and most characteristic fish of the intermediate zone and, while a very occasional specimen may be found just over the edge of the other zones, it is safe to state that at points only 10 metres over the boundary it is completely absent. That the ecological preferences of *C. obliquidens* are for areas in which rocks give way to sand is shown by its occurrence elsewhere in situations similar to those prevailing in the intermediate zone (viz. in the north bay at Nkata Bay, at Likoma Island, and at Mbamba Bay).

The gut contents of sixty-four specimens ranging from 7·5 to 11·7 cm. in length were examined in detail, several more were casually examined, and a few collected elsewhere were examined for comparative purposes. The food was found to consist almost entirely of loose Aufwuchs. A very occasional ostracod and once even a mayfly nymph and chironomid larva were seen, but the only real variation of the diet observed was the presence in a few of the guts of the spherical gelatinous colonies of algae which grow on the *Vallisneria* and, to a lesser extent, among the rocks, a very few tiny fragments of *Vallisneria,* and a few sand grains. As the gelatinous colonies pass through the gut undigested and as the higher plant fragments and sand grains were almost certainly picked up inadvertently this species can be classified for practical purposes as a stenotypic feeder whose food consists exclusively of loose Aufwuchs.

As Trewavas (1935) has said " this species is a *Pseudotropheus* in all except dentition ", and in particular it bears a remarkable resemblance to *P. zebra* both in structure and in general habits. Apart from colour differences the general appearance of the two species in life is almost identical. The similarity extends to the structure and mode of action of the mouth which seems to be identical in the two species, and, as observations both in nature and in aquaria reveal, each species scrapes rock surfaces in an identical manner. The teeth of *C. obliquidens,* although superficially quite different from those of *P. zebra* because of the oblique nature of the outer row, are actually very similar and consist of an outer row of bicuspid teeth and several inner rows of tricuspid teeth. One important difference in the feeding behaviour of the species has however, been noted, and that is that *C. obliquidens* obtains some of its food by scraping the *Vallisneria* which grows in the intermediate zone. Exactly the same movements of the mouth take place as when rocks are being scraped. The fish commences scraping near the base of a leaf and slowly moves towards the tip. Although the leaves yield somewhat to the pressure exerted they do not bend so much as one might expect. When a fish leaves a leaf a distinct difference can be seen between the browsed and unbrowsed portions. In spite of its ability to feed on the Aufwuchs growing on the *Vallisneria* this species does not enter the sandy shore where this plant also grows.

The competitive relationships existing between this and other species are discussed at the end of the next section.

Pseudotropheus lucerna Trewavas

Unlike the rest of the members of the genus *Pseudotropheus,* which appear to be confined to the rocky shore, *P. lucerna* exhibits a very well marked preference for the intermediate zone where it appears to be not uncommon. It has also been taken under similar conditions in the north bay at Nkata Bay. By contrast only a single specimen of this species has been taken on the rocky shore during the whole of the time that work was in progress there, and a single specimen was taken under rocky shore conditions at Ruarwe, though as the latter had young in the mouth it was not feeding there.

The gut contents of twenty-eight specimens (including the one from the rocky shore) were examined. All these contained loose Aufwuchs accompanied in several cases by grit. Among the Aufwuchs in some guts were seen fragments of filamentous algae such as grows on the leaves of *Vallisneria*. It may be, therefore, that this species browses on *Vallisneria* as does *C. obliquidens* but this has not been actually observed. The presence of grit in more than half of the guts examined also indicates that it picks up material from the bottom and it seems that it may grub about at the bases of the *Vallisneria* plants as well as, almost certainly, scraping material from the rocks. Further observations on the feeding behaviour of this species are, however, called for.

The mouth structure and its dentition are rather similar to those of *P. zebra* but differ in that the lower jaw is much straighter on its anterior border and tends to be shorter than the upper jaw, and in that the tricuspid teeth are smaller, more numerous, and more close set. The significance of these differences remains to be proved but a straight-edged lower jaw may be more efficient than a rounded structure in skimming material from sandy surfaces, and the tendency towards shortening of the lower jaw perhaps shows a similar correlation.

Aulonocara nyassae Regan. (Figs. 82–85)

Only five specimens of this species have been encountered within the limits of the littoral zone forming the subject of this account and all have been taken in the intermediate zone. Another specimen has been found in the north bay at Nkata Bay under similar conditions and eight more specimens were collected at Mbamba Bay, on the opposite shore of the lake, again under similar conditions. There seems to be little doubt, therefore, that this species prefers situations where both sand and rocks are present.

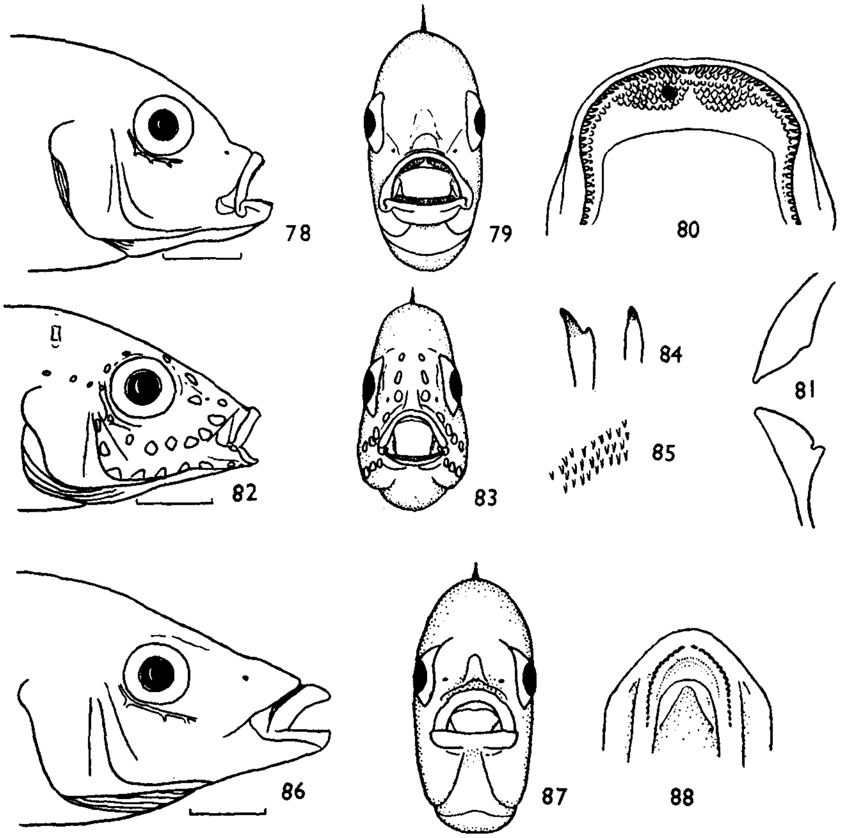
All five specimens collected in the intermediate zone had eaten insects—hydropsychid and chironomid larvae, baëtid nymphs, and some mangled and unidentified but apparently terrestrial insects, one had taken a few ostracods, two contained molluscs (*Corbicula* and *Melanoides*) and one had eaten a prawn (*Caridina*). All the nine specimens collected elsewhere had eaten similar aquatic insects, leaving no doubt that this species is an insect eater.

Its adaptations towards this kind of diet are fairly clear but it is less easy to point to adaptive features correlated with its habitat preferences. The mouth is somewhat protrusible and the teeth of the outer row in both jaws are all functionally conical although the median teeth actually have a small subsidiary cusp (Fig. 84). Their sharp, recurved, nature renders them eminently suited to the picking up of insects. The arc of posterior teeth consists of three rather irregular rows of sharp backwardly-directed conical teeth (Fig. 85) well suited to the holding of insects. A few of the central teeth of the lower pharyngeal bone are enlarged, a structural feature that will facilitate the crushing of large insects and the molluscs which form part of the diet.

The function of the deep pits associated with the cephalic portion of the lateral line system is at present entirely conjectural but it may be that they are concerned with the reception of impulses produced as a result of movements of the prey.

Hemitilapia oxyrhynchus (Boulenger). (Figs. 86–88)

This species, while occurring on the sandy shore, is much more abundant in the intermediate zone of which it is one of the characteristic fishes. Its preferences for this zone can be correlated with the more abundant growth of *Vallisneria* there than on the sandy shore, for it is from the Aufwuchs growing on this plant that most of its nutriment is obtained.



Figs. 78–81.—*Cyathochromis obliquidens.* 78. Head (lateral). 79. Anterior view showing mouth. 80. Dentition of upper jaw. 81. Opposing outer teeth of upper and lower jaws.

Figs. 82–85.—*Aulonocara nyassae.* 82. Head (lateral). 83. Anterior view showing mouth. 84. Outer teeth. Left, near centre of jaw ; Right, from lateral portion of jaw. 85. Inner teeth.

Figs. 86–88.—*Hemitilapia oxyrhynchus.* 86. Head (lateral). 87. Anterior view showing mouth. 88. Dentition of lower jaw.

The gut contents of twenty specimens, including two from the sandy shore, ranging from 8·7 to 13·9 cm. in length plus two specimens from the equivalent of the intermediate zone in the north bay at Nkata Bay were examined. Almost all these contained only the Aufwuchs scraped from the leaves of *Vallisneria,* and fine sand particles. One had in addition picked up a specimen of the little lamellibranch *Corbicula* and a mayfly nymph, one had swallowed a few fragments of *Vallisneria,* another had eaten a few ostracods, and one contained a little zooplankton. Some of the fine sand grains were perhaps taken in with the Aufwuchs among which they had settled after periods when the bottom was somewhat disturbed, but their constant presence may indicate that some food is picked up from the bottom—as the rather unexpected occurrence of *Corbicula* also indicates—but no observations on bottom feeding in this species were made.

H. oxyrhynchus has a rather long snout and a rather wide spade-like lower jaw such as one might expect in a species which digs in the sand. The dentition is quite simple as can be seen from Fig. 88, and only the outer row of teeth appear to be of importance. These are set obliquely and the anterior edge of each tip lies internal to the posterior edge of its anterior neighbour, the result being a fairly broad scraping surface.

Observations have been made on the distinctive feeding behaviour of this species, particularly at Likoma Island, where it was very common among beds of *Vallisneria* under intermediate zone conditions. It swims up to a leaf of *Vallisneria*, turns on its side so as to get the flat grass-like leaf between its jaws, and nibbles. The exact mode of action of the jaws has not been determined but presumably the outer teeth serve as scrapers and remove the Aufwuchs. The leaf itself is not damaged.

Haplochromis compressiceps (Boulenger)

This species occurs also on the sandy shore, but as the four specimens caught were all obtained from the intermediate zone it can be listed here. The specimens ranged from 15·2 to 21·7 cm. in length. One was empty, one contained fish remains, one contained some very fragmentary insect remains including a terrestrial beetle, and one contained a few plant fragments and some gelatinous algal colonies.

There is no doubt that this is a predacious species. In nature it often hovers stationary in the water much as does the European pike. Its much compressed body and its somewhat greenish tinge will render it fairly inconspicuous when it hunts among weed beds. The local fishermen, who are very observant, claim that this species bites out the eyes of other fishes.

Lethrinops spp. cf. *praeorbitalis*

Specimens of two species close to *L. praeorbitalis* and *L. laticeps* were caught in the intermediate zone and were referred to as R. INT. 4 and R. INT. 5 respectively. According to Dr Trewavas, to whom specimens were sent, one of these is *L. praeorbitalis* but the definitions of this species and *L. laticeps* are in need of revision and it is safest not to name them at present. R. INT. 4 (nine guts) fed almost exclusively on chironomid larvae, but in four of the seven guts, of R. INT. 5 examined, were found nematodes, plentifully in three cases, as well as chironomid larvae. As these were always dead even though the fish was examined shortly after capture it would seem that these are specially sought for in the sand and are not normal inhabitants of the alimentary canal.

One of these species, believed to be R. INT. 5, was seen digging in the sand in a similar manner to *L. furcifer*, but was not seen to discharge sand through the opercular apertures as does that species.

Among the other fishes recorded from this zone mention may be made of *Chiloglanis* sp. as no member of this genus was previously known to occur in L. Nyasa. In July 1955 quite a number of young of this genus (only about 20 mm. in length) were found among the marginal rocks and stones, and they occurred also under similar conditions in the North Bay. The species concerned may have been *C. neumanni* Boulenger, an adult of which was collected by Mr D. Harding elsewhere in the lake.

(d) *Crocodile Creek*

Serranochromis robustus Castelnau

Although recorded from the lake proper this species (recorded as *S. thumbergi* by Trewavas, 1935) is definitely more common in Crocodile Creek where numerous small specimens have been encountered among vegetation. Gut contents of eleven specimens 2·0 to 4·9 cm. in length showed that, at this stage, they feed on insects and crustaceans. A small case-making caddis larva was the most frequently recorded food closely followed in order of abundance by mayfly nymphs. Chironomid larvae, mosquito larvae, and cyclopoid copepods came next in sequence, and cladocerans, harpacticoid copepods, a mite, and, in the smallest specimen, testaceous rhizopods, were seen. Among the Crustacea *Eucyclops euacanthus*, *Attheyella bidens*, and *Euryalona orientalis* were definitely recognised.

Food appears to be taken partly from the bottom and partly from the open water.

Tilapia shirana Boulenger

This species visits the creek and apparently breeds there (Fryer, 1956 c). Three specimens 8·6 to 14·5 cm. in length had fed on similar detritus to that eaten by specimens collected in the lake. Several small specimens 14 to 14·5 mm. in length were collected in May 1955. These contained tiny chironomid larvae, ostracods, cyclopoid and harpacticoid copepods, rhizopod tests, tiny algae and detritus. The young stages are therefore more selective in feeding behaviour than adults and take a percentage of animal matter.

Tilapia of the *saka-squamipinnis* group

Juvenile specimens of members of this group are not infrequently captured in Crocodile Creek but large adults have not been seen. The guts of several specimens 6 to 11·2 cm. in length contained very similar material to those of specimens from the lake proper but reflected the nature of the substratum in being more "muddy".

In March, April and May 1955 several shoals of young *Tilapia* of this group or, less likely, *T. karongae*, were present. These had fed like the larger specimens, but a few animals (chironomid larvae, copepods, mites) were also seen in the guts examined. If these fishes had been born in the creek then it would suggest that they were *T. saka* (see Lowe, 1952), but the time of the year at which they were seen accords more with Lowe's data regarding the breeding season of *T. squamipinnis* !

Barbus innocens Pfeff. (Juveniles)

Juvenile specimens of this species seem to be not uncommon in the creek. The food taken by ten specimens 3·8 to 4·9 cm. in length indicates that at this stage of its existence *B. innocens* is a general feeder on bottom material for the guts contained mainly detritus among which however, algal cells, chironomid larvae, cyclopoid and harpacticoid copepods (the latter all apparently *Attheyella bidens*), cladocerans and mites were recognised.

Clarias mossambicus Peters

This species lurks on the bottom and is seldom seen but is probably fairly common in the creek, of which it is perhaps the most distinctive species. Eight specimens 33 to 57 cm. in length were collected. These contained terrestrial insects (beetles, termites, ants, Orthoptera), remains of a small fish (once), plant fragments and seeds. One specimen was crammed with seeds which it seemed quite incapable of digesting. It is well known as a general feeder.

The long barbels must be useful in the detection of prey in murky water such as that in which it occurs here.

Clarias mellandi Boulenger

Only one specimen 40·6 cm. in length was obtained. It contained five anisopterid dragonfly nymphs, an unidentified insect and several plant seeds.

Other fishes of Crocodile Creek

A few small *Barilius microcephalus* have been seen in the creek. Two which were captured had eaten mainly terrestrial insects (in this case adult midges) and a spider, thus collecting their food from the surface as in the lake. *Alestes imberi* also enters the creek. The guts examined contained mainly terrestrial insects. A few *Haplochromis similis* also occur. The few specimens collected contained mainly bottom detritus and some indetermined fibrous material together with a little filamentous algae. *Barbus paludinosus* Peters has also been recorded, the two guts examined containing a mass of both plant and animal matter and detritus picked up from the bottom. A small *Barbus* (a juvenile *B. rhoadesii* ?) although only 7·5 cm. in length had eaten another fish. A number of small unidentified cichlids and cyprinids up to about 3·5 cm. in length have also been examined. These contained mostly tiny chironomid larvae and copepods.

THE FOOD AND ECOLOGY OF THE INVERTEBRATES

The food of the fishes, which constitute more or less the end points of all the food chains in the littoral zone, has already been considered, but in order to fully comprehend the economy of the communities concerned it is necessary to know also something about the food and food requirements of the more important invertebrates. An attempt was therefore made to ascertain the type of food taken by some of the invertebrates, and the results are presented here together in some cases with relevant details of the general biology of the species. As before, each zone is considered in turn. No mention is made of the intermediate zone whose shore harbours some rocky shore species and whose main invertebrate fauna is practically identical with that of the sandy shore.

(a) *The rocky shore*

Potamonautes lirrangensis Rathbun

This crab, until recently believed to be endemic to L. Nyasa and known as *Potamon orbitospinus* Cunnington (Bott, 1955) is very common on the rocky shore and can sometimes be seen lurking under rocks. Its numbers can, however, be easily under-estimated and, as is shown by the way in which specimens appear from beneath rocks when bait is being used, the rocks must hide a considerable population of this species. While females with large broods of young are sometimes caught in deep water small independent specimens are particularly common near the shore line and it may be that the early stages are passed through close inshore ; individuals venturing into deeper water as they get bigger.

Although it lurks under rocks by day *P. lirrangensis* obviously forages over considerable distances by night for it is often found entangled in gill nets set on the sandy shore as much as 100 m. from the rocks.

This species takes a variety of foods for, while it will feed readily on fishes entangled in gill nets—to which it sometimes causes considerable damage—it has been seen out of water feeding on the algal felt left above the water line by the falling lake, and algal material, as well as fragments of terrestrial plants, has been seen in the gut of specimens examined.

Chironomid larvae

The difficulty attendant on the taxonomy of African chironomid larvae needs no emphasis and consequently no attempt has been made to identify the species encountered. From an ecological point of view however, the majority of the species living among the Aufwuchs on the rocks, all of which are of small size, can be regarded as Aufwuchs feeders, for the food in the alimentary canal of specimens belonging to various species consisted of diatoms and fragments of filamentous algae.

Ostracods

The ostracods of the rocky shore are represented chiefly by two species of *Cypridopsis*, both possibly undescribed. As in the case of the chironomid larvae they can be readily classified as Aufwuchs eaters. The food seems to be exclusively algal and they show a marked predilection for diatoms, the gut often being crammed with these algae.

Schizopera consimilis Sars

This species, while exceedingly common among the Aufwuchs of the rocks, is not confined to this micro-habitat but occurs also on the sandy shore. The few gut contents examined appeared to contain pulverised material of plant origin, presumably derived from the Aufwuchs, and there is little doubt that this is another Aufwuchs eater.

Neoperla spio (Newman) nymphs

Nymphs of this species of stonefly occur typically in " fairly rapid stony streams " (Hynes, 1953) and their occurrence among the rocks of the lake-shore bears further testimony to the turbulent state of the water there. The fact that specimens were found only among the rocks is in keeping with Hynes' field observations that they avoid silty places and vegetation.

Little information on the seasonal cycle was obtained save that an empty nymphal skin was seen in early September (before the commencement of the rains) and a predominance of small specimens was noted in January (during the rains). Hynes (1952) concluded that the main period of eclosion of this species in the Belgian Congo is during the first half of the rainy season.

The examination of a number of gut contents confirmed Hynes' (1953) observation that it is carnivorous, for chironomid larvae, a mayfly nymph, numerous ostracods, *Schizopera*, and once some cyclopoid copepods including *Mesocyclops leuckarti*, presumably swilled in from the plankton, were recorded as food. That the species is carnivorous from an early age is shown by the fact that a specimen only 4 mm. long contained four specimens of *S. consimilis* and two tiny ostracods. Ostracods, incidentally, appear to be always ingested whole.

Afronurus spp. nymphs

Mayfly nymphs belonging to two species of *Afronurus* occur commonly under stones on the rocky shore but their gut contents indicate that they obtain their food from the upper surfaces whither perhaps they venture at night. Seventeen guts, embracing both species, showed that both fed on algae among which diatoms predominated. This material is probably swept from the rock surface by the brushlike maxillae.

Hydropsychid larvae

Larvae of two species of Hydropsychidae occur on the rocky shore and one in particular is very common there. Although confused at first the two can be separated quite readily, one having short furcae, a fattish body and a sluggish disposition, while the other has longer furcae a more slender body, and is more active. The latter is much the commoner of the two and occurs in large numbers but seems to be localised in certain niches which are not easy to define but which are perhaps connected with the proximity of a suitable food-bringing current. In such situations half a dozen or even more specimens may occur very close together while nearby a much larger rock may not harbour a single specimen. As shown by the gut contents of twenty specimens this is a herbivore, for all contained algae, including diatoms, the only animal matter found being one tiny chironomid larva and a chironomid head capsule.

The other species, of which six guts were examined, appears to be more carnivorous, and eats ostracods and chironomid larvae but takes some algae.

A record of a hydropsychid larva having eaten a small specimen of its own or a related species made before the two species were recognised as distinct probably refers to this species.

The diet of Hydropsychidae obviously varies much from species to species for Slack (1936) found larvae of an unidentified British species to be largely herbivorous but cites records of other species having been found to be decidedly carnivorous.

Eubrianax larvae

Larvae of a psephenid beetle (popularly referred to in American literature as water pennies) of the genus *Eubrianax* are very common under stones on the rocky shore, and have, though rarely, been seen on the upper surfaces.

They are slow moving algal-eating creatures which feed on the Aufwuchs from which they crop *Calothrix* as well as eating the loose matter such as diatoms.

Elmid larvae

Larvae of two species of elmid beetles occur among the rocks, one being fairly common and the other very rare. The commonest feeds on algal matter including diatoms.

Leeches

Two species of leech occur among the rocks. One, an elongate red species attaining a length of about 25 mm. is very common and seems to occur particularly on surfaces fairly tightly embedded in the substratum. It appears to feed almost entirely on chironomid larvae, which it engulfs whole, but one individual contained eleven specimens of the planktonic *Diaptomus kraepelini.* How these had been procured is a complete mystery.

The other species, a small, broad, greenish species, is much less common. With one exception the guts examined were empty, the full one being gorged with red blood.

(b) *The sandy shore*

Caridina nilotica Roux

This atyid prawn is fairly common in the beds of *Vallisneria* where at times it attains a density of well over 300 per square metre. Although a capable swimmer it always seems to keep near the bottom. Numerous gut analyses indicate that it eats detritus, but the gut contents themselves are not very revealing for they always contain a very finely pulverised mass of particles whose origin is difficult to determine.

Cyclopoid copepods

All three species of *Microcyclops* occurring on the sandy shore are herbivorous, eating diatoms and other small algae, *Eucylops dubius* is also a herbivore. No truly carnivorous cyclopoids have been encountered, but *M. nyasae* has been seen with an occasional rotifer in the gut as well as algae.

Baëtid nymphs

Baëtid nymphs are common among the beds of *Vallisneria,* but their numerical density is apparently less than that of *Cardina.* When disturbed they swim briskly to the nearest leaf of *Vallisneria* along whose longitudinal axis they align themselves and thus become fairly well camouflaged. Their food is algal and is presumably browsed from the leaves of the plants among which they live.

Caenis sp. nymphs

Nymphs of *Caenis* are less common than baëtid nymphs. Needham & Lloyd (1930) suggest that the modification in this genus of the anterior pair of tracheal gills into a gill cover to protect the rest of the gills is an adaptation against respiratory smothering, and as such may well be useful in the present species during times when much silt is brought into suspension by rough weather.

Chironomid larvae

Although living in a different environment and belonging to different species from those of the rocky shore the sandy shore chironomid larvae appear to have a similar diet.

Dragonfly nymphs

Both anisopterid and zygopterid dragonfly nymphs occur on the sandy shore, the latter being the commoner of the two. The food of the zygopterid nymphs includes baëtid nymphs and ostracods but only indetermined chitinous fragments have been seen in the very few anisopterid nymphs examined.

Melanoides tuberculata

This species occurs both in the beds of *Vallisneria* and on the bare sand but is commonest in the former habitat. In Lake Victoria, Fish (1955) records it as digesting cellulose. The few guts examined in L. Nyasa appeared to contain pulverised algal material, presumably scraped from the leaves of the *Vallisneria* by the finely toothed radula which appears well suited to the collection of such material.

Lanistes procerus

This large gastropod frequents the beds of *Vallisneria* but is sometimes to be found washed up on the beach after rough weather. It feeds by tearing off and swallowing quite large pieces of *Vallisneria,* a function for which its broad, stout-toothed radula is well suited. The fact that pieces are torn off and not abraded is shown, not only by the size of the pieces swallowed, but by the presence in one gut of two structurally undamaged and obviously accidentally ingested ostracods. This species cannot apparently digest cellulose and its feeding mechanism would appear to be inefficient insofar as many undamaged plant cells are ingested and can be found still quite green in the faecal pellets. Some of the Aufwuchs necessarily taken in with the *Vallisneria* may be digested but some diatoms are defaecated while still possessing green contents.

Corbicula africana

This species lives buried in the sand and appears to be quite common. It subsists on detritus filtered from its feeding current.

(c) *Crocodile Creek*

The most important macroscopic invertebrates of Crocodile Creek are chironomid larvae, baëtid nymphs and *Caridina nilotica* whose food is similar to that found in these groups on the sandy shore. A zygopterid dragonfly nymph is also very common and appears to prey largely on baëtid nymphs as five of the eight guts examined definitely contained these insects. Chironomid larvae and a tiny bug were also recorded as prey. Some anisopterid nymphs examined had eaten chironomid larvae and cylopoid copepods.

A few brief notes on the ecology of certain other invertebrates follow.

Bugs

Ranatra vicina Sign, *Notonecta* and *Naucoris* are all carnivorous suctorial feeders as is the surface dwelling gerrid, and their part in the food cycle of the creek can be inferred from what is known of their relatives elsewhere. In captivity a specimen of *Naucoris* sp. was seen feeding both on a snail (*Gyraulus costulatus*) and on a small anisopterid larva. A tiny *Micronecta*-like bug appeared in large numbers along the sandy slopes of the overflow lagoon in May and June 1955 and appeared to be confined to this microhabitat ; its preferences thus being similar to those of the European *Micronecta poweri* (D. & S.). These bugs were feeding on detritus which included large numbers of minute green algal cells.

Crustacea

To gain an insight into the detailed interrelationships of the Copepoda, Cladocera and Ostracoda present in the creek would require a detailed study in itself, but from what is known of these groups it can be stated that the cyclopoid copepods belong mostly to genera which have been shown to be herbivorous (Fryer, 1957 b) and include some (e.g. *Eucyclops agilis*) whose feeding habits have been studied in detail elsewhere. On the other hand *Macrocyclops albidus oligolasius* is a carnivore. The Cladocera present feed mainly on detritus and small algae but, by virtue of the different strata which the various species occupy, they must tap different sources of these materials. The few ostracods present are bottom dwellers and one at least is a vegetarian.

Molluscs

A species of *Limnaea*, rather scarce in the creek itself, very quickly colonised the overflow lagoon whilst it was in existence and multiplied there abundantly. Many died when the water receded again.

Of the two small molluscs *Segmentorbis angustus* and *Gyraulus costulatus* which are common in the creek the former is the most abundant. Both occur among rank vegetation and both were found to contain detrital matter and tiny algal fragments in the gut.

FOOD WEBS IN THE MAJOR HABITATS

(a) *The rocky shore*

Here the fundamental basis of all organic production is the algal film covering the rocks. Within the narrow " trophic zone " the total productive area is enormously increased by the irregular nature of the substratum. An accurate estimate of this increase is scarcely possible but it must be in the region of three times that of an unbroken substratum. Estimates of total organic matter (taken as loss in weight by dry weight after incineration) present per unit area of rocks of measured area, whose surfaces were scraped clean of Aufwuchs and its attendant organisms, gave very variable results as can be seen from the following figures.

TABLE 5

Amount of organic matter present on submerged rocks

Amount of organic matter/100 sq. cm. in mg.	Approximate depth of rock in cm.
86·6	91
100	76
180	62
243	51
211	38
134·5	32
563	23

The only real correlation appears to be that between the very shallow water in the last case, with its attendant freedom from the grazing activities of the larger fishes, and the production of an excessive amount of organic matter. So many and varied are the factors influencing organic production of this kind, however, that much more detailed work would be necessary before any sort of generalisations could be made, and the most that can be said is that, in shallow water, the production of a standing crop of at least 560 mg. per 100 sq. cm. is possible.

Data collected relating to grazing rates are still most inadequate but it can be remarked that the amount of organic matter present per 100 sq. cm. in the shallowest water was four to six times as much as that present in completely filled guts of specimens of *Labeotropheus fuelleborni* 9·8 cm. in length and *Psuedotropheus zebra* 8·5 cm. in length. The alimentary canal of these species takes at least twelve hours to empty. No conclusions are drawn from these data which can be taken as no more than a pointer to conditions of supply and demand of the basic food on the rocky shore.

The links in the food chains on this shore are very short, the main flow being Aufwuchs→fishes, often direct, and seldom with more than one intermediate stage. (Fig. 89).

(b) *The sandy shore*

Fig. 90, when compared with its counterpart for the rocky shore, shows at a glance one of the fundamental differences in the trophic organisation of the two habitats. Here the availability of several primary food sources stands in marked contrast to the single main source on the rocky shore. Partly, though not entirely, because of this, there is a greater diversity of secondary foods on the sandy shore for, in addition to similar foods to those available on the rocky shore (chironomid larvae, mayfly nymphs, etc.), there are others such as molluscs, prawns and cyclopoid copepods which are unrepresented in the latter zone.

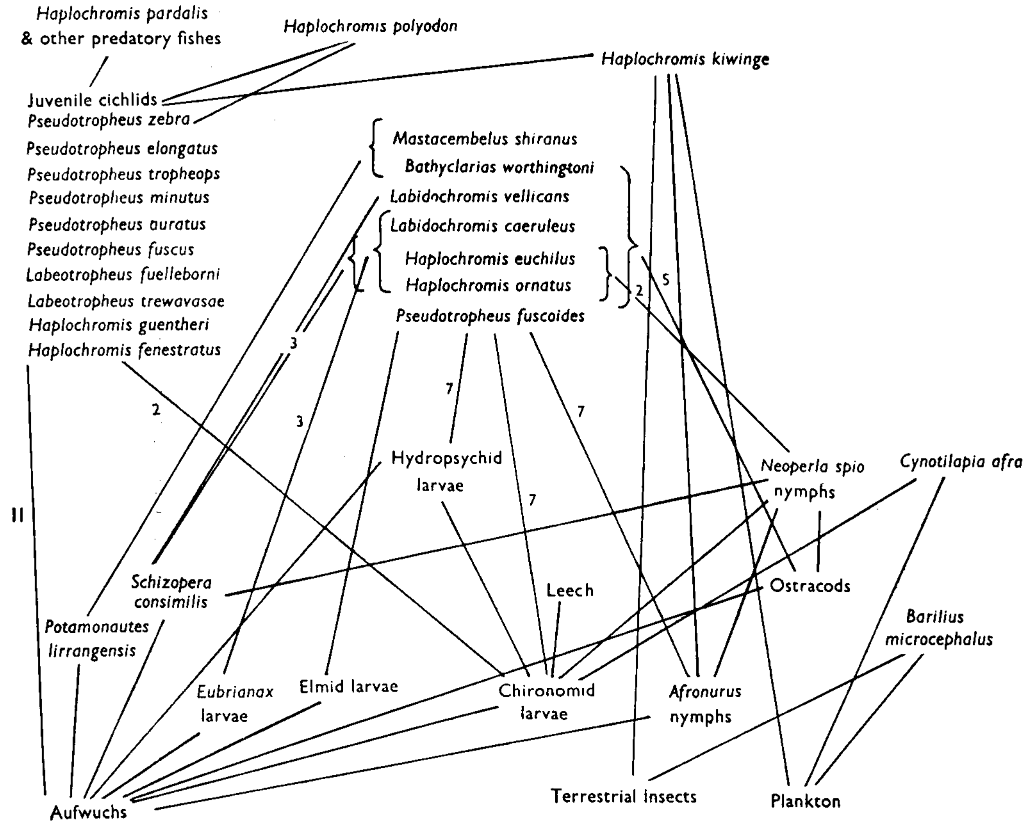


Fig. 89.—Food web on the rocky shore.

(c) *The intermediate zone*

The food web of the intermediate zone is not illustrated as it is essentially the same as that of the sandy shore. Here, however, there is an additional primary food source in the form of Aufwuchs growing on the rocks which are present and, consequently, certain additional secondary foods.

(d) *Crocodile Creek*

The food web of Crocodile Creek (Fig. 91) indicates clearly that the main source of food in this habitat is the bottom where algae are able to grow and where material brought down in suspension by the feeding stream settles. In its dependence largely on one source of food the economy of the creek

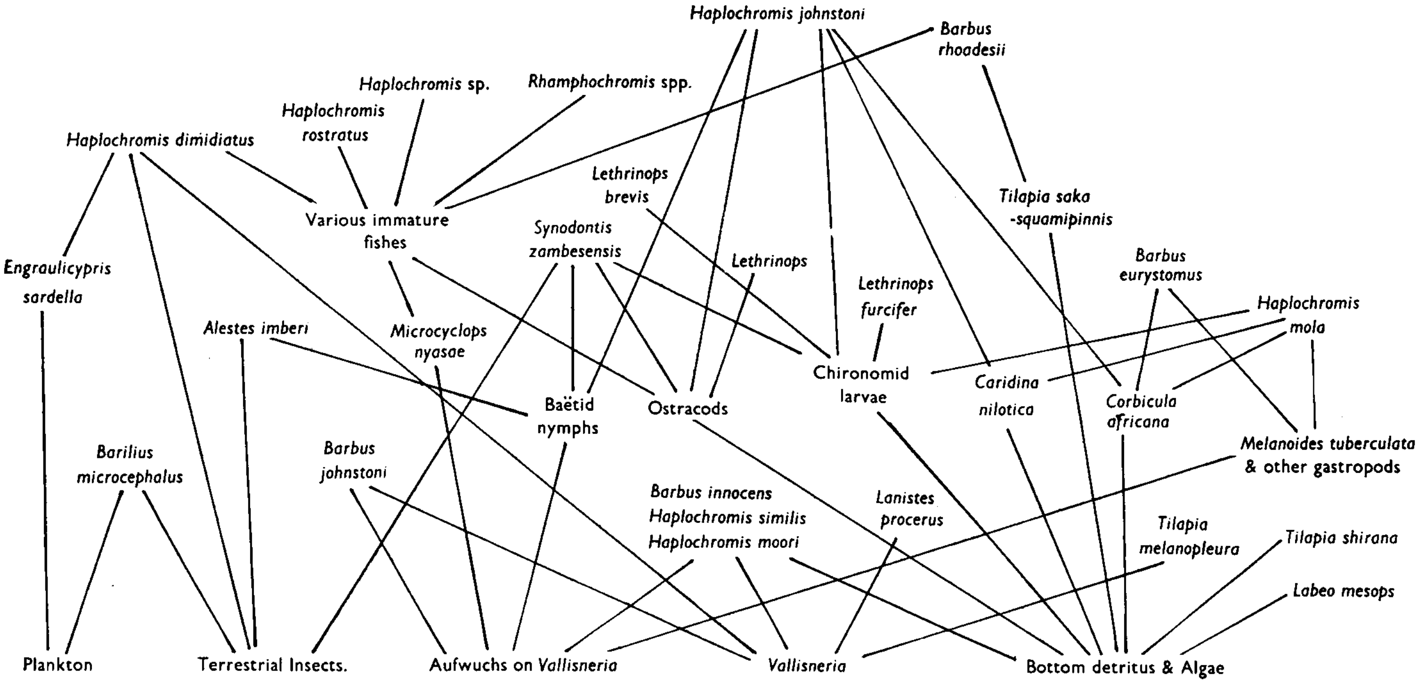


Fig. 90.—Food web on the sandy shore.

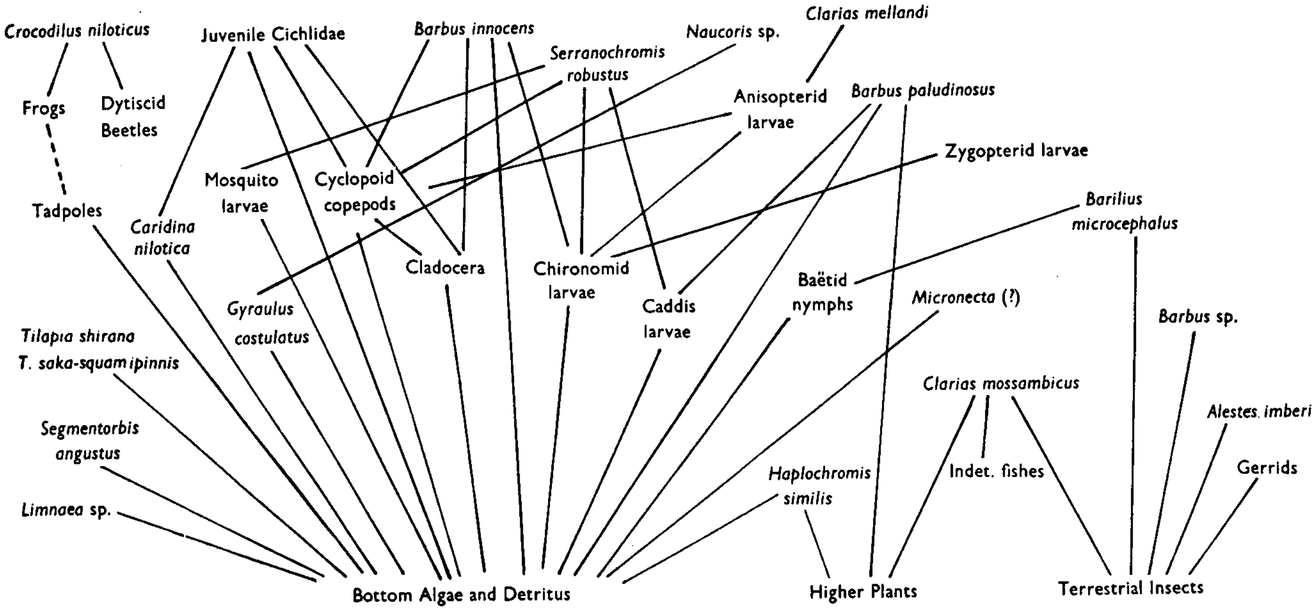


Fig. 91.—Food web in Crocodile Creek

resembles that of the rocky shore rather than that of either of the other two lacustrine habitats with which the creek has much greater physiographical affinities.

The relative poverty of the fish fauna of the creek can be partly explained when its dependence on bottom algae and detritus is realised, for this source of food, and the invertebrates depending on it, are removed or very greatly reduced in quantity when the creek is scoured by floods, and there must inevitably be a time lag, whose length depends on the duration and intensity of the rains, before algae and invertebrates can recolonise the bottom of the creek, and the weeds which are also removed can redevelop as shelter. This periodic scarcity of food, which requires more detailed study, is probably as important, and perhaps even more important, so far as the fishes are concerned, than the purely mechanical effects of scouring. This also probably explains why most of the fishes present are general feeders rather than exploiters of one specialised food source.

PROBLEMS OF COMPETITION AMONG THE FISHES

In each lacustrine community several species of fishes, some very closely related, co-exist. Some of the problems connected with this co-existence and with the competitive relationships of the various species are considered in this section.

(a) *The rocky shore*

In a previous section the account of gut analyses made it clear that many fishes feed directly on the algal Aufwuchs of the rocks, and that several others eat similar invertebrates. The fish population among the rocks is also very dense. These bare facts indicate the probability of competition for food. How then do the various species obviate competition with their neighbours ?

Firstly the fishes can be split into several obvious groups based on food preferences, viz. algal browsers, invertebrate eaters, fish eaters, and plankton feeders, with two other possible categories, surface feeders, and scale eaters, including only *Barilius microcephalus* and *Genyochromis mento* respectively. Obviously the members of one " feeding group " do not compete directly for food with those of another group, though within each group competition for food might be expected. Preferences have been found, however, either in food or in general ecology, which enable certain species with similar habits to co-exist in the same general habitat.

Of the invertebrate feeders *Bathyclarias worthingtoni* and *Mastacembelus shiranus* live actually beneath the rocks, thus frequenting a different microhabitat from that occupied by the other species which at most go beneath rocks for temporary shelter. Both differ from other invertebrate feeders, save for a single record concerning *Melanochromis melanopterus*, in including crabs in the diet. They differ between themselves both in diet and in general ecology. *B. worthingtoni* takes a considerable number of crabs, particularly as it gets bigger, and ostracods play an important part in its diet : *M. shiranus* takes few crabs and must necessarily be restricted to eating small specimens, and has not been recorded as eating ostracods. Other differences have also been noted, e.g. one

B. worthingtoni had eaten fishes, never recorded in *M. shiranus*, and the latter hydropsychid larvae which have not been seen in the gut of the former.

Because of its eel-like form *M. shiranus* will be able to enter and feed in crannies inaccessible to *B. worthingtoni*. It also occurs right up to the shore-line where the latter is not found. Thus, while there is an overlap in both food and habitat preferences, the two species largely occupy separate niches.

There are six other important " invertebrate eaters ", all cichlids, as well as one species, *Melanochromis melanopterus*, of which too few specimens have been collected to permit a true interpretation of its feeding niche. Of these *Labidochromis vellicans* occupies a rather different niche from the other species, living closer inshore (Fig. 93) and having more skulking habits. Because of its small size it can take food from crannies inaccessible to all save the smallest specimens of other species and to *L. caeruleus*, and must be partially isolated in this respect even when its horizontal range overlaps that of its possible competitors. In spite of its small size this species seems capable of eating even the largest insects available on the rocky shore and is not debarred from competing with other species on this account.

Although the number of specimens of *L. caeruleus* available was small there are slight indications that it differs somewhat from *L. vellicans* in its food preferences. Thus mayfly nymphs figured in the gut contents of some of the specimens of this species but are very seldom seen in *L. vellicans*, and *Eubrianax* larvae occurred in three guts but were represented only by a single specimen in the more numerous guts of *L. vellicans* examined. On the other hand chironomid larvae and ostracods occurred much less frequently than in *L. vellicans*. It is tempting to suggest that these slight differences are correlated with the slight differences in pharyngeal dentition of the two species : the more robust dentition of *L. caeruleus* being an adaptation to the crushing of rather hard-bodied insects such as mayfly nymphs and psephenid larvae.

Young *Haplochromis kiwinge*, up to about 10 cm. in length, take a proportion of their food from the rocks, but also eat zooplankton, which is their most important single article of diet, and some terrestrial insects. Their relatively unspecialised mouth probably debars them from picking up ostracods from the rocks. On the whole they have a rather distinct feeding niche.

The food of the "invertebrate eaters" is tabulated in Table 6; foods being arranged in order of importance based on the number of occurrences and relative abundance of the different categories in the guts examined. While the data are meagre in some cases the indications are that no two species have identical preferences. This must help to obviate serious competition, but a good deal of general competition for food probably takes place. *L. vellicans* and *Haplochromis ornatus* have very similar diets but must seldom come into contact because of their different horizontal ranges, and the same possibly holds good for *Haplochromis euchilus* and *Pseudotropheus fuscoides*.

It is interesting to compare the ecological relationships of this assemblage of fishes with those of a small community of freshwater fishes studied by Hartley (1948) in England. After analysing considerably more data than was available for the species considered here Hartley concluded that his community was

TABLE 6

Food preferences of six invertebrate-eating cichlid fishes from the rocky shore. Foods are arranged in order of importance. Figures in brackets indicate the number of guts examined.

Labidochromis vellicans (26)	*Labidochromis caeruleus* (7)	*Haplochromis kiwinge* (Juv) (26)	*Haplochromis euchilus* (6)	*Haplochromis ornatus* (6)	*Pseudotropheus fuscoides* (6)
Chironomid larvae Hydropsychid larvae Ostracods Other dipterous larvae	Hydropsychid larvae Mayfly nymphs Chironomid larvae *Eubrianax* larvae	Zooplankton Mayfly nymphs Terrestrial insects Chironomid larvae	Mayfly nymphs Chironomid larvae Ostracods Hydropsychid larvae	Chironomid larvae Ostracods Mayfly nymphs Hydropsychid larvae *Schizopera*	Mayfly nymphs Chironomid larvae
Also recorded Mites, *Schizopera*, Mayfly nymphs, *Diaptomus*, *Eubrianax* larvae, Algae	Also recorded Ostracods, Mites, Case-bearing caddis larvae, *Corethra* larvae	Also recorded Algae, Hydropsychid larvae	Also recorded Fish, *Neoperla* nymphs, *Eubrianax* larvae, Terrestrial insects, *Schizopera*, Prawn, Snail	Also recorded *Neoperla* nymphs, *Eubrianax* larvae, Elmid larvae, Mites, Algae.	Also recorded Hydropsychid larvae, *Diaptomus*, Terrestrial insects (?) Snail, Algae.

" a loosely organised assemblage in which the members are distinguished by no more than the varying proportions on which they draw upon the constituents of a common stock ". While this statement is broadly applicable to the species considered here the range of foods is much less than that taken by the omnivorous species in Hartley's community. Hartley also points out that his species show " considerable flexibility of feeding behaviour ". They could, therefore, easily adjust their diet if one food became scarce, while here several of the species concerned show very specialised adaptations towards collecting certain foods and could probably not switch so easily, particularly as the other feeding niches on the rocky shore are already occupied by specialised species. It is concluded therefore that a much more delicate state of dynamic balance exists in the present case than in that considered by Hartley.

A much more complex state of affairs exists among the algal-eating fishes for no fewer than twelve common species subsist largely or entirely upon Aufwuchs (Fig. 92), without taking into account *Pseudotropheus elongatus* of which only a few specimens have been seen and *P. williamsi* which also eats insects and is rare on the shore under consideration.

One species, *Haplochromis guentheri*, exhibits sufficient selectivity in feeding to warrant the assumption that it competes only to a limited extent with the other algal browsers with which it lives. The predominance in the guts examined of filamentous blue-green algae (*Lyngbya* ?), very seldom seen in the guts of other species, as well as the presence of occasional ostracods and other animals, indicates that while it can be broadly classified as an algal browser it occupies a distinct and otherwise unexploited feeding niche.

As indicated in Fig. 92 the algae taken by the other algal browsers can be split into two main types—*Calothrix* and " loose Aufwuchs ". Most species collect only the latter, a few may collect both, and *Varicorhinus nyasensis* appears to collect mainly *Calothrix*. While the distinction between eaters and non-eaters of *Calothrix* is certainly concrete and not theoretical its significance is obscure for the *Calothrix* eaten seems always to pass through the gut largely unaltered. Even if one assumes that the taking or non-taking of *Calothrix* is of ecological importance only *V. nyasensis*, which also takes an occasional insect, can be regarded as occupying a distinct feeding niche on these grounds. Of the other three species, *Labeotropheus fuelleborni*, *L. trewavasae* and *Pseudotropheus tropheops*, which include *Calothrix* in their diet the first and the last can and do exist without it on occasion. This is proved by observations made at Mbamba Bay (see p. 233) and by the capture of several specimens of these species at Nkata Bay whose guts contained no such algae. While these two species take identical foods there are great differences in their methods of food collection (pp. 172 and 180). It seems possible that, because of these differences, and because *L. fuelleborni* swims always close to rock surfaces while *P. tropheops* " hovers " over the rocks, that the former species may be able to collect food from situations which, if not actually inaccessible to *P. tropheops*, are seldom frequented by it. These differences in " feeding areas " are not great and there is no doubt that both species often take their food from the same situations and overlap in food preferences to a great extent.

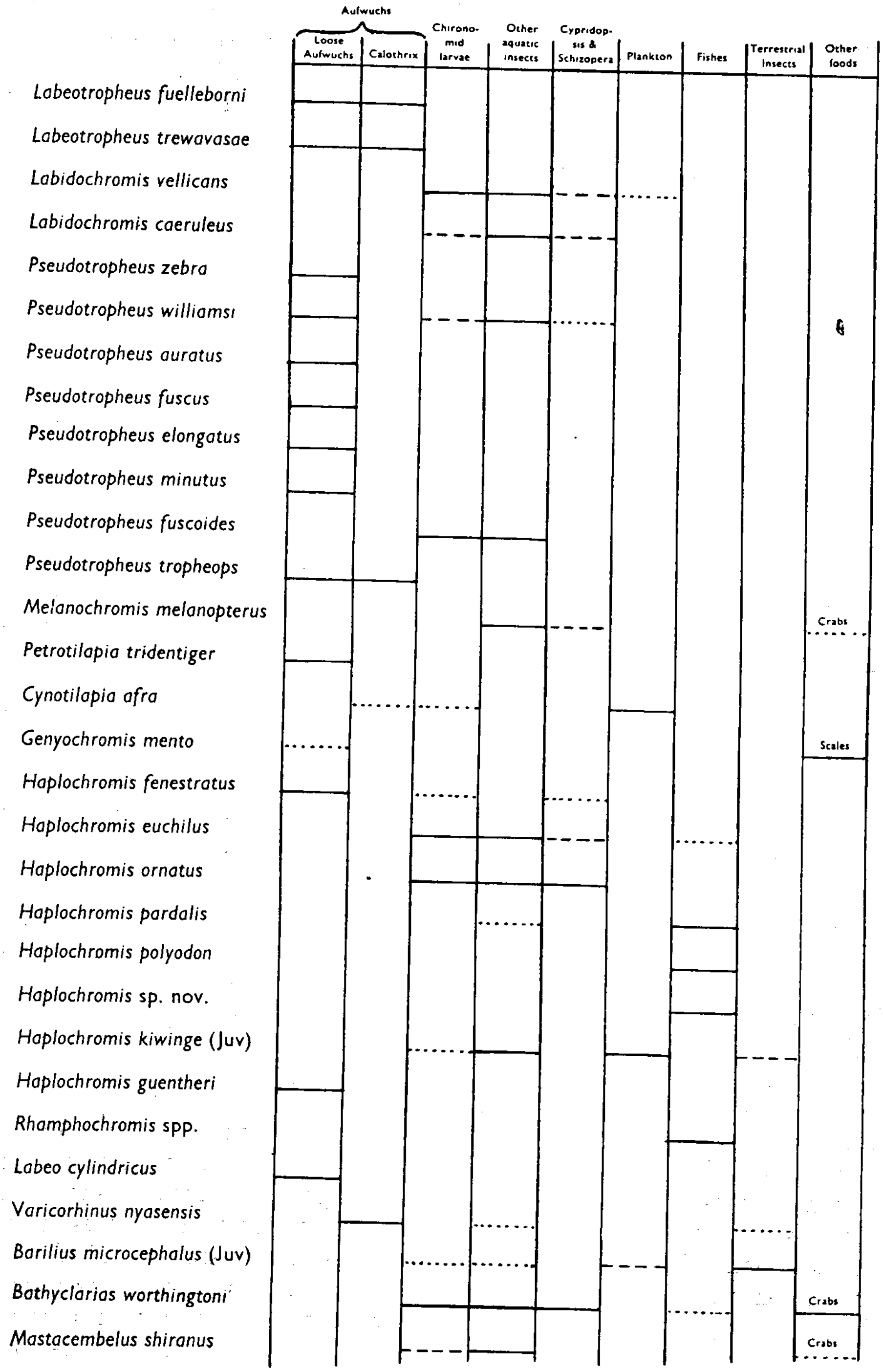


Fig. 92.—Diagrammatic representation of the main foods of the rocky shore fishes. A full line indicates a major food source; a broken line a frequent source and a dotted line an occasional source.

At the moment it is quite impossible to point to any difference in habitat preferences between the two sibling species of *Labeotropheus*. The two were in fact not recognised as distinct species until the field work was completed! The mouth structure and dentition are identical in the two species, gut contents are quite indistinguishable, and the two fishes live side by side among the rocks on the same shore.

There are no fewer than seven common Aufwuchs eating species which do not eat *Calothrix*. Of these *Pseudotropheus fuscus* and *P. minutus* live close inshore and have a different horizontal distribution from the rest (Fig. 93). The horizontal distribution of the former species is known from observations while that of the latter is inferred from catch data. *P. fuscus* is skulking in habits and the same is probably true of *P. minutus*. There is, however, a very marked size difference between the two species which will permit *P. minutus* to exploit with its narrow mouth crannies which are inaccessible to all save young specimens of *P. fuscus*. Thus while the two probably compete, there can be seen means whereby competition may be minimised.

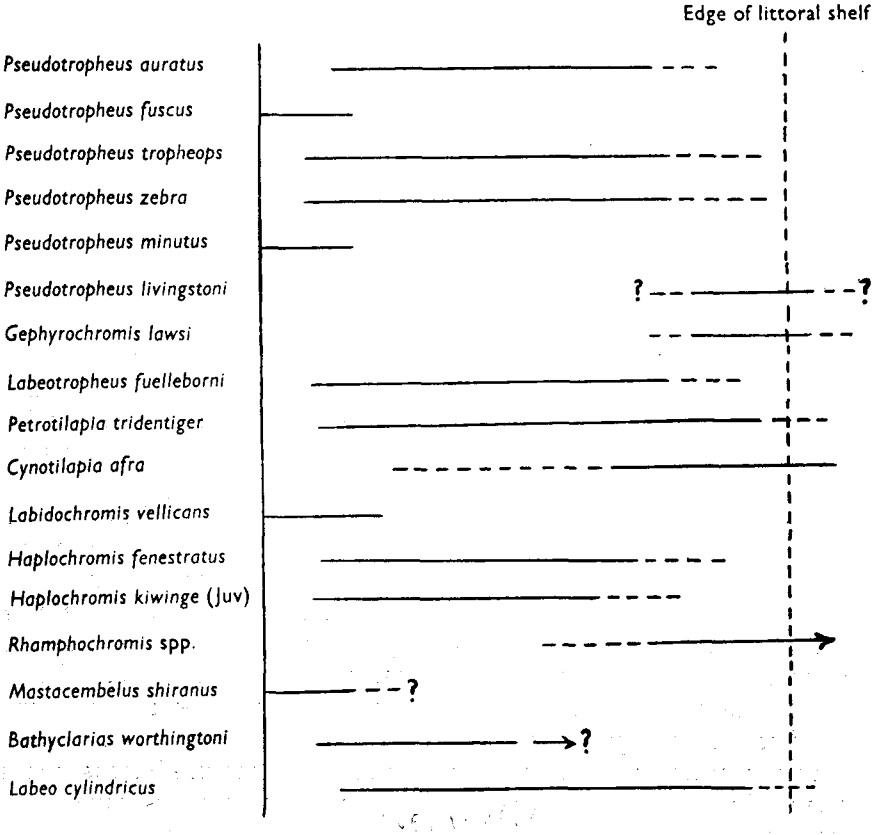


Fig. 93.—Diagram showing approximate horizontal distribution of some rocky shore fishes.

Of the remaining five species *Haplochromis fenestratus*, while feeding largely on loose Aufwuchs, occasionally supplements its diet with a few chironomid larvae and ostracods, and it collects its food in a manner which differs from that of the other species. Because of its narrow mouth it may be able to collect food from cracks which are inaccessible to the other species.

Labeo cylindricus appears to take its food largely or entirely from horizontal surfaces and therefore leaves untapped parts of the habitat used as a source of food by species with the same food preferences.

Pseudotropheus zebra and *Petrotilapia tridentiger*, while having strikingly different teeth, nevertheless collect their food by apparently identical means but by a method which differs from that employed by *Pseudotropheus auratus*, though in all three cases the food taken is identical and all three co-exist with no spatial isolation. The difference in food collecting mechanism may in some way assist *P. auratus* to exploit the available food source in a different manner from its relatives but no evidence has been found to show that this is so. It has proved impossible to find differences between *P. zebra* and *P. tridentiger* either in the food collected or in the method of collection, and the reason why the two co-exist in this way seems to be that they do not compete because of a superabundance of food. Such an explanation of the co-existence of closely allied species has been put forward for titmice (Hartley, 1953) and for herbivorous cyclopoid copepods (Fryer, 1957 b). In the writer's opinion this superabundance of food plays an important part in permitting the co-existence of numerous closely allied species which occur in large numbers and which, while differing markedly in their methods of food collection, would nevertheless come into competition if the food supply was limited.

Elucidation of the means whereby the piscivorous species avoid competition is rendered very difficult by the fact that one can seldom identify the partly digested victims with absolute certainty. However, the species of *Rhamphochromis* occur, in general, at the fringe of the rocky shore and must therefore compete only to a small extent with species living closer inshore such as *Haplochromis polyodon*. Again species such as *Bagrus meridionalis* and the clariids which visit the shore differ markedly in behaviour from the piscivorous cichlids and therefore probably tend to encounter different fishes.

The predators, which take a considerable toll of the non-predacious rocky shore fishes, probably play an important part in regulating their numbers. At present there appears to be an unlimited amount of Aufwuchs available on the rocky shore. Because of this it is conceivable that, in the absence of predators, the population of fishes, dense as it is, could increase even more. This would lead to increased competition for food and living space, and the present community equilibrium would be upset—possibly with the extermination of certain species. The presence of predators, however, will prevent this, and by reducing the effects of interspecific competition will tend to favour the survival of certain non-predacious species.

This role is quite the reverse of that assigned to the predacious fishes of African lakes by Worthington (1937, 1940, 1954), whose views have recently been questioned (Fryer & Iles, 1955). This theory is elaborated in Part II, but here it is of interest to note that a similar role of predation has recently and quite independently been postulated by Sokoloff (1955), who attributes the ability of two very closely related species of *Drosophila* larvae to co-exist in the slime-fluxes of trees to the effects of predation on ovipositing females and the interference with ovipositing females by other insects, which holds the drosophilid populations at a reasonably low level and thus obviates competition.

The dynamic balance of the community is also probably controlled in part by the predators. Thus any increase in numbers of the Aufwuchs feeding fishes at the expense of the invertebrate eating fishes is likely to be counteracted by increased predation on the Aufwuchs feeding fishes with a subsequent return to stable conditions.

The possibility of a further type of competition among the rocky shore fishes, namely competition for breeding grounds, will be discussed in Part II.

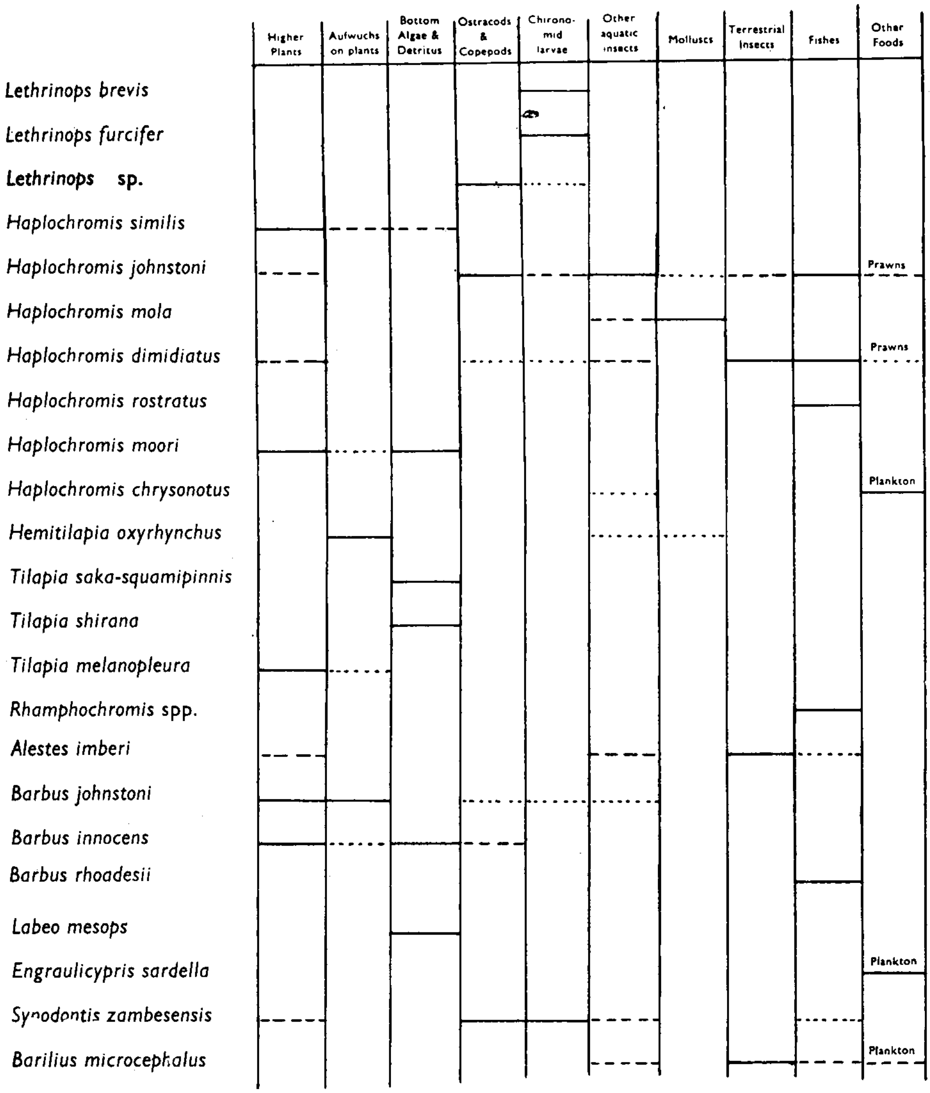


Fig. 94.—Diagrammatic representation of the main foods of the sandy shore fishes. Conventions as in Fig. 92.

(b) *The sandy shore*

Fig. 94 shows the foods eaten by the most important sandy shore species. Here, while there is a strong possibility of general competition for food, there is no one foodstuff which, like the Aufwuchs on the rocky shore, is used exclusively or almost exclusively as a source of food by several species. While there is a good deal of overlap in food preferences there are only a few cases in which direct competition may be expected ; the two outstanding cases being those of *Lethrinops brevis* and *L. furcifer*, which are both specialised feeders on chironomid larvae, and of *Tilapia shirana* and members of the *saka-squamipinnis* group of the genus both of which feed on bottom detritus and which also take rather similar food to *Labeo mesops*.

The last case is the simplest. *L. mesops* is only a visitor to the sandy shore and it swallows large sand grains, probably often collected in deep water, and must compete but little with the species of *Tilapia* which, while utilising the same food source, more carefully skim the substratum and do not ingest large sand grains. *T. shirana* is quite rare on the sandy shore which indicates that, under the conditions prevailing there, it cannot complete very successfully with the representatives of the *saka-squamipinnis* group.

It is not possible to explain the co-existence of *Lethrinops brevis* and *L. furcifer* save on the grounds that the food supply must be sufficiently plentiful to obviate serious competition between them, though, as already noted these species spend much of their time in an apparently diligent search for food.

Apart from these cases the fishes are either specialised feeders occupying a niche virtually unexploited by other species ; e.g. the mollusc eating *Haplochromis mola*, or, like the members of Hartley's community mentioned above, eat a variety of foods so that, should pressure on any one food become great, they can probably switch to another.

(c) *The intermediate zone*

The remarks concerning the sandy shore apply to a large extent to the intermediate zone, but certain other problems arise, the most interesting of which concern *Aulonocara nyassae, Pseudotropheus lucerna* and *Cyathochromis obliquidens*.

A. nyassae might be expected to compete with *Haplochromis johnstoni* which is common in this zone. Although little is known of the habits of *A. nyassae* there is some evidence, obtained both at Nkata Bay and at Mbamba Bay, that some of its food (hydropsychid larvae) is collected from rocks. *H. johnstoni* has not been found to eat hydropsychid larvae and seems to have a definite preference for weed beds, so the two may not compete to any great extent.

Little is known of the general habits of *P. lucerna* save that it is markedly restricted to the intermediate zone and that it takes much of its food from the rocks. Its virtual absence from the rocky shore, where suitable food is abundant, can probably be attributed to the competitive influence of the numerous other species of the genus and their allies which occur there and which take similar food. Absence of suitable food must be an important factor debarring it from the sandy shore. It seems to be a hanger-on in a restricted niche in which it must have some advantages, one of which may be its wide mouth which will enable it to scrape a greater area per unit of time than a narrower mouthed species, and thus compensate to some extent for the greater paucity of food in this zone than on the rocky shore. The lesser abundance of Aufwuchs in the intermediate zone than among the rocks is doubtless a major factor governing the comparatively rare occurrence of other species of *Pseudotropheus* in this zone and as such probably assists the survival of *P. lucerna.*

More is known of *C. obliquidens* whose great similarity in structure, food preferences, and feeding mechanism to *Pseudotropheus zebra* has already been pointed out (p. 205). It browses on the Aufwuchs both of the rocks and of the *Vallisneria*, but does not occur in zones where either of these sources of food is present alone. Its great numerical abundance in the intermediate zone shows that here it is a very successful species and can compete very effectively with *P. zebra*, a few specimens of which are occasionally seen in this zone but which, by comparison with *C. obliquidens* is definitely rare. Its dual feeding behaviour may well be a contributary factor to this success. Onto the rocky shore, however, it very seldom ventures and the obvious inference is that here *P. zebra* has some selective advantage. Its absence from the sandy shore may be due to similar causes, namely that it can compete successfully with browsers on the vallisnerial Aufwuchs where rocks are also available as an important source of food, but it is unable to do so when this food alone is available. Moreover *C. obliquidens* is probably derived from rock-dwelling ancestors and long standing instincts and breeding behaviour connected with rocks would require to be changed before it could completely desert this kind of substratum.

(d) *Crocodile Creek*

The position in Crocodile Creek is rather similar to that on the sandy shore though the number of species involved is less. Here occur several species whose food preferences overlap to a considerable extent but which are fairly general feeders capable of utilising a variety of foods and presumably able to compensate for the scarcity of one kind of food by turning to another. There are also some species which occupy a distinct niche, viz. the bottom scraping vegetarians of the genus *Tilapia* and young weed-dwelling *Serranochromis robustus* which actively seek out animal prey both among the weeds and on the bottom.

INTER-HABITAT MOVEMENTS AND RESTRICTIVE ECOLOGICAL FACTORS

An outstanding feature of the littoral zone of L. Nyasa is the way in which most of the species represented are restricted to one major habitat. This is seen most strikingly if one observes the fishes with a mask and passes from a rocky to a sandy shore. On the former one sees myriads of fishes which disappear with startling suddeness as one passes onto the sand which, at first glance, presents a deserted appearance, but which is later seen to house a variety of fishes which differ markedly from those present among the rocks.

Inter-habitat movement can be dismissed very briefly as so little takes place. *Barilius microcephalus*, whose food requirements are independent of the nature of the bottom is the only fish which can be found commonly on both the rocky and sandy shores. *Varicorhinus nyasensis*, a rocky shore species, is known to move onto the sandy shore, and apparently up Crocodile Creek, when sexually mature. Young *Tilapia* of the *saka-squamipinnis* group appear to move about at certain times of the year though the reason for this is not understood. Both they and *T. shirana* move into Crocodile Creek either for breeding or for brooding the young. *Alestes imberi* enters Crocodile Creek on occasion, *Haplochromis similis* has been found there, and *Barbus innocens* is found in the creek and on the sandy shore, but none of these species frequents the rocky shore. The only invertebrate which appears to move regularly between major habitats is the crab *Potamonautes lirrangensis* which lives among the rocks but forages on the sand by night. The copepod *Schizopera consimilis* apparently finds conditions on both rocky and sandy shores suitable for its existence ; otherwise the picture is one of stenotopy.

The reasons for this stenotopy vary from species to species but the most obvious and widepread is the demand for a particular kind of food which, in turn, depends on the nature of the substratum. It is indeed virtually impossible to separate these two limiting factors as usually one could not operate in the absence of the other. The most obvious case is that of the specialised rock-scraping fishes which depend on Aufwuchs and, ultimately, on the rocks on which it grows. Similar factors restrict the distribution of numerous other fishes, e.g. the diggers for chironomid larvae, the mollusc eaters, and the browsers on *Vallisneria* on the sandy shore. Demand for a particular kind of food restricts certain invertebrates to one habitat in a similar way, e.g. the snail *Lanistes procerus* feeds on *Vallisneria* and is therefore restricted to the sandy shore.

A few fishes, notably the piscivorous species, could, in theory, satisfy their nutritional requirements in any of the habitats yet they are fairly well restricted to one of them. Here it seems that the various species have evolved habits enabling them to prey with greater success on the fishes of one habitat rather than another. Their case is strictly comparable with that of the birds of prey in Britain among which, for instance, the sparrow hawk frequents woodland, the merlin, moorland, etc., and which feed largely on the small birds of these habitats.

A factor preventing the successful penetration of lacustrine predators into Crocodile Creek may well be the turbidity of the water which, apart from being objectionable to a species accustomed to the clear waters of the lake, would hamper the feeding activities of an active predator hunting by sight more than those of fishes taking other kinds of food.

Shelter is probably important in restricting the distribution of certain invertebrates such as the nymphs of *Afronurus* and the larvae of *Eubrianax*, both of which could probably collect and utilise the Aufwuchs growing on the *Vallisneria* just as well as that growing on the rocks. Coupled with this may well be an inherent demand for current such as Wu (1931), cited by Welch (1935) has shown to exist in the Simuliidae. The need for a suitable current and a stable substratum certainly confines the two netspinning hydropsychid larvae to the rocky shore.

A few special cases merit consideration. The scale-eating fish *Genyochromis mento* could conceivably obtain its food from fishes on the sandy shore, though it is doubtless advantageous to scrape scales from a common and rather inactive species, and it thus tends to have its distribution restricted by that of its principal " host " *Labeo cylindricus* which fulfils these conditions. It may be also that *G. mento*, being as it is, so obviously descended from rock-dwelling ancestors, has evolved a pattern of behaviour an integral part of which is a background of rocks, which is not easily changed. A similar suggestion has already been put forward as a partial explanation of the restriction of *Cyathochromis obliquidens* to the intermediate zone. Such an ancestral behaviour pattern can scarcely be discounted as a major factor restricting the distribution of *Cynotilapia afra* to waters off the rocky shore, for it is now almost completely independent of the rocks either for food or shelter and feeds mainly on plankton which can be obtained over a variety of substrata. This ancestral behaviour pattern must exert a particular strong effect on all species during the breeding season when definite environmental conditions are necessary for nest making, etc.

While the restriction of lamellibranchs to the sandy shore is easy to understand as the species represented in L. Nyasa require a penetrable bottom in which to embed themselves, the similar restriction of gastropods is puzzling. *Lanistes procerus* is restricted by its food preferences but there seems to be no reason why the rocks should not provide suitable food for some of the other species. The exposed nature of the environment probably hinders the colonisation of the rocks. That this is so is indicated by the presence of *Physopsis* sp. among the rocks in a very sheltered corner of the north bay at Nkata Bay. The presence of innumerable fishes on the rocky shore, among which are several species which would eat molluscs if the opportunity arose is also perhaps partly responsible for their exclusion. The finding of a mollusc in the guts of specimens of *Genyochromis mento* and *Pseudotropheus fuscoides* indicates that such colonisation may take place but that fishes quickly find and eat such adventurous individuals.

While competition cannot be ignored it appears to play only a small part in restricting species to a single major habitat, though it may well have done so during the course of evolution of the parent forms of the fishes. There are exceptions to this generalisation (notably the restriction of *Cyathochromis obliquidens* and *Pseudotropheus lucerna* to the intermediate zone as discussed on pp. 228 and 229), but at the present time the majority of species are so specialised in their food preferences and, more particularly, in their methods of food collection, that these aspects of their biology alone usually restrict them to one major habitat, and competition is virtually restricted to that between species *within* a habitat.

It is obvious, then, that the phrase " the fauna of L. Nyasa " is as vague to the ecologist as is "the fauna of Great Britain ", and one must henceforth regard the animals of this great lake as comprising a number of very discrete faunas which are as distinct from one another as are the faunas of an English Oak Wood and an expanse of moorland.

COMPARISONS WITH OTHER AREAS

Although work was concentrated on the shore at Nkata Bay it was possible to pay brief visits to other parts of the lake and make comparative observations. While, as might be expected, minor differences were apparent, it appears that conditions on the rocky, sandy and " intermediate " shores at Nkata Bay are fairly typical of those prevailing in similar habitats throughout the lake.

The sandy shore studied is apparently somewhat impoverished, perhaps due to its restricted area and the paucity of weed beds. Less attention was paid, however, to sandy shores elsewhere than to rocky shores.

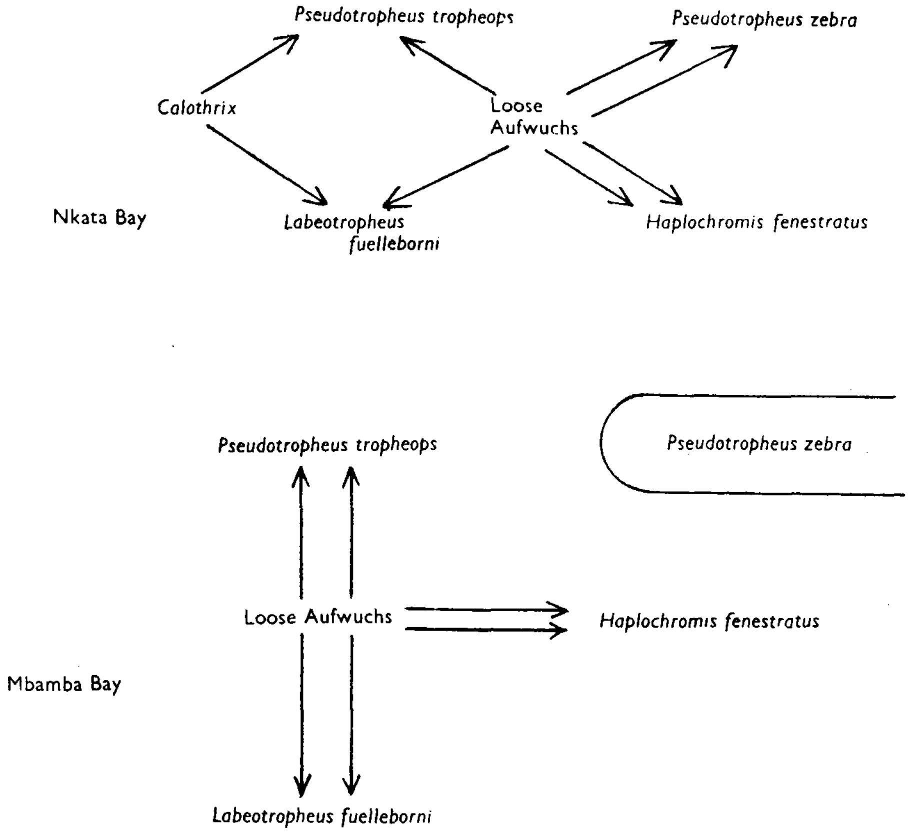


Fig. 95.—Suggested competitive relationships between some rocky shore fishes at Nkata Bay (where *Calothrix* and loose Aufwuchs are available as food), and at Mbamba Bay (where only loose Aufwuchs is available).

At Likoma Island (about five miles off the eastern, Moçambique, shore), where a total of five days, intensive field work was carried out, and at Ruarwe (about forty miles north of Nkata Bay), conditions were very similar in general respects to those prevailing at Nkata Bay. Some rather striking differences were noted, however, at Mbamba Bay (on the Tanganyikan shore) during a two-day visit. Here the rocks are granitic in nature as they are at Likoma

Island and to a large extent at Ruarwe, and not composed of schists as they are at Nkata Bay. They differ, however, from those of Likoma and Ruarwe in having more angular projections, such as is typical of certain granites. Further, no *Calothrix* was found in the scrapings made from these surfaces, though this alga was present on the rocks both at Likoma and Ruarwe. Here too was a faunistic difference. *Pseudotropheus zebra*, which is very common on rocky shores studied elsewhere, was either absent or exceedingly rare. This fish is not one which includes *Calothrix* in its diet so its absence is not correlated directly with the absence of this alga. On the other hand the commonest fish was *P. tropheops*, and *Labeotropheus fuelleborni* was also common. Both these fishes eat *Calothrix* at Nkata Bay and elsewhere. None was found in their guts at Mbamba Bay, indicating that they were no more successful in finding it than the ecologist. *Haplochromis fenestratus*, another loose Aufwuchs eater, was also very common.

The general nature of the environment was similar to that in which *P. zebra* has been found elsewhere, and considering the wide distribution of this species in the lake it can scarcely be supposed that it has not had the opportunity of colonising this area. It may be excluded by the angular projections of the rocks which hinder its " sucking " method of feeding but do not impede the nibbling and chiselling of *P. tropheops* and *L. fuelleborni* respectively. There is also the possibility of its exclusion by competition. Because of the absence of *Calothrix*, *P. tropheops* and *L. fuelleborni* would, of necessity, make greater demands on the loose Aufwuchs than is the case in habitats where this alga is present. By doing so they may have pushed out *P. zebra*. (Fig. 95).

In a collection of rock fishes from Benji Island (about six miles off shore near Domira Bay) made by Messrs P. B. N. Jackson and K. Howard, the general facies was similar to that of similar habitats in the north but produced several specimens of what appears to be an undescribed species of *Pseudotropheus*.

On the rocky shores which shelve very steeply, e.g. in parts of Likoma Island, it is noteworthy that *Cynotilapia afra*, which at Nkata Bay occurs particularly at the edge of the littoral shelf, is to be found very close to the shore-line.

A NOTE ON PRODUCTIVITY IN LAKE NYASA

The central problem in limnology is that of productivity so it is useful to consider what light the present study has shed on the productivity of Lake Nyasa. In a series of papers Rawson (summarised in Rawson, 1955) has demonstrated that in large deep lakes in North America an inverse relationship exists between increase in mean depth and productivity (based on yield of fish, standing crop of net plankton, and weight of bottom fauna). While detailed quantitative data are still lacking, the impression gained as a result of everyday observations on these characteristics is that the generalisation applies to Lake Nyasa, with the exception of the shallow South East arm south of Boadzulu Island which must be treated as a separate entity. The rest of the lake, however, cannot be treated simply, for the biological economy of each major habitat has been shown to depend ultimately on a different kind of production. While there is nothing startlingly new in this statement it is believed that the importance of the algal Aufwuchs on the rocks has been shown to exceed that demonstrated in any other lake, either tropical or temperate, and attention is therefore directed emphatically to this source of food in rocky-shored tropical lakes.

Lake Tanganyika harbours a number of cichlid fishes with remarkably similar structural features to those of the rock-scraping Nyasan cichlids and, Poll (1950) recorded that two of them eat material scraped from rocks, and has even more recently presented evidence to show that the rock fishes of this lake derive much of their food from epilithic algae. (Poll, 1956 a). During a very brief visit to Mpulungu at the southern tip of the lake the writer saw several species feeding from the rocks in an almost identical manner to their Nyasan counterparts. It seems, therefore, that the algal Aufwuchs is also very important in Lake Tanganyika.

The fundamental importance of the littoral zone of Lake Nyasa (resulting from the morphometry of the basin and the hydrological conditions prevailing in the lake) has already been emphasised, and the peculiar conditions prevailing lead one to propose a series of indices of productivity for habitats rather than one or more general indices for the lake as a whole. Three of these are :—

(1) The plankton productivity — An index of the productivity of the pelagial zone.
(2) The Aufwuchs productivity — An index of the productivity of the rocky shores.
(3) The macrophytic plant and periphyton productivity. — An index of the productivity of the sandy shores.

In addition it is necessary to find some index of productivity for the profundal region. At present this is difficult or impossible. To some extent the emerging " lake-flies " may represent the productivity of this zone, but as these appear to be represented largely if not entirely by *Corethra edulis* Edwards, which in the larval stages probably feeds entirely in the pelagial zone, they are of negligible value in this respect. From the still limited information on the profundal region of the lake it would appear that its contribution to the general productivity is extremely slight. If chironomid larvae do live beneath the thermocline then they must bring back from the profundal regions some of the material which has accumulated there and cannot be brought into circulation by water movements and must, when rising to the surface, provide a transient food source for pelagic fishes.

Summarising these indices and bearing in mind the enormous area of the lake the general picture is one of paucity, but individually the two littoral habitats may be highly productive.

In the area particularly studied the standing crop of animals on the rocky shore is undoubtedly heavier than that on the sandy shore. In many parts of the lake, however, the high productivity of rocky shores is offset by their steepness and hence narrowness, while many sandy shores, while perhaps never supporting a permanent fish fauna as dense as that of rocky shores, are often extensive ; a fact of some importance from the point of view of fisheries.

Work carried out by the East African Fisheries Research Organisation has led to the suggestion being put forward (Anon., 1952, 1954) that the level of production in *shallow* tropical lakes is determined by the *rate* at which nutrient salts can be taken up, built into organic matter, and decomposed to give nutrient salts again. Thus anything which hastens the breakdown of organic matter helps to boost productivity. The work of herbivores in breaking down plant protein is particularly stressed in this connection.

It is difficult to fit this hypothesis to deep lakes such as Nyasa where material is constantly being lost below the thermocline and is apparently not returned by overturns, but it may to some extent be applicable to the littoral zone, and particularly to the rocky shore where very large numbers of herbivorous fishes and a dense fauna of algal eating invertebrates hasten the breakdown of plant matter. Further the faecal matter of these organisms is deposited in close proximity to the algae and must remain and be broken down largely in the area in which it was deposited in spite of the turbulence of the water.

The high productivity of the littoral zone may be due in part to its favourable position to receive salts swilled into the lake from the surrounding land (p. 159) but another contributory factor may be the transverse rocking of the thermocline which can take place in large lakes and for which Mr D. Harding tells me he has some evidence in Lake Nyasa. Such transverse rocking may occasionally bring water from the hypolimnion to the surface around the lake shore, but apart from this unlikely event it seems probable that the effects of turbulence as the thermocline moves up and down over the irregular bottom in the sub-littoral region will result in the passage of water from the hypolimnion as it were around the edges of the thermocline and into the epilimnion. Further, currents running over the irregular bottom near the lake shore will tend to cause the interface between the epi- and hypolimnion to be more disturbed than in the open water, and vertical eddies will be set up which will bring water from the hypolimnion into the epilimnion. This will enrich the marginal waters of the lake. Whether these factors do indeed exert a profound effect remains to be proved, but it cannot be denied that the total biomass per unit volume is infinitely greater in the littoral zone than in the deeper water. Relevant to this question are the results of a study of the algae of several East African lakes carried out by Ross (1955) who found that, besides supporting much benthic algae, the inshore waters of all the lakes studied, " except the very smallest and shallowest " had a higher phytoplankton productivity than had the more offshore waters. This too may be due in part to the proximity of the land as a source of nutrients, and to movements of the thermocline.

SUMMARY OF PART I

An account is given of the fauna of part of the littoral zone of Lake Nyasa, at Nkata Bay, and of the ecology and interrelationships of its individual constituents.

The main physiographical features of the littoral zone studied are outlined. The shore at Nkata Bay is partly rocky and partly sandy and includes a small zone in which " intermediate " conditions prevail. A small swampy estuary (Crocodile Creek) is also present.

Each major habitat is quite distinct and each has a distinctive fauna. These faunas are described and the feeding habits and general ecology of the individual species, and particularly the fishes, are described. The fishes, most of

which belong to the family Cichlidae, are numerous, both specifically and numerically, and many of them show striking adaptations to their mode of life, particularly in the structure of the mouth and in the dentition. These adaptations are described and illustrated.

Food webs are constructed for the major habitats and their structure is briefly discussed.

As each major lacustrine habitat, and particularly the rocky shore, harbours a large number of closely related species, many of which take similar, or even identical foods, competition might be expected. Data bearing on this problem are analysed.

Whilst most insect eating fishes on the rocky shore take broadly similar foods each appears to show certain preferences which tend to minimise competition. These differences are in some cases accentuated by differences in the vertical or horizontal distribution of different species.

Many herbivorous fishes on the rocky shore take similar or identical foods though in some cases they have different feeding mechanisms. Some species are spatially isolated by virtue of their ecological preferences, but several closely allied species co-exist in the same microhabitat and take the same foods. Such co-existence is at variance with the so-called Gaussian hypothesis and seems to be possible because of a superabundance of the algal food on which these species feed.

On the sandy shore the fishes are usually either specialised feeders occupying an otherwise almost unexploited feeding niche or are general feeders which can probably shift their emphasis from one kind of food to another should any one kind become scarce.

In the intermediate zone the situation is similar to that on the sandy shore but two of the most important species, which are related to rocky shore species, are probably restricted to this zone because of an inability to compete with their relatives on the rocky shore and because of a lack of features suited to life on sandy shores.

In Crocodile Creek the number of species is small and almost all are general feeders.

The importance of predators in maintaining a dynamic balance on the rocky shore is pointed out.

Most species of all groups are restricted to one major habitat. Demand for a certain type of food or substratum appear to be the main factors restricting distribution. The significance of such inter-habitat movements as take place is indicated.

Brief comparison with other areas in the lake is made.

A note on the productivity of Lake Nyasa is given and attention is directed particularly to the great production of algal Aufwuchs on rocky shores and to the accompanying rich faunas.

PART II

THE ECOLOGY AND EVOLUTION OF A GROUP OF ROCK-FREQUENTING NYASAN CICHLID FISHES KNOWN AS THE " MBUNA "

INTRODUCTION

The most outstanding zoological feature of Lake Nyasa is the inclusion in its fauna of a large number of fishes belonging to the family Cichlidae. More than 180 species, of which all save four are endemic, are now known to exist there. According to Trewavas (1935) these can be assigned to twenty-three genera. Among them are nine genera which she states are " more closely related to each other than to any other genus, though it is very difficult to find an absolute character to distinguish them". It is with the ecology and evolution of the members of these genera that the present paper deals.

THE CHARACTERISTICS OF THE MBUNA

The nine genera referred to by Trewavas together with the number of species now recognised for each are, *Pseudotropheus* (13), *Labeotropheus* (2), *Melanochromis* (5), *Cyathochromis* (1), *Petrotilapia* (1), *Cynotilapia* (1), *Labidochromis* (2), *Genyochromis* (1) and *Gephyrochromis* (2).

The last mentioned genus was listed by Trewavas (1935) as *Christyella*, a name shown later (Trewavas, 1947) to be synonymous with *Gephyrochromis* under which Boulenger (1915) had described it, erroneously giving Lake Tanganyika as its provenance.

The present study of both the structure and ecology of members of these genera has confirmed and emphasised Trewavas' contention that they are closely related. They do indeed appear to constitute a distinct group of the Cichlidae which is probably worthy of at least tribal rank. This distinctness is recognised by the African fishermen who, while giving separate names to some of the species concerned, refer to the group as " Mbuna " (in Chitonga) or " Chindongo " (in Chinyanja). As certain complexities would be involved in the erection of a supra-generic taxonomic unit for the reception of these genera they are here referred to simply as the " Mbuna ".

Systematically the Mbuna can be characterised as follows : Cichlidae of small size, seldom more than 20 cm. in total length and frequently smaller. Body moderately elongate, with two incomplete lateral lines. Scales denticulate. Nape covered with large numbers of small scales. Scales on cheek small. Snout short. Dentition various, but always with a short series of three to nine conical postero-lateral teeth on each side of the upper jaw, usually enlarged ; and always with several rows of teeth anteriorly which may be conical or, more usually, bi- or tri-cuspid. Lower pharyngeal bone triangular, approximately equilateral, with tendency to be indented on posterior margin. Apophysis for upper pharyngeal bones formed by the parasphenoid in the middle and the basioccipital at the sides. Dorsal fin with fifteen to nineteen (usually seventeen to nineteen) spines and seven to eleven soft rays. Anal fin with three spines and seven to nine soft rays.

Left ovary of female markedly atrophied, right functional. Both testes of male functional. Representatives of several genera at least are mouth brooders, young being carried by female.

Colour pattern various but some or all specimens of all species show one or more of the following characteristics : Dark vertical bars, usually six to eight below the dorsal fin. Horizontal bars, one mid-lateral and one above it. A cross bar on snout. A dark sub-marginal band on dorsal fin. A dark spot near the upper posterior margin of the operculum. One or more bright orange or yellow spots on or near the posterior margin of anal fin in male and sometimes in female.

Lacustrine species, littoral in habits, and associated with rocky shores.

Confined to Lake Nyasa.

They differ most markedly from the rest of the Nyasan cichlids in the possession of lateral conical teeth, in the large number of small scales in the nape region, the reduction of the left ovary of the female, and often in the coloration. In general they also have different habitat preferences from the other cichlids of the lake. The general form of a number of species can be seen from the illustrations of Boulenger (1915), Regan (1921) and Fryer (1956 a, 1956 d, 1957 a), while a series of illustrations showing the range of mouth structure and dentition is given in Part I.

The group is particularly interesting from an evolutionary point of view as all stages of divergence are represented from trivial specific differences to striking generic adaptations to different ways of life.

There is little doubt that the Mbuna evolved in the lake, and although some remarkably similar species occur in Lake Tanganyika Trewavas (1948) refutes the suggestion that they are in fact closely related, particularly on the grounds of a fundamental difference in the structure of the pharyngeal apophysis at the base of the skull. It would appear that the Mbuna and their ecological equivalents in Lake Tanganyika constitute a remarkable case of parallel evolution in isolated stocks which had rather similar genetical material at their disposal.

THE SPECIES STUDIED

The following species have been studied.

Pseudotropheus tropheops Regan
Pseudotropheus novemfasciatus Regan
Pseudotropheus auratus (Boulenger)
Pseudotropheus fuscus Trewavas
Pseudotropheus fuscoides Fryer
Pseudotropheus elongatus Fryer
Pseudotropheus minutus Fryer
Pseudotropheus sp. nov.
Pseudotropheus zebra (Boulenger)
Pseudotropheus williamsi (Günther)
Pseudotropheus livingstonii (Boulenger)
Pseudotropheus elegans Trewavas
Pseudotropheus lucerna Trewavas
Petrotilapia tridentiger Trewavas
Cyathochromis obliquidens Trewavas
Cynotilapia afra (Günther)
Labeotropheus fuelleborni Ahl.
Labeotropheus trewavasae Fryer
Genyochromis mento Trewavas
Labidochromis vellicans Trewavas
Labidochromis caeruleus Fryer
Melanochromis melanopterus Trewavas
Melanochromis vermivorus Trewavas
Melanochromis brevis Trewavas
Melanochromis perspicax Trewavas
Melanochromis labrosus Trewavas
Gephyrochromis moorii Boulenger
Gephyrochromis lawsi Fryer

Of these all except *P. novemfasciatus*, *P. elegans*, the new *Pseudotropheus*, the last four species of *Melanochromis* listed, and *G. moorii* have been studied alive or have at least been examined in a fresh condition after capture. The exceptions have been studied only in the preserved state. As treated here *P. tropheops* includes the species and subspecies described as *P. tropheops tropheops* Regan, *P. t. gracilior* Trewavas, *P. microstoma* Trewavas, and *P. macrophthalmus* Ahl. Reasons for regarding these forms as constituting one variable species will be given elsewhere.

TAXONOMY

The taxonomic relationships of the Mbuna present some extremely perplexing features at both the generic and specific level. While a detailed account of these is not called for here, a few remarks relevant to the biological and evolutionary study call for comment.

One of the tantalising features of the taxonomy of the group is the difficulty experienced in defining several of the genera, notably those which group themselves most closely around *Pseudotropheus*. The distinctions between some members of this genus and the genera *Melanochromis* and *Gephyrochromis* are so fine that, were one considering the border-line cases alone, one would not hesitate to merge the genera concerned into one taxonomic unit. On the other hand the extreme forms of *Melanochromis* and *Gephyrochromis* are sufficiently distinct from *Pseudotropheus* to merit independent generic status. Thus *G. lawsi* is obviously closely related to *P. lucerna* and *P. elegans* and there could be few complaints if it were regarded as being a member of the genus *Pseudotropheus* as it at present stands defined, yet it is obviously congeneric with *G. moorii* which exhibits sufficient non-*Pseudotropheus* features to merit generic separation. Similarly *P. fuscoides* rests uneasily between *P. fuscus* on the one hand and species of *Melanochromis* on the other.

Even more perplexing are cases where fishes which, in their basic anatomy, appear to belong to one particular genus, nevertheless exhibit such well-marked divergence in one characteristic (dentition) that they have been assigned to separate genera. Three striking cases of this phenomenon are found among the Mbuna. The monotypic genera *Cynotilapia*, *Cyathochromis* and *Petrotilapia* are all very similar in anatomy to species of *Pseudotropheus*, and particularly to *P. zebra* and its nearest allies, yet all show extreme modification of the teeth, and all differ widely one from another in this respect. In fact in features other than the dentition they are probably more like *P. zebra* than are certain species which are currently regarded as members of its own genus !

One has, therefore, the choice of recognising these highly specialised and undoubtedly adaptive features by bestowing generic distinctness upon them, and thereby to some extent obscuring the phylogeny of the group as a whole ; or lumping all the species concerned into one genus whose members would then show an unusually wide range of dental patterns. Neither system is entirely satisfactory. The former procedure, adopted by Trewavas (1935) in her preliminary grouping of the genera, is followed here. In order to correctly express affinities and yet take into account divergent specialisation of single characteristics one would in effect require a three-dimensional system of nomenclature. Such a system has yet to be devised.

Many taxonomic problems are presented also at an infra-generic level. Most of these concern the genus *Pseudotropheus*. As it stands at present this genus comprises a somewhat heterogeneous assemblage of species which appear to represent at least three diverging lines of evolution. While these lines have diverged to such an extent that one familiar with the group can recognise the fact (particularly in the field), it is extremely difficult to define them so that their representatives may be given taxonomic standing. This would not matter greatly were it not for the fact that such genera as *Cyathochromis* and *Melanochromis* (and others) can be recognised as being closer to one line than to another, a state of affairs which leads to apparent unorthodoxy when one tries to express phylogeny as, for example, in Fig. 99, p. 260. In such cases it would appear that evolution has gone on at different rates in the different lines and that, to take one example, although the trend towards the condition seen in *Cyathochromis* probably arose after the *Pseudotropheus* group had begun to undergo divergent specialisation, it proceeded with such rapidity that its present-day manifestation merits generic recognition; whereas *P. zebra* and *P. tropheops*, which may well have been diverging for a longer period of time, are still regarded as members of the same genus.

These taxonomic difficulties are to be interpreted as some of the results of the recent, probably rapid, and still continuing evolution of the group of fishes concerned.

INTRASPECIFIC VARIABILITY

Some of the species are structurally stable and show relatively little morphological variability, though they may be variable in colour (see below), while others, even when comprising a single population, are very variable in certain morphological characteristics as well as in colour. Even the stable species are not easily characterised by reference to ratios such as are used in classical fish taxonomy as certain parts of the body exhibit allometric growth. For instance in all those species of which sufficient material has been available for study, there is a progressive increase in body depth in relation to length as the fish increases in size, as can be deduced from the graphs already published which show the relationship between standard length and body depth in the species of *Labidochromis* and *Labeotropheus* (Fryer, 1956 a, 1956 d).

The most variable species studied is *Pseudotropheus tropheops*. In fact it is so variable that it was formerly considered to represent three species, for one of which a subspecies was described. Details of this variability are given elsewhere, but here it can be mentioned that it affects such structural characteristics as the width of the tooth band of the lower jaw, the diameter of the eye, the interorbital width and the snout length, as well as coloration. In fact it affects just those characteristics of the animal which were utilised as a basis for specific differentiation by systematists in their pioneering studies on the group when the amount of available material was limited. All these characteristics appear to vary in a completely random manner.

COLOUR PATTERN

In spite of the remarkable range of coloration and colour variation to be seen among the Mbuna, some of which is mentioned in the next section, it is nevertheless possible to designate certain features of the colour pattern as being characteristic of the group. Some of these, such as the frequent presence of a broad black submarginal band on the dorsal fin, were recognised as such by Trewavas (1935) even in preserved material. One can in fact describe a " basic colour pattern " one or more features of which it is usually possible to trace in any individual of the Mbuna group.

A fish having such a basic colour pattern would have two horizontal bars, one in the mid-lateral line and one above it ; a cross bar on the snout (a continuation of the lower horizontal bar) ; a dark submarginal band on the dorsal fin ; traces of six to eight dark vertical bars below the dorsal fin ; a dark spot near the upper posterior edge of the operculum, and one or more intense yellow or orange spots on or near the posterior margin of the anal fin.

Such a pattern, with the exception of the vertical bars, is shown most clearly today by *Pseudotropheus auratus*. Species in which the horizontal bars are best developed tend to show little sign of vertical bars and vice versa, though both can sometimes be seen in a single individual of certain species.

The appearance of dark vertical bars in the very early stages of development of several species, including *Petrotilapia tridentiger* in which they can seldom be distinguished in the adult, perhaps indicates that the ancestral Mbuna exhibited such a pattern, though the possibility that they also represent a larval specialisation cannot be ruled out.

Some of the features of the colour pattern are sporadic in their occurrence and may or may not be found in different individuals of a given species. This applies particularly to the dark submarginal band of the dorsal fin. Such sporadic occurrence suggests that it is a primitive characteristic in process of being lost. It is interesting to compare this state of affairs with that found in the best studied case of the ecology and evolution of a group of closely related and geographically isolated species, namely that of " Darwin's Finches " of the Galapagos Islands studied by Lack (1947). Among these birds are four species belonging to three genera in which a rufous wing bar occurs in some but not all individuals. So far as is known this wing bar is functionless. It seems probable that the dark sub-marginal band of the Mbuna is similarly functionless in such species as *Pseudotropheus tropheops* and *Petrotilapia tridentiger* in which it may be well developed, feebly developed, or completely absent : but the fact that it is always well developed and very clearly apparent in some species (*Pseudotropheus auratus*, *Labidochromis caeruleus*) suggests that here it has been adopted as a specific recognition signal or plays some part in the courtship display and is therefore preserved by natural selection. Such a function would accord well with the suggestion that its presence is a primitive characteristic.

COLOUR VARIATION, SEXUAL DIMORPHISM AND COLOUR POLYMORPHISM*

The actual coloration of the Mbuna is exceedingly diverse, though individual species are usually either dark or very brightly coloured. This diversity is complicated by random variation, by the fact that the colour of sexually active individuals, and particularly the males, often differs from that of non-breeding fishes of the same species ; because sexual dimorphism in coloration is exhibited by some species ; and by the fact that some species are polymorphic in respect of coloration. In addition, colour changes, which are very striking in the case of the males of *Pseudotropheus auratus*, also take place according to the emotional state of the animal. These topics are discussed in turn.

Colour variation

As opposed to colour polymorphism, namely the existence of several quite distinct types of coloration, there is, in some species, a considerable amount of colour variation of the most random type. This is seen most strikingly in *Petrotilapia tridentiger* and *Pseudotropheus tropheops*. Females of *P. tridentiger* may be a more or less uniform dull brown, almost black, or have the brownness tinged with blue, or be quite orange ventrally. Others which, however, may represent a polymorphic form, may be completely gold and very similar in colour to the familiar golden carp. This may be a polymorphic form as very small gold specimens are to be seen in nature—indicating that this colour is retained throughout life—and that it is definitely not associated with sexual activity. In aquaria, however, it tends to fade and once dark vertical bars began to develop in a specimen which showed no sign of these when captured. Apart from the fact that the brightness and intensity of the coloration seems to increase as the gonads ripen this colour variation seems to be quite haphazard even within a single well isolated population. The males are almost equally variable but tend to be a bright blue when sexually active. Some have a most brilliant orange throat ; in others the throat is blue or brownish ; and in some the entire belly is golden yellow.

Besides exhibiting a distinct colour polymorphism one of the forms of *Ps. tropheops* is just as variable in colour as is *P. tridentiger* described above.

Such random colour variation indicates that in these species specific coloration is unimportant in mating activities. Some other characteristics such as the formation of the mouth and dentition may be important in preventing the successful completion of any interspecific mating behaviour in which these two species might become involved and it is perhaps significant that *P. tridentiger* has a dentition quite unlike that of any other species and that there is only one species—the somewhat doubtfully distinct *Ps. novemfasciatus*—with a similar mouth to *Ps. tropheops*. It would certainly appear significant

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* Colour polymorphism is called polychromatism by some authors. Ford (1940) prefers to use polyphasy in the more general sense and to restrict the term polymorphism to a condition of balance of the genes involved, or to the transient condition leading to such balance. As Hovanitz (1953) says, however, " in actual field work it is not always practical to separate true polymorphism from that polyphasic condition which is due to recurrent mutation ". The term polymorphism is used here partly for the reason given by Hovanitz and partly because it seems that true polymorphism in the sense defined by Ford is involved.

that those species with the most distinctive coloration (*Pseudotropheus auratus* and *Labidochromis caeruleus*) appear to be among the least variable in this respect.

Sexual dimorphism

Sexual dimorphism in the Mbuna, so far as it concerns coloration, may be either transient, when it is associated with ripeness of the gonads, or permanent. Transient sexual dismorphism is shown for example by *Pseudotropheus minutus* in which males with unripe gonads resemble the females in their dark and sombre coloration, but differ from them when the gonads are ripe by developing a body pattern of alternating blue and nearly black vertical bars. Another example is provided by *Labeotropheus fuelleborni* in which the breeding male assumes a bright blue coloration, and indeed a rather similar state of affairs holds good for most of the Mbuna.

Permanent sexual dimorphism is shown by *Cyathochromis obliquidens* and *Pseudotropheus auratus.*

Males of *C. obliquidens* are very handsomely coloured, with blues and yellows predominating, and have three or four intense orange spots on the anal fin, while the females are much more sombre and are a light yellowish brown in colour with a grey bronze sheen, have no spots on the anal fin, and always exhibit the two horizontal bands of the basic colour pattern.

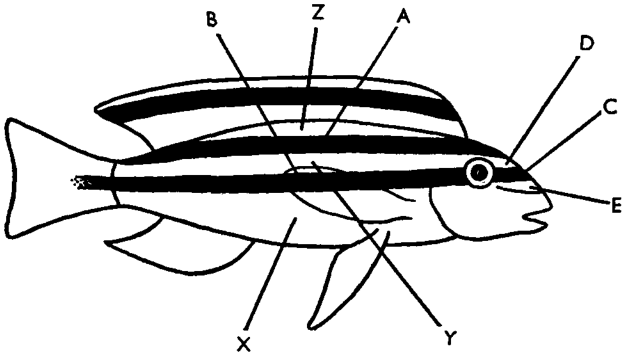

Fig. 96.—Colour pattern of *Pseudotropheus auratus.* (Diagrammatic). For significance of lettering see text.

More striking is the difference in colour between the sexes of *P. auratus.* Females have the two dark, almost black, horizontal bands of the basic colour pattern very clearly demarcated on the flanks on a ground colour of gold, and invariably have a very distinct dark sub-marginal band on the dorsal fin. Each of the dark horizontal bands is edged with blue. Typical males on the other hand, have exactly the same colour *pattern* but the ground colour is almost black and the horizontal bands are a brilliant electric blue*.

The male is, however, subject to remarkable and rapid changes in colour. These changes require further study but their essentials can be understood from the following description. References refer to Fig. 96. A typical male

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* Trewavas' (1935) statement that these bands in the male are gold was based on preserved specimens in which the colour had disappeared.

was caught, quite undamaged, in a net. Bands A, B, D and E were blue and the rest of the body including band C was almost black. This fish was dropped into a can of water in the boat and there underwent a remarkable colour change, assuming the female coloration, i.e. bands A and B changed from blue to black, bands D and E changed from blue to gold, and the rest of the body, with the exception of band C which remained black, changed from black to gold. On being allowed to settle in the laboratory the typical male coloration was re-assumed. The fish was lifted out of the water and it again changed quickly to the colour of the female. On being returned to the water the male coloration was again gradually reassumed. This latter process was carefully watched and took place as follows. Bands A and B gradually became less and less distinct as the gold on either side became suffused with blue-black. At the same time the entire belly region (X) became darker as a black pigmentation spread throughout a formerly gold area. The dorsal parts were now blue black with the bands scarcely distinguishable. Gradually, however, bands A and B then became more and more distinct but the colour was now blue and not black, while the bands above and between them, and the belly region, previously gold, became distinct and black !

The significance of the above phenomenon remains obscure. It is possible, however, that the male, when not sexually active, is the same colour as the female. Against this is the fact that the few specimens caught which had a female colour were indeed all females. Trewavas (1935) noted a marked discrepancy in the sex ratio of preserved specimens in the British Museum, of which thirty-seven were females and seven were males. Specimens with male coloration were seen rarely at Nkata Bay and elsewhere during the present study so it may be that some of the alleged females in the British Museum are actually immature males. One field observation is relevant to this question. A specimen seen guarding a territory, and therefore presumed to be a male, was in a " half way stage " in coloration, bands Z and Y being " bluish gold " instead of black and the belly region X being a mixture of gold and black pigment.

Sexual dimorphism, either transient, or permanent, is fairly general throughout the Mbuna, the only exceptions noted being some of the colour phases of the polymorphic *Pseudotropheus zebra* and the monomorphic *Labidochromis caeruleus* both males and females of which are similarly and most strikingly coloured. (See Fig. 8 in Fryer, 1956 a).

Colour polymorphism

Colour polymorphism is shown by at least four species of the Mbuna, *Labeotropheus fuelleborni*, *L. trewavasae*, *Pseudotropheus zebra*, and *P. tropheops*. Further, the most striking colour form of one species is, as nearly as possible, identical with that of another species of a different genus.

The normal coloration of *L. fuelleborni* is a rather dull blue grey though the male assumes a brighter " breeding dress " from time to time. One female, however, captured at Benji Island in the southern part of the lake, was " peppered " with black and orange pigment. This specimen was only studied after preservation but the colour pattern, while similar to that found in some of the females of *L. trewavasae*, seems to differ sufficiently to be regarded as distinct.

Among the relatively small number of specimens of *L. trewavasae* collected 50 per cent of the females were " normal " in coloration and 50 per cent exhibited what is here called an " orange blotch " pattern. This consists of a series of small groups of pigment spots, some black, others orange, on a rather dirty white ground. The entire body is so coloured. The degree of black pigmentation, i.e. the total area occupied by the black blotches, varies from individual to individual. In some fishes the black blotches occupy at least 40 per cent of the body, in others no more than about 20 per cent. The degree of development of the black pigmentation may differ on the two sides of a single fish. Always, however, the pigment was aggregated into distinct blotches, being in this respect quite different from the peppered pattern seen in *L. fuelleborni*. Apart from its reappearance again in *Pseudotropheus zebra* (see below) this pattern is quite unique not only among the Mbuna but among the Nyasan cichlids as a whole. This form occurs both in the Nkata Bay area and Ruarwe some forty miles to the north, these being the only stations from which *L. trewavasae* has so far been recorded. A sight record at Kajizinge, between these stations, also almost certainly refers to this form.

A more complex state of affairs exists in the case of *P. zebra*. Here both males and females may either exhibit a pattern of alternating blue and black vertical bars (BB) whose intensity varies somewhat according to the state of the gonads, or they may be entirely sky blue in colour (B), or they may be almost white (W). In addition a small percentage of the females exhibit an " orange blotch " pattern (OB) such as was described above for *L. trewavasae*. These colour-forms are shown in Plate 2. In addition one white specimen exhibited a very small number of black blotches such as are to be seen in the OB pattern.

The occurrence of the OB pattern in two different genera was at first taken simply as an indication of their fundamentally similar genetic makeup and was considered as additional evidence that the two genera concerned, which differ markedly in mouth structure, are closely related. So far as the Nyasan cichlids are concerned this opinion is still held. However, similar polymorphism, in one form of which the distribution of the black pigmentation is virtually the same as in the two Nyasan species, occurs among the cichlids of Lake Victoria in several species of *Haplochromis* and in two monotypic genera related to *Haplochromis* (Greenwood, 1954, 1956 a, 1956 b, 1957 and personal communications), and is to be seen again in two species of *Haplochromis* of L. Kivu. In Lake Victoria Greenwood considers that no reliability can be placed on this characteristic as an indicator of phyletic relationship save that its repeated occurrence probably reflects the oligophyletic origin of the Lake Victoria species flock. Nevertheless he thinks it " suggestive " that two of the species which exhibit it, *Haplochromis sauvagei* (Pfeffer) and *Macropleurodus bicolor* (Boulenger), show similarities in fundamental syncranial morphology. Taking a broad view, therefore, the conclusion seems to be that the occurrence of a similar pattern in certain individuals of fishes in three widely

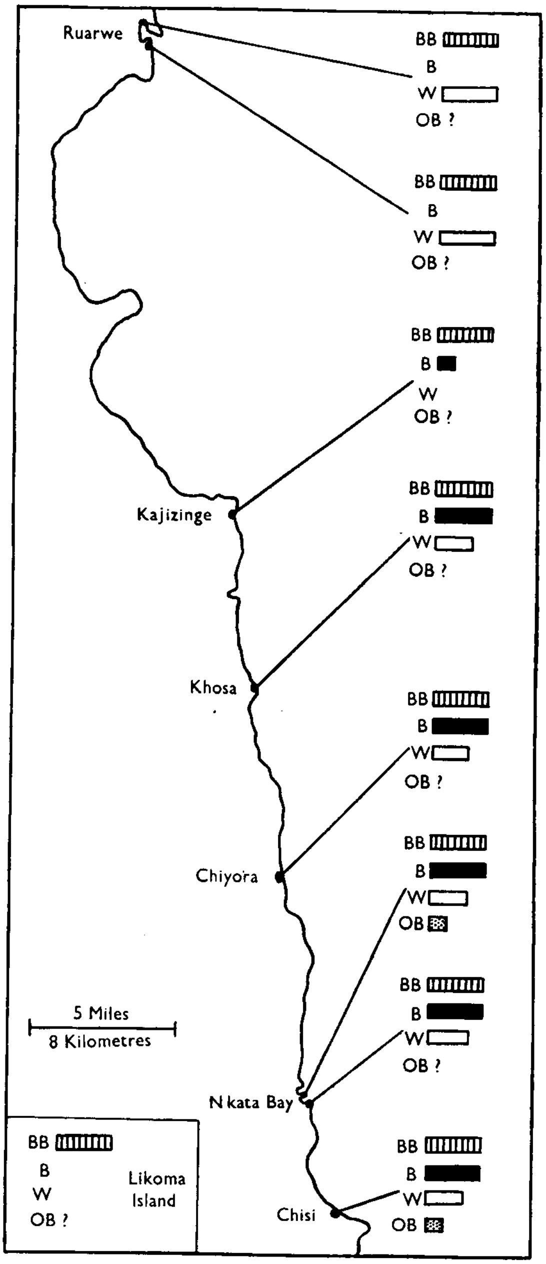

Fig 97.—Distribution of colour forms of *Pseudotropheus zebra* in a region in the north-west of Lake Nyasa and (inset) Likoma Island. Degrees of abundance indicated by the segments are, Common : Present : Rare : Absent.

separated lakes is indicative of the oligophyletic origin of their present-day cichlid faunas.

The distribution of the various colour forms in *P. zebra* is not uniform. Fig. 97 shows the approximate proportions of the various colour forms, as estimated by visual observations, in several localities along a forty mile stretch of shore which is predominantly rocky and is interrupted by sandy beaches of only minor extent, together with the state of affairs at Likoma Island which lies on the opposite side of the lake and is separated from the other localities by about forty miles of open water of great depth. At Benji Island, about 130 miles south of Nkata Bay, no blue or white specimens were seen or collected by my colleagues who specially looked for them there. While it was unfortunately not possible to make observations at as many points as would have been liked in part of the area shown on the map the indications are that the incidence of the various colour forms does not necessarily change gradually. If this were so one would have expected the white form, which is very conspicuous when present, to be more common at Kajizinge than at Nkata Bay, though it was in fact not seen there at all.

There is no obvious correlation between the distribution of the various colour forms and the environment, which is very uniform on rocky shores. It seems possible, however, that some of them, particularly W and B, will be more obvious than their fellows to predators, and particularly to fish-eating birds such as cormorants, darters, kingfishers, fish eagles and ospreys, all of which presumably possess colour vision.*

Pseudotropheus tropheops also exhibits colour polymorphism. While very variable in colour and in the degree of development of a colour pattern a "typical" individual can be readily recognised. In addition a form which is rather light in colour and has a number (usually eight) of narrow horizontal orange stripes on the flanks is also common, at least at Nkata Bay. Both males and females of this form are to be found. In males in breeding dress the horizontal stripes tend to be obscured by the development of darker pigment and bluish vertical bars. At first this was taken to be a distinct species, but no constant morphological differences between it and the " typical " form could be found, and Dr E. Trewavas, to whom a specimen was sent, agreed that it was indistinguishable from her preserved material of *P. tropheops*.

Another form, again originally taken to be a distinct species, is typically very pale, almost silvery, in colour and has eight dark vertical bars, of which six lie below the dorsal fin and extend some way into it. The dorsal fin thus has six distinct patches of black pigment at its base. The two horizontal bands of the basic colour pattern are also quite well developed. This pattern has been seen on a juvenile taken from the mouth of a female which had the same pattern. Unfortunately all save one of the young of this specimen had been spat from the mouth during capture so the opportunity of ascertaining whether or not mixed broods were produced did not arise. This form is rather rare at Nkata Bay but was found to be much more common at Ruarwe. A few specimens have been seen which are in some ways intermediate in coloration between this form and the typical form, the ground colour being dark,

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* See Addendum, p. 280.

the bars less distinct, and the vertical ones not extending or only very slightly extending into the dorsal fin. The whole problem in this case is thus rendered very obscure.

Besides these, a single specimen of *P. tropheops* which was completely orange in colour was collected at Cape Maclear in the south ; and at Nkata Bay a specimen was found which had six horizontal rows of distinct yellowish spots ventrally. (See also notes on the orange shoulders of males of this species at Likoma Island given in a subsequent section).

It must be emphasised that in all cases of polymorphism recorded above no evidence has been obtained to indicate that the different forms have different ecological preferences. All co-exist and can frequently be seen together.

Nothing is known about the genetical basis of colour polymorphism in *P. zebra* and *L. trewavasae* except what can be inferred from the fact that the OB pattern appears to be strictly sex limited and that complete dominance is the general rule. In general the different types of coloration are exceptionally clear cut, which indicates that they are the result of the expression of single genes or chromosome sections. The occurrence of a few flecks of black pigment in a white specimen of *P. zebra* may possibly be the result of modifiers. The sex limited nature of the OB pattern makes it seem probable that the female is the heterogametic sex, and it seems likely that there is in operation a mechanism involving the linkage of the gene or gene complex concerned with its expression with a recessive lethal such as has been shown by Goldschmidt and Fischer and by Gerould to be responsible for similar female polymorphism in certain butterflies. (Both cases quoted by Huxley 1942).

While no obvious selective advantages can be seen for the various polymorphic forms—and particularly for the conspicuous white form of *P. zebra* —it might be inferred from the distribution of the various forms that colour differences have selective significance or at least may be linked with hidden characteristics which are themselves of selective significance, though the possibility that the composition of isolated populations is influenced by genetic drift cannot be ruled out. If drift is not at work then the differences in the frequency of the various forms of *P. zebra* over relatively short distances may well be interpreted as indicating that the selective advantage of the various colour phases (not necessarily based on the colour itself), varies from locality to locality, the differences being correlated with slight differences in the environment in different areas. That the alleles concerned have exactly similar selective values is extremely unlikely as has been shown by several genetical studies which, incidentally, reveal also that apparently insignificant morphological characteristics may go hand in hand with other characteristics of obvious selective value, such as longevity, fecundity, and similar viability factors, most of which would be difficult or impossible to discover during field studies.

Colour per se may have positive or negative selective value in different localities where conditions differ slightly as it appears to have in the snail *Cepaea nemoralis* (L) (Cain & Sheppard, 1950, Sheppard, 1951) but not in another polymorphic snail *Bradybaena similaris* (Komai & Emura, 1955). This seems improbable in the present cases where the colour differences are clear cut and not subtly intergrading, and particularly when it is remembered that the OB pattern occurs in fishes in other lakes which frequent quite different habitats from those occupied by the Mbuna.

The number of females obtained which had young in the mouth was few and as very small juveniles are not particularly suitable for studying the development of pigmentation this rather promising possibility of finding out something of the genetics of polymorphism in the group remains largely unexplored. It is worth while noting, however, that the entire brood of a " normal " female of *Labeotropheus trewavasae* (twenty-two fishes) whose members were large enough to exhibit distinctive pigmentation were all " normal ".

DISTRIBUTION

All species of the group are strictly confined to L. Nyasa. Brooks (1950) attempted to marshall such scanty evidence as was available to show that some species of the group are geographically isolated in one part of the lake. This was scarcely justified and we are still not in a position to make many assertions concerning the intra-lacustrine distribution of the various species. However recent collections made at strategic points on both east and west shores, together with records from the north and south ends of the lake (based chiefly on the Christy collection (Trewavas, 1935)), indicate that several species occur all round the lake wherever suitable conditions exist. It would be easy to base speculations on negative evidence but until the lake has been much more carefully explored the fact that a given species has not been recorded from a locality cannot be taken as proof of its absence. A table showing the essential facts of the known distribution of the various species is given in appendix 1.

That *some* species do not occur wherever there are rocky shores is shown by the work at Nkata Bay which is now by far the best worked area of rocky shore in the lake. Here certain species which are fairly well represented in the Christy collection were not found.

The fact that Brooks' evidence was incomplete and that the apparent case of northern and southern subspecies of *Pseudotropheus tropheops* has been shown to be the result of chance association of phenotypes of a very variable species in limited collections (Fryer, unpublished data) does not mean that geographical speciation is denied. As is made clear in subsequent sections the evidence is all in favour of such speciation.

GENERAL ECOLOGY AND HABITS

Although the various species of Mbuna have diverged in habits and many show striking morphological differences correlated with these habits, all species nevertheless have one fundamental requirement in common. None is ever found far from rocks. Most species are very closely associated with rocky substrata from which they obtain their food, and even those species such as *Cynotilapia afra* and *Genyochromis mento* whose feeding habits differ most strikingly from those of their relatives, and which could presumably collect all their food from non-rocky situations, are far from being emancipated from rocky shores. This broad similarity in ecological preferences emphasises the close phyletic relationship of the various genera.

Apart from *Cynotilapia afra* which has to some extent taken to a pelagic mode of life yet is still found only on rocky shores, all the other species are benthic in habits and are usually to be found swimming within about 1 metre of the bottom. They are graceful fishes whose movements are usually unhurried, and whose main activity in life appears to be the collection of food. They occur on rocky shores in prodigious numbers, their density being at least six or seven (and sometimes even more) per square metre of the bottom on the shore studied in most detail (see Part I, p. 164). When alarmed they usually flee for only short distances and seek shelter beneath a rock at the earliest opportunity.

Their very close association with rocks is startlingly revealed when one observes, as is often possible, a region where a rocky shore suddenly ceases and gives way to a sandy beach. As the rocks cease, so do the Mbuna, and within a few yards of one another one can see areas in which Mbuna abound and in which they are completely absent. Where rocky shores grade more gradually into sandy beaches the change in fauna is naturally less rapid, but is nevertheless very striking, particularly in that almost all species cease to occur as soon as there is any considerable admixture of sand in the substratum ; but two species *Cyathochromis obliquidens* and *Pseudotropheus lucerna*, which are virtually absent among the rocks, and which are completely absent from the sand may be here very common.

Almost all are shallow water forms. As the depth of water in excess of 6 or 7 metres increases there is a progressive diminution in number of Mbuna and, as a general rule, it is true to say that very few of these fishes venture to depths of more than about 20 metres. This means that they are restricted to a very narrow strip around the margin of the lake and offshore islands. For instance, even on the rocky shore studied at Nkata Bay where there is a well marked littoral shelf, a depth of 20 metres is attained within about 70 metres of the shore, and on large tracts of shore the slope is much steeper than this and there are indeed points at which the rocks descend almost vertically to depths in excess of 20 metres.

A very striking and important feature of the ecology of these fishes is that a large number of species can always be found living together on rocky shores. For example eighteen species were recorded on a single rocky shore at Nkata Bay, and a further two species occurred on a contiguous strip where rocks occurred among sand.

Detailed information on the individual ecological preferences of the species studied has been presented in Part I ; most of this, together with additional relevant information, is summarised in the next two sections.

FOOD PREFERENCES

Two basic foods are available to rock frequenting fishes of small size. One of these is the algal felt (Aufwuchs) growing on the rocks, which consists essentially of diatoms and other loose algae (loose Aufwuchs) and more firmly attached filaments, particularly of the blue green alga *Calothrix*, which, however, is not digested when eaten (see Part I, p. 173). The other is the invertebrate fauna which consists mainly of small insect larvae and certain crustaceans (ostracods and harpacticoid copepods).

The Mbuna have exploited both these sources of food. A given species is usually rigorously restricted to one or other of these diets and in most cases the feeding mechanism is highly specialised to facilitate the collection of one or other of these foods. Within each feeding group, however, the differences in food preferences between individual species are usually remarkably small and are frequently indistinguishable. Thus all the herbivores eat Aufwuchs and the only difference between the various species seems to be that some collect the indigestible *Calothrix* whilst others do not.

It is noteworthy that no species of Mbuna has become piscivorous, but *Melanochromis melanopterus* seems to possess potentialities whose exploitation would permit the inclusion of fish in the diet and, on one occasion, a small fish was found in the gut of this species. The other fishes of the environment have been exploited, however, namely by *Genyochromis mento* which feeds by rasping scales from its larger and less active brethren. (Fryer, Greenwood & Trewavas, 1955). This absence of piscivorous species may not be unconnected with the prevalence of small size within the group. (In aquaria all species, whether carnivorous or herbivorous feed greedily on the eggs or fry of their fellows if opportunity to do so offers).

The food of the species studied is listed below.

Labeotropheus fuelleborni	Aufwuchs (including *Calothrix*)
Labeotropheus trewavasae	Aufwuchs (including *Calothrix*)
Pseudotropheus zebra	Loose Aufwuchs
Pseudotropheus livingstonii	Loose Aufwuchs
Pseudotropheus williamsi	Insects + some loose Aufwuchs
Pseudotropheus lucerna	Loose Aufwuchs
Pseudotropheus tropheops	Aufwuchs (including *Calothrix*)
Pseudotropheus fuscus	Loose Aufwuchs
Pseudotropheus fuscoides	Insects
Pseudotropheus elongatus	Loose Aufwuchs
Pseudotropheus minutus	Loose Aufwuchs
Pseudotropheus auratus	Loose Aufwuchs
Melanochromis melanopterus	Insects and (in one large specimen) crabs
Petrotilapia tridentiger	Loose Aufwuchs
Cyathochromis obliquidens	Loose Aufwuchs
Cynotilapia afra	Zooplankton + very small amounts of Aufwuchs and insects
Genyochromis mento	Fish scales and fins + traces of Aufwuchs
Labidochromis vellicans	Insects
Labidochromis caeruleus	Insects
Gephyrochromis lawsi	Loose Aufwuchs

INDIVIDUAL ECOLOGICAL PREFERENCES

While all species occur among or near rocks it is possible to point to certain ecological preferences of a few species, other than those of food, which will tend to keep them isolated from their near relatives and allow them to inhabit the same general habitat without competing to any great extent. Perhaps the most striking example of this is the occurrence in rocky areas with an admixture of sand of *Cyathochromis obliquidens* and *Pseudotropheus lucerna*, but similar cases occur among the species living among the rocks themselves. Thus among the insect eaters *Labidochromis vellicans* usually occurs very close inshore and has a different horizontal range from its relatives, and the same holds good to a very marked degree for *Pseudotropheus fuscus* among the Aufwuchs eaters and apparently also for *P. minutus*. On the other hand the few specimens of *P. livingstonii* taken all came from deeper water than that frequented by the majority of the Mbuna, and, at Nkata Bay at least, the same applies to *Gephyrochromis lawsi*. At Florence Bay the latter occurs on a shore which is shingly rather than truly rocky and thus appears to have preferences which keep it isolated from the rest of the Mbuna, though these preferences cannot yet be distinctly defined.

The differences in general ecological preferences and in food preferences are shown in Table 7. Ecological separation is particularly weak among the the Aufwuchs eaters. Here, although the difference between eaters and non-eaters of *Calothrix* is an established fact in some areas of the lake, its significance is doubtful as *Calothrix* is not digested. Further, species which eat it when it is available can subsist without it in those areas in which it does not occur (see p. 233). It seems, however, that by including *Calothrix* in their diet when it is available these species relieve pressure on the loose Aufwuchs, and it is possible that certain species which can co-exist when *Calothrix* is available cannot always do so when both are competing for loose Aufwuchs alone (see Part I, p. 233).

Although the possession of different feeding mechanisms is listed in Table 7 (see also p. 258) as a possible means of ecological separation this is done without much confidence in its effectiveness, for the species concerned often take identical foods. In fact it seems that different mechanisms have been evolved in order to achieve the same end rather than that divergence in order to permit the exploitation of slightly different conditions has taken place. Further, although in theory the small *Pseudotropheus minutus* will be able to feed in crannies inaccessible to the larger *P. fuscus* with which it co-exists, the gut contents of the two are in fact indistinguishable.

Even assuming these slender and somewhat academic differences to be sufficient to partially obviate competition between certain species there still remain some, such as the very well studied *Pseudotropheus zebra* and *Petrotilapia tridentiger*, which co-exist, employ an identical feeding mechanism, and eat exactly the same kind of food. This intimate co-existence without obvious competition, which is of considerable evolutionary importance, seems to be due to a large extent to the superabundance of algal food among the rocks. (See p. 226 and also subsequent sections of this paper).

BREEDING HABITS

It is much more difficult to obtain information about the breeding habits of species living among rocks than of their allies living on sand. Some at least of the latter species construct nests at which their behaviour can be observed. No evidence of nest-building has been observed among the Mbuna, and indeed it is difficult to imagine how any such structure could be constructed among the rocks.

TABLE 7

The ecological niches of the Mbuna.

ROCKY SHORES												ROCKS AMONG SAND	SHINGLE
Invertebrate eaters			Mixed feeders	Scale eaters	Aufwuchs eaters							Aufwuchs eaters	Aufwuchs eaters
Semi-Pelagic plankton feeders	Inshore skulkers	Non-skulkers			Eaters of loose Aufwuchs and *Calothrix*		Eaters of Loose Aufwuchs only						
					Feeding mechanism Type 1	Feeding mechanism Type 4	Inshore skulkers		Non-skulkers		Deeper water		
							Large species	Smaller species	Feeding mechanism Type 3	Feeding mechanism Type 2			
Cynotilapia afra	*Labidochromis vellicans*	*Labidochromis caeruleus* *Pseudotropheus fuscoides* *Melanochromis melanopterus*	*Pseudotropheus williamsi*	*Genyochromis mento*	*Labeotropheus fuelleborni* *Labeotropheus trewavasae*	*Pseudotropheus tropheops* *Pseudotropheus novemfasciatus*?	*Pseudotropheus fuscus*	*Pseudotropheus minutus*	*Pseudotropheus auratus* *Pseudotropheus elongatus*	*Pseudotropheus zebra* *Pseudotropheus elegans* ? *Petrotilapia tridentiger*	*Pseudotropheus livingstonii*	*Cyathochromis obliquidens* *Pseudotropheus lucerna*	*Gephyrochromis lawsi*

All the evidence obtained points to the fact that breeding takes place among the rocks, i.e. that there is no migration to other habitats, and that the young are reared there. Summarising the somewhat fragmentary evidence obtained it would appear that during breeding periods the male assumes a " breeding dress " and establishes a territory among the rocks over which it keeps a zealous watch and from which it actively chases all intruders ; that egg laying is preceded by a definite sequence of courtship behaviour, and that after fertilisation the eggs are picked up and brooded in the mouth of the female. Breeding takes place throughout the year. There is no evidence to show that pairs continue to associate after fertilisation of the eggs. Notes on these various aspects of the breeding behaviour are given below.

Territoriality

That breeding males of several species defend territories is established beyond doubt. Such behaviour can be regularly observed during underwater observations. The territory may be a cleft among the rocks or even a flat, exposed area of rock offering no semblance of shelter. Because of the very irregular nature of the substratum it was virtually impossible to decide whether different species have different territorial preferences, though *Labeotropheus fuelleborni* was seen most often with territories in clefts, and an exception must be made for *Cyathochromis obliquidens* which frequents areas where rocks occur among sand, and which on two occasions was seen occupying a territory which consisted of an excavation in the sand alongside, or in one case under, a rock.

The territory is usually small and the centre of attraction may be, as in one case where *Pseudotropheus auratus* was watched, only about 60 cm. long and no more than about 20 cm. wide. When on guard in its territory a male of any species usually moves little more than a metre in any direction from the centre of the territory except to pursue intruders. On such occasions it may chase them for a couple of metres before returning to its territory. Guarding males are very bold and on one occasion a male of *Pseudotropheus tropheops* was seen to drive away a predatory *Haplochromis* considerably larger than itself. Dice (1952) quotes Collias as stating that defence of a territory is usually directed against individuals of the same species and that alien species are nearly always permitted to enter a territory without molestation. This is not so among the Mbuna.

After observing a fish in its territory it is usually difficult to locate it on a subsequent occasion, but in one case, due to the fortunate coincidence of a male of *P. auratus* which exhibited a peculiarity of coloration selecting a territory near to a readily recognisable " landmark ", it was possible to establish that it was present in the same restricted territory on two consecutive days.

Some guarding males at least do not cease to feed whilst occupying territories as they have been observed to browse on the rocks in between periods of guard duty.

The significance of territoriality in the Mbuna is probably to give some measure of protection to the eggs which are presumably shed by the female in the territory of the male at the end of courtship, and are then taken into the mouth.

It is not known whether a male fertilises the eggs of more than one female during a period of sexual activity, but this is not unlikely. Although aquarium studies are needed before this can be proved, the impression gained in the field is that there is no prolonged association between a pair of fishes but that courtship takes place if a " ripe " female ventures into the territory of a male, and is presumably carried to completion if the female is ready for oviposition. As there is no evidence to indicate association of " ripe " males with brooding females it seems quite probable that the male remains in its territory as long as its physiological condition is such as to sustain such behaviour, and it seems likely that further females will be received as readily as the first.

Courtship behaviour

Full details of the courtship behaviour of any one species are unknown, but it is possible to mention a few observations made in nature. The most frequently seen part of the courtship, and one which takes place in several, perhaps all, species is " tail chasing ". During this process a male and female swim round and round very rapidly in a tight circle so that the snout of each follows its partner's tail. As many as thirty circles may be described by the participating fishes, after which there is frequently a brief pause followed by more tail chasing. It seems probable that the bright orange or yellow spots developed on the anal fin of the male, and occasionally of the female, are made use of during this behaviour. Tail chasing appears to be the first part of the courtship behaviour, for fishes have been seen to commence it immediately after encountering one another.

Other aspects of courtship behaviour have also been seen. Once a male of *Pseudotropheus tropheops* was seen displaying in front of a female. It swam backwards and forwards along a very short " beat ", violently wagging its tail as it did so, and even repeated this behaviour several times after the apparently disinterested female had moved away.

On another occasion a male of *P. tropheops*, whilst occupying a territory, was approached by a female of its own species. No tail chasing took place on this occasion but the two fishes lay side by side, head to tail, and moved slowly round several times, the body of the male quivering violently throughout the entire process. No sign of eggs or milt was observed during this process. The female eventually moved away but even after its departure the male was observed to have one more bout of violent quivering.

On one occasion a male and female of *Pseudotropheus fuscus* were observed tail chasing, between bouts of which they indulged in a form of fighting, each fish seizing the jaw of its partner. No biting elsewhere took place. This was later found to be part of the mating behaviour of certain cichlids and excellent photographs showing identical behaviour in a pair of the South American *Aequidens portalegrensis* (Hensel) are given by Innes (1951).* From time to time this particular pair of *P. fuscus* withdrew under a rock, but although search was made no eggs were seen.

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* On the other hand Baerends & Baerends van Roon (1950) describe similar behaviour, which they call " mouth fighting," as taking place between rival *males* of both *Hemichromis bimaculatus* Gill and *Tilapia natalensis* (= *T. mossambica* Peters).

Two exceptional occurrences are worthy of mention. On one occasion three individuals of *P. tropheops* (sex uncertain) were seen tail chasing. On another occasion a male of *P. auratus* guarding its territory was approached by a dark-coloured fish, almost certainly a female of *P. fuscus*, and certainly not of its own species, with which it immediately commenced frenzied tail chasing. After a brief pause a second bout took place, and the stranger then moved away. It would appear that this behaviour was elicited by some signal common to both and that the cessation of tail chasing represented the point where the courtship behaviour of the two participants diverged and was no longer mutually stimulating. The phenomenon of attempted courtship between closely related species has been reported for other groups, e.g. butterflies (Tinbergen 1953), in which group its occurrence is common knowledge to naturalists, birds (Lack, 1947), and snails (Diver, 1940). Tinbergen (1953) states that a male stickleback may react even to a small tench entering its territory, by commencing its mating behaviour—in this case zig zag dancing, so it is not surprising that such behaviour should be occasionally elicited by closely related species of Mbuna. The observation just cited, incidentally, supports the belief that tail chasing is the prelude of courtship.

Brooding the young

No Mbuna has been seen to deposit eggs and no free eggs have been seen. Judging from the avidity with which eggs are eaten in aquaria by many rocky shore fishes (including herbivores) it seems probable that they are picked up by the female immediately after fertilisation or they would otherwise be quickly eaten by other fishes. As the courtship behaviour appears to be based on visual stimuli it is supposed that this takes place by day.

The brooding of young in the mouth of the female is probably common to the group as a whole, and has definitely been established for *Pseudotropheus tropheops*, *P. fuscus*, *P. zebra*, *P. lucerna*, *P. williamsi*, *P. elongatus*, *Petrotilapia tridentiger*, *Cyathochromis obliquidens*, *Labidochromis vellicans*, *Labeotropheus fuelleborni*, *L. trewavasae* and *Genyochromis mento*.

The number of young which can be brooded in the mouth is small. As eggs and young tend to be spat from the mouth when brooding females are captured, the only reliable numerical data on brood size are those obtained from a few fishes collected by stunning. Details of these samples are given in Appendix II. Only fishes whose mouths were obviously crammed to capacity are considered. These data indicate that in *Pseudotropheus tropheops* and the two species of *Labeotropheus* the number of young reared per brood must seldom exceed thirty and is usually considerably less than this. In fact the number of eggs produced by a ripe ovary is sometimes less than thirty, and as few as seventeen have been seen in a ripe ovary of *Pseudotropheus zebra*. One specimen of *Labidochromis vellicans* with its mouth apparently crammed to capacity carried only ten young. *Genyochromis mento* and *Pseudotropheus fuscus* apparently produce somewhat larger broods than do these species but the maximum number of young seen in any mouth was forty-six (in *P. fuscus*) and it is doubtful whether all these could have been retained until the young were of sufficient size to fend for themselves.

The size of brood is small in comparison with that of many other mouth-brooding cichlids. For example the numbers found to be carried by various species of *Tilapia* by Lowe (1955) ranged from 65 to 711, and the number carried by species of *Haplochromis* and *Lethrinops* in Lake Nyasa seems, with few exceptions, to be greater than that carried by the Mbuna. (General observations and information from T. D. Iles). In relation to the size of the parent the eggs are particularly large, being larger than those of some of the mouth-brooding species of *Tilapia* which do not begin to breed until they attain a considerably larger size than is ever attained by some of the Mbuna. The largest eggs measured were those of *Labeotropheus* spp., their axes being about 6·0 × 4·0 mm. Eggs of *Pseudotropheus tropheops* usually measure about 4·5 × 2·5 mm.

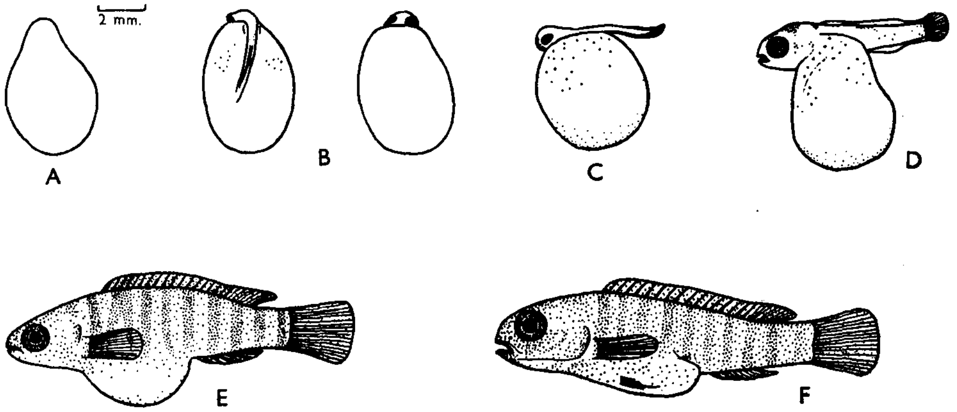

Fig. 98.—Developmental stages of *Labeotropheus* during the period of oral incubation. (Note : Both species of *Labeotropheus* are involved in the sequence portrayed here, but in the very early stages of development they appear to be indistinguishable).

There is an efficient correspondence between the number of ripe ovarian eggs and mouth-capacity. This is achieved in part by the functional development of only a single ovary which produces a small number of large yolky eggs.

Eggs of the Mbuna are a rich golden yellow in colour and are approximately spherical when taken from a ripe ovary, but become broadly ovate and develop a terminal papilla after laying.

Stages in the ontogeny of *Labeotropheus* passed through during the period of oral incubation are shown in Fig. 98. Study of various developmental stages of other species indicates that this sequence is typical of the Mbuna as a whole. Unfortunately it is not possible to put a time scale to the early stages of development but, by analogy with other cichlids, it seems probable that the period of incubation does not exceed about four weeks.

The largest Mbuna taken from the mouth of a female (*Labeotropheus trewavasae*) had a length of about 16 mm. Young Mbuna (species uncertain) 19 mm. in length have been collected in the most inshore waters of rocky shores, and others, believed to be *Pseudotropheus tropheops*, 20 mm. in length have been seen swimming independent of parental control. The young begin to feed during the period of oral incubation and may begin to take food before all traces of the yolk sac have disappeared. The female parent does not feed during the period in which eggs or young are being carried in the mouth.

In all species for which adequate data are available breeding takes place throughout the year. As females with young in the mouth have been seen with a ripening ovary the indications are that a female produces several broods per year.

The smallest female of *Pseudotropheus zebra*, which attains a length of 11 cm., which has been found with a ripe ovary had a length of 7·6 cm. Comparable figures for *P. tropheops* are 13 cm. and 7·2 cm.

The possibility of homogamy

Kosswig (1947) suggested that homogamy might have been important in promoting rapid speciation in the cichlid fishes of African lakes, and Steinmann (1953), thinking particularly of the coregonid fishes of Europe, suggests that insufficient attention has been paid to this possibility. It is therefore worth while mentioning some very scanty observations which are relevant to this matter. While on one occasion a swarm of thirty to forty BB pattern individuals of *Pseudotropheus zebra* were seen together, and on another occasion a small group of the B form were seen in association it may be more significant that a B male and a BB female were seen " tail chasing ".

These colour forms of *P. zebra* provide particularly good material for the study of selective mating as envisaged by Kosswig and further observations may throw valuable light on this problem. To date the evidence, while scanty and indecisive, does not indicate the existence of homogamy in polymorphic species.

Competition for breeding grounds

As each species seems to require a definite territory for mating purposes and as the fish population of rocky shores is very dense it is theoretically possible that there could be competition for breeding grounds. However, this contingency does not seem to arise on account of the fact that breeding takes place throughout the year, and that, at any given time, only a fraction of the total male population is occupying territories. One can always find territorial males but their numbers are few in relation to the total population and their territories are usually well separated. In this they differ markedly from the nest-building *Haplochromis heterodon* Trewavas of the same lake in which, in certain areas, many males simultaneously occupy contiguous territories (Fryer, 1956 c).

ADAPTIVE RADIATION

While the adaptive radiation of the Mbuna is restricted in so far as the group is confined to rocky shores, within this major habitat almost all available niches have been exploited. The one striking omission is that of a piscivorous species.

Just as the birds of the subfamily Geospizinae of the Galapagos Islands (Lack, 1947), and of the family Drepaniidae of the Hawaiian Islands (Amadon, 1947 and 1950) differ adaptively among themselves in the structure of the beak which has become modified and specialised to facilitate the collection of certain foods, so do the members of the Mbuna differ in mouth structure and in dentition, each being highly specialised in structure and having a feeding mechanism suited to the collection of a certain type of food.

There can be little doubt that the ancestral Mbuna were rock scrapers, and at the present time numerous species are specialised exponents of this art. Most species are herbivores which scrape the algal Aufwuchs from rock surfaces, but it is interesting to see that at least four different types of feeding mechanism, with which are associated an even greater number of types of buccal dentition, have been evolved to this end. These feeding mechanisms can be listed as follows :

(1) The *Labeotropheus* type—Found only in the two species of *Labeotropheus.*

(2) The *Pseudotropheus zebra* type—Found in *P. zebra*, *P. williamsi**, probably in *P. livingstonii* *P. elegans*, and *P. lucerna*, and also in *Petrotilapia tridentiger* and *Cyathochromis obliquidens.*

(3) The *Pseudotropheus fuscus* type—Found in *P. fuscus*, *P. fuscoides* *P. auratus*, *P. minutus*, and probably *P. elongatus.*

(4) The *Pseudotropheus tropheops* type—Found in *P. tropheops* and probably in *P. novemfasciatus.*

Each of these feeding mechanisms has been described in Part I. The feeding mechanism of *Gephyrochromis lawsi*, which is also a rock scraper, is unknown but from the structure of the mouth it can be inferred that it is probably similar to the *Pseudotropheus tropheops* type. Although the dentition of *Petrotilapia tridentiger* and *Cyathochromis obliquidens* is strikingly different from that of the species of *Pseudotropheus* with which they are grouped, and although these two also differ strikingly from one another, yet all share a common feeding mechanism. In most cases this feeding mechanism is associated with an exclusively algal diet, but in the case of *P. williamsi* the teeth are rather sharper than those of its relatives and insects are also eaten.

A similar but more marked divergence is seen in group (3) where *P. fuscoides*, whose mouth structure and dentition are basically similar to those of the herbivores listed, is essentially an insect eater. It seems probable also that some of the species of *Melanochromis*, with which *P. fuscoides* is closely related, will have similar feeding mechanisms.

One member of this genus, *M. labrosus*, known only from a single specimen, has its lips produced into pointed lobes and, by analogy with another Nyasan cichlid, *Haplochromis euchilus* Trewavas which has similar lips and whose feeding habits have been observed, it can be inferred to use these lobes to detect the movement of insects living among the algal Aufwuchs of the rocks, which are then snapped up. Its dentition is suitable for dealing with such food.

While employing a feeding mechanism of the *P. zebra* type, *Cyathochromis obliquidens* has become established under conditions where rocks occur among sand, and is able to utilise its feeding mechanism for scraping algae from the strap-like leaves of *Vallisneria*, though it is still also a rock scraper. *P. lucerna*,

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* Also eats insects.

which has a " *P. zebra* type " of mouth and dentition and presumably a similar feeding mechanism, lives under similar conditions to *C. obliquidens*.

Cynotilapia afra is undoubtedly an offshoot from the *Pseudotropheus* stock and more particularly from the *zebra* group of the genus. In fact at first glance it is easy to confuse a blue and black barred *P. zebra* and *C. afra* which resemble each other in form and coloration. The mouth structure too is very similar in the two species but *C. afra* differs strikingly in dentition (cf. Figs. 16–18 and 28–31 in Part I). This species has ventured, or has been forced away, from the rocks and now leads a semi-pelagic existence in the inshore waters where it feeds largely on zooplankton. In spite of this partial emancipation from the rocks *C. afra* is nevertheless found only in open water just off rocky shores, and occasional individuals are seen or captured among the rocks from which they still occasionally pick up a little food.

Genyochromis mento, while showing resemblances in dentition to the species of *Pseudotropheus*, has utilised its ability to scrape in quite a different way and has the remarkable habit of removing scales from other fishes (Fryer, *et al.* 1955).

The two species of *Labidochromis* obviously diverged early from the primitive stock and took to feeding on insects and other small invertebrates among the rocks, and their dentition is now very specialised for this purpose and differs markedly from that found in any other genus of the group.

Adaptive radiation within the group can be seen in part from Table 7 and from Fig. 99.

THE PHYLOGENETIC RELATIONSHIPS OF THE MBUNA AND THEIR EVOLUTIONARY HISTORY

The suggested relationships of the various species are most readily understood by reference to Fig. 99.

Any attempt to outline the evolutionary history of the Mbuna or the means whereby divergence took place must of necessity be largely theoretical, but since as much information on the ecology and general habits of the group is available as for any comparable group of species in the African lakes, to which so much attention has been directed by students of evolution, it is worthwhile trying to interpret the available facts.

The Mbuna are probably among the most long-standing of the cichlids of L. Nyasa. This is shown clearly by the fact that all the genera, which comprise more than one-third of the cichlid genera present, are endemic, and by the fact that these genera, which appear to be monophyletic in origin, and which are all closely related, have nevertheless evolved some highly complex yet widely differing specialisations. It seems highly probable, therefore, that the Mbuna commenced their adaptive radiation early in the history of the lake.

It is not known from what form the Mbuna stemmed ; but it seems likely that they arose from a *Haplochromis*-like ancestor, and probably from a riverine species. The most generalised present-day species of *Haplochromis* are such fluviatile species as *H. wingati* (Boulenger) and *H. bloyeti* (Sauvage). A consideration of their structure reveals no reason for precluding such a generalised type from being ancestral to the Mbuna.

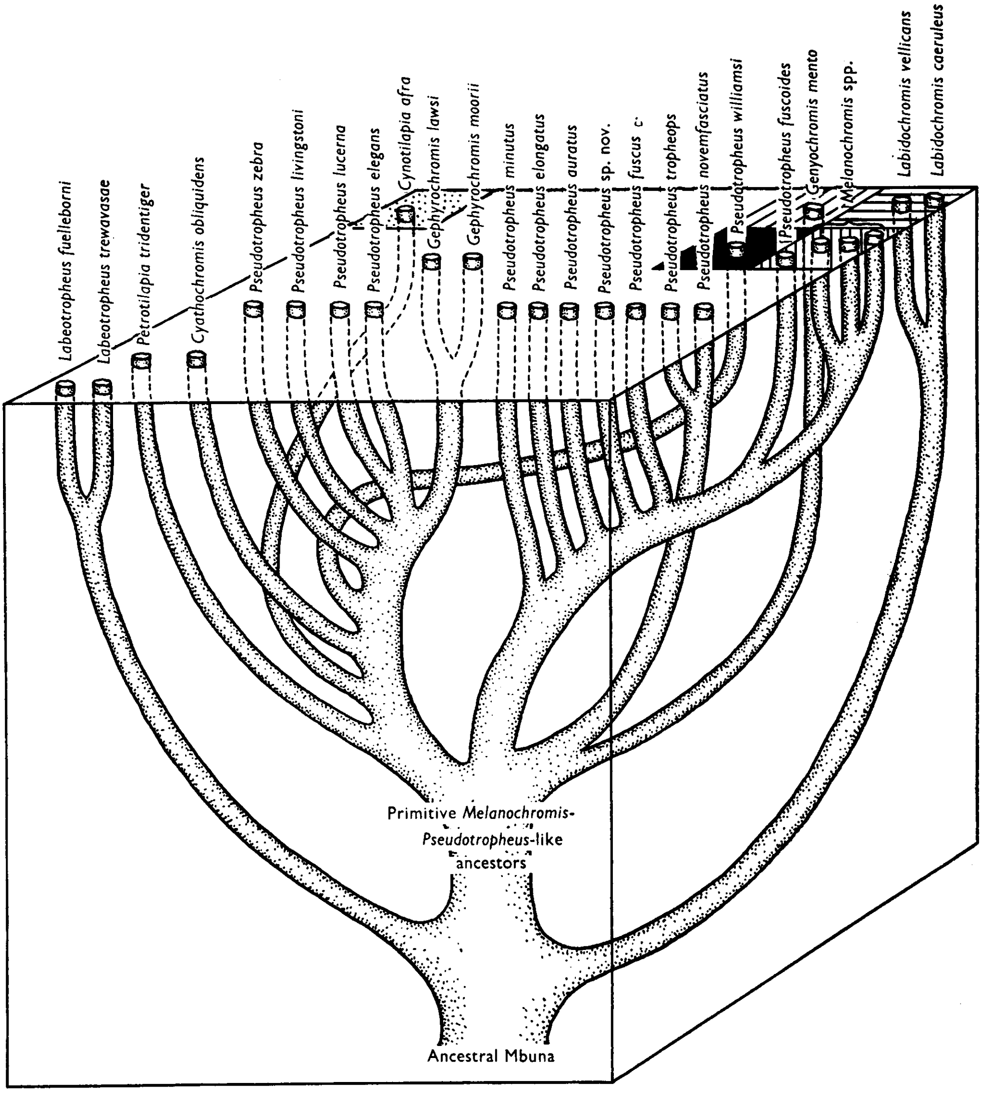

Fig. 99.—Suggested phylogenetic relationships of the Mbuna. Note : Proximity to the base of the " tree " does not necessarily denote primitiveness but indicates rather that divergence of that line probably took place early in the history of the group. Further, the fact that other genera are shown arising from between the *Pseudotropheus* branches does not necessarily mean that they are more closely related to certain species of *Pseudotropheus* than are the various *Pseudotropheus* species to one another. On the other hand, the genus *Pseudotropheus* is at present rather ill-defined and merges almost imperceptibly with *Melanochromis* and *Gephyrochromis* as is reflected by the figure.

The variously marked areas on the upper surface of the cube indicate different feeding habits. Stippling : Plankton feeders. Oblique lines : Scale eaters. Horizontal lines : Invertebrate pickers. Vertical lines : Invertebrate eaters. Solid black : Mixed feeders. White : Algal browsers.

A clue as to what the intermediate stages in the evolution of the Mbuna may have been like is given by the structure of some of the species of *Haplochromis* living in Lake Victoria. Here, where it is presumed with good reason that evolution has not gone on in isolation for as long as is the case in Lake Nyasa, one group of species of *Haplochromis* shows a distinct tendency towards the evolution of a *Pseudotropheus*-like type, and has given rise to *H. nigricans* (Boulenger) which is scarcely separable from *Pseudotropheus.* The gap between this species and the generalised *Haplochromis* type is, however, bridged by *H. nuchisquamulatus* (Hilgendorf) (Greenwood, 1956 b). Again, there is in Lake Victoria a *Haplochromis* with many features, and particularly those of dentition, similar to those of *Cyathochromis obliquidens.* This is *H. obliquidens* Hilgendorf. According to Greenwood (1956 b) this species probably arose from a form like *H. lividus* Greenwood, which exhibits certain incipient *obliquidens* characteristics, and which itself probably stems from a form like *H. nuchisquamulatus* whose affinities with the generalised *Haplochromis* type are not difficult to perceive. In Lake Nyasa, where isolation has prevailed for a longer period than in Lake Victoria, it is only natural that such intermediate forms should have become extinct in the face of competition from the more specialised species, but it seems fairly safe to assume that the structure of some of the species of *Haplochromis* living in Lake Victoria today gives a reasonable indication of the kind of fishes from which the present-day Mbuna arose.

Certain fragments of information on this matter can also be gleaned from the ontogeny of the extant species. For instance the early developmental stages of some of the Mbuna (e.g. *Pseudotropheus tropheops*) have a rounded caudal fin such as is to be seen in the generalised species of *Haplochromis.*

The occurrence of the OB colour pattern in two genera of the Mbuna and in species of *Haplochromis* in Lakes Victoria and Kivu and in genera clearly derived from *Haplochromis* in Lake Victoria is not at variance with the suggested ancestry of the Mbuna.

An important feature in the evolution of the group was probably the early assumption of an algal diet. Fishes as a whole tend to be carnivorous and the adoption of the habit of feeding on the sward of algae growing on rock surfaces probably allowed the Mbuna to get off to a flying start as it were when they first colonised the lake. The main trend in the history of the group has been towards perfection of this habit.

The first fundamental split was probably that where certain forms took to eating insects and other small invertebrates living among the algae. This early invertebrate-eating offshoot is probably represented today by the two species of *Labidochromis* which are more specialised for the collection of this type of food than any other member of the Mbuna. It is significant, however, that this line, while apparently successful in certain niches, has given rise to only two species which survive today, one of which is rare.

Study of the morphology and habits of the other genera indicates that the scraping of algae from rocks offered better opportunities for radiation, and it is towards this type of trophic specialisation that they tended to evolve, though some became secondarily modified to facilitate the collection of invertebrates, and others such as some of the more generalised species of *Melanochromis* perhaps never became very specialised in this way. This general trend of evolution was accomplished in different ways and one genus, *Labeotropheus*, became a highly specialised rock scraper of a type which appeared to offer no further opportunities for radiation, though two sibling species of this genus exist at present. The other lines, however, produced a number of rock scrapers specialised to varying degrees. It seems likely that so many species were tending towards the exploitation of this type of feeding habit that competition began to make itself felt and some species, particularly those which were the least specialised, began, or continued, to include the rock dwelling invertebrates in their diet. These species would be similar to the present day *Pseudotropheus fuscus* and *P. aurutus* which are the least specialised of the rock scrapers, and from them, by a sharpening of the anterior row of teeth in each jaw and a slight enlargement of the pharyngeal teeth, arose such forms as *P. fuscoides* and the species of *Melanochromis*.

Even among the highly specialised algal eating rock scrapers it seems that there has been a tendency to diverge in feeding habits and become at least partly insectivorous. An excellent example of this stage of evolution is to be seen today in *Pseudotropheus williamsi*, which, while possessing a mouth structure and feeding mechanism identical with those of its close relatives such as *P. zebra*, which are stenotopic algal feeders, nevertheless eats a mixture of algae and insects (such as mayfly nymphs living on and under the rocks).

One species of *Melanochromis*—*M. labrosus*—has apparently become so specialised as an invertebrate eater that it has developed sensitive lobes on the lips to facilitate the detection of its prey.

Meanwhile a certain amount of partitioning of the habitat was going on. *Pseudotropheus fuscus*, and possibly *P. minutus* (or their immediate ancestors) were able to establish themselves in the most inshore waters and feed from the rocks there with less competition from other species than in waters a little further from the shore.

Other fishes with rock haunting, algal-eating ancestors sought to escape competition by colonising new habitats. Two species managed to find a new niche in areas where rocks occur among sand and were able to flourish there without changing their diet. These were *Cyathochromis obliquidens* and *Pseudotropheus lucerna*. The same may be true also of *Gephyrochromis lawsi* which is also an algal eating rock scraper and which was found to be common on a beach which was shingly rather than truly rocky, and where very few other members of the Mbuna occurred.*

Two other species underwent even more radical changes in habits and came to occupy entirely different niches. One, represented today by *Genyochromis*

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* Dr Trewavas writes, " Five specimens of *Gephyrochromis moorii* were collected in a fine-meshed seine during the Survey of 1939 on the lake shore near the mouth of the River Rukuru (nr. Karonga). This is a sandy shore with sparse reeds. Two stomachs examined contained a green mass of diatoms, mostly *Navicula*, with a few very fine sandgrains. It seems that the horizontally directed lower series of teeth in this species acts as a dredge-lip for scooping the bottom-diatoms from the surface of the sand ". Two specimens were recently collected by Mr D. Harding from a similar habitat on the eastern shore of the lake, indicating that such conditions are perhaps optimal for the occurrence of this species.

mento, utilised its ability to scrape by turning to the other fishes in the environment and scraping scales from their bodies. To this end it gradually acquired a strong, prominent, lower jaw and rigid dentition whose ancestry is, however, still very clearly seen. The other, which has become the present day *Cynotilapia afra*, pushed out into the open water and has taken to feeding on plankton. This species, which is phylogenetically close to *Pseudotropheus zebra*, may be regarded as almost pre-adapted towards plankton feeding for its mouth, whose opening and closing mechanism is the same as that of *P. zebra*, is very mobile and capable of being quickly opened to a large gape. Its sharp outer conical teeth may serve to prevent the escape of plankton but more likely indicate that before leaving the rocks it had begun to include insects in its diet, and in fact chironomid larvae taken from the rocks are still occasionally found in the gut of this species today.

Throughout the process of radiation specialisation towards rock scraping by algal eaters continued and today a remarkable array of feeding mechanisms and types of dentition directed towards this end are to be seen, particularly in the genus *Pseudotropheus*.

It is significant that, basing biological success on numerical abundance of species, the algal eaters are the most successful. This was made abundantly clear during the work at Nkata Bay and elsewhere where algal eaters predominate and where the only really common invertebrate-eater is *Labidochromis vellicans*. By adopting certain habits or habitat preferences some species have ruled out the possibility of occurring in abundance ; e.g. the habitats frequented by *Cyathochromis obliquidens* are of small extent in Lake Nyasa, and the diet of fish scales exploited by *Genyochromis mento*, which is only a modified form of parasitism, can only be indulged in within certain limits. It is conceivable, however, that the obviously recent evolution of plankton eating by *Cynotilapia afra* may lead to the development of one or more numerically abundant species.

MECHANISMS OF EVOLUTIONARY DIVERGENCE

Throughout the above historical reconstruction, details of *how* evolutionary divergence took place have been ignored and the controversial question of whether such divergence was allopatric or sympatric has been avoided. These topics must now be discussed. Such a discussion seems all the more necessary as Poll (1956 b), who describes the complex species associations of littoral fishes found in Lake Tanganyika, which are remarkably similar to those of Lake Nyasa and which may consist of twenty to thirty species in the same habitat, seeks to explain their existence in a manner rather different from that outlined here. He points out that some of these species exhibit dental specialisations which permit them to take different foods but, impressed by the similarity of many co-existing species, says " Néanmoins, si l'on distingue un certain nombre d'adaptations particulièrs, le nombre d'espèces actuellement mélangées dans la même habitat est si grand que l'étude ecologique est incapable d'expliquer une telle association." Of the fishes inhabiting deeper water he says " Il semble bien que le lac actuel n'est pas responsable ni capable de nous expliquer nne telle diversité."

By way of explanation he refers to changing conditions during the history of the lake and the well authenticated evidence of geographical isolation within the basin and concludes that the factors responsible for the formation of numerous endemic species are " les variations locales des conditions d'existences, parmi lesquelles la salinité, les variations de niveau de l'eau, donc de la profondeur d'habitat, et les variations de la nature du fond sont les plus importantes." He then goes on to say " Au cours des temps, les variations physico-chemiques des habitats, ont permit l'accumulation des espèces. Nous devons admettre, en effect, leur apparition successive dans des conditions locales successivement différentes. Dans la suite, la confluence des habitats ou l'uniformisation de leurs conditions d'existence a permis le mélange des espèces et leur co-existence au sein d'associations polyspécifiques extraordinaires telles qu'on les observe de nos jours." No explanation of how these " associations polyspécifiques extraordinaires" manage to survive in apparently stable communities is offered, nor is it made clear how the various species " accumulated ", and the so-called " uniformisation " of conditions seems to be a somewhat nebulous concept.

The following account, while in general agreement with some of Poll's ideas, differs in many ways ; particularly in that it seeks to describe in detail how ecological studies, when related to the results of genetical research, enable the origin of such associations to be explained without recourse to vague postulates about changing salinities, and also how, after being evolved, such communities can be maintained.

Before discussing these topics, however, it is necessary to review a few facts relating to the history and topography of Lake Nyasa.

The environmental background

Nyasa is an ancient lake. Its exact age is unknown, but according to the most recent paper by Dixey (1941) on the subject it is believed to have been first formed about the Middle Pleistocene. On the basis of radioactive determinations the duration of the Pleistocene period has been estimated as about 1,000,000 years (Zeuner, 1946). On this evidence the age of the lake would be only about 500,000 years. However, in an earlier paper Dixey (1938) states that " features broadly corresponding to the Nyasa Shire Rift (apart from the deep basin in which Lake Nyasa lies) . . . existed as far back as the late Jurassic or early Cretaceous ". Later, during Miocene times, an uplift occurred which was " accompanied or followed " by further rifting to which Dixey attributes the subsidence which gave rise to the basin now occupied by Lake Nyasa. On this evidence, therefore, the present lake could conceivably have come into being in Miocene or Pliocene times. If this were so, then on the basis of radioactive determinations (Zeuner, 1946) the maximum age of Lake Nyasa could be as much as 12 or 13 million years.

Whether or not the lake is as old as this it is not possible to say with certainty, but there does seem to be good evidence (in addition to that provided by its present day fauna) to show that it is older than Dixey's most recent estimate. This evidence is the occurrence of fossils, including molluscs and the remains of *Mastodon* and *Hippopotamus*, in lacustrine deposits (the

Chiwondo beds) in northern Nyasaland. On the basis of their fossil content these beds were originally assigned to the Pliocene (Hopwood, in Dixey, 1927), and Dixey (1932) speaks of them as being of " late Tertiary or early post-Tertiary age ". In his latest paper, however, Dixey (1941) quotes later work by Hopwood which suggests that they are not much older than Mid-Pleistocene. In a personal communication Dr Hopwood has kindly stated his present opinion on the age of these beds, the dating of which is entirely dependent on the inference to be drawn from their fossil content. Since the earlier estimates were made it has been possible to make comparison with more recently discovered deposits elsewhere, and the indications are " that one is probably not far wrong in placing the Chiwondo beds in the lower Pleistocene (=Villafranchian of Europe) ". It is to be noted that the Chiwondo beds rest, and not simply but with strong unconformity, upon other *lacustrine* strata which themselves must therefore have been laid down by Lake Nyasa. If one takes Zeuner's estimate of the duration of the Pleistocene as being correct, therefore, one must conclude that Lake Nyasa came into existence at least one million years ago and possibly a good deal earlier than this.

It is difficult for a zoologist to assess the significance of geological evidence such as is presented by Dixey and perhaps unwise for him to question its validity, but certainly an age of one million years or more, which must be attributed to Lake Nyasa on the basis of the fossils of the Chiwondo beds, is far more in accord with the zoological evidence presented by the present day fauna than is the figure of 500,000 years. The latter figure is even less than that attributed to Lake Victoria where differentiation of cichlid fishes has gone on to a much smaller extent than it has in Lake Nyasa.

Bearing in mind that, as is shown below, conditions appear to have been particularly favourable to speciation in Lake Nyasa, and also that in horses it seems possible that a change of generic magnitude could be effected in about one million generations (see Huxley, 1942, p. 61), a zoologist, without taking cognisance of any geological evidence, would probably favour an age much more closely approximating to the minimum (upwards of one million years) than to the maximum (about 12 million years) of the two possibilities indicated above. When the geological evidence and the degree of differentiation of the present day cichlid fish faunas of Lakes Victoria and Tanganyika are taken into account, an age of one to two million years seems not an unreasonable estimate for Lake Nyasa.

Geological evidence indicates that the lake originally occupied only the northern part of its present basin and that it stood at a considerably higher elevation that it does today (Dixey, 1926, 1941). Its present form and level were only arrived at after a complex series of downthrusts and faults. There must therefore have been many ecological changes during the history of the basin. Changes still take place today in the form of annual fluctuations in lake level, and rather longer term fluctuations of a similar kind, some of which, with a ten or eleven years cycle, are believed to be connected with sun spot activity.

Making allowance for its considerable irregularities, the total length of the shore-line of Lake Nyasa and its included islands probably exceeds 1000 miles (1600 kilometres). In the not very distant geological past it was even longer than this. This shore-line, while consisting of remarkably few major habitats (see p. 155) is nevertheless by no means uniform. It consists largely of alternating rocky shores and sandy beaches. Even in areas where rocky shores predominate these are frequently interrupted by sandy beaches, sometimes in the form of small coves, sometimes more extensive. This fragmentation of the major habitats along the shore-line is believed to have been of outstanding importance in the process of evolution of the Mbuna and of other fishes in the lake.

The configuration of the shore-line is not permanent even from year to year and must have changed considerably in places during quite recent times (geologically speaking). For example, what are now predominantly sandy shores many miles in extent along the alluvial Kota Kota plain were, in a not very remote epoch, under 150 feet of water, and the shore-line in that region may then have been much more rocky. It is also generally agreed that considerable fluctuations in the levels of African lakes took place during the pluvial and interpluvial periods which roughly correspond with the glacial and interglacial periods of the Pleistocene glaciation in the northern hemisphere. It seems highly likely that the present day islands of the lake such as Likoma, Chisamulu, Benji and Boadzulu were connected with the mainland during these interpluvial periods, and that it was then that they received their fauna of rock fishes which later became isolated by a rise in lake level. Alternatively they could have become populated as the lake gradually extended southwards in comparatively recent times.

It is against such a background that the evolution of the Mbuna must be considered.

The process

The Mbuna are confined to rocky shores or, in the case of two species, to regions where rocks occur on sand. They are completely absent from sandy or reed-fringed shores. Even a small sandy gap in a rocky shore is a very effective barrier and it is safe to say that, in normal circumstances, a stretch of sandy beach twenty yards wide is quite sufficient to inhibit the movement of Mbuna across it. This is no wild supposition but a statement based on many observations in the field.

Similar effective barriers of small extent have been described by other writers. Thus Dowdeswell & Ford (1953) found that on small islands narrow windswept necks of land as little as 150 yards in length effectively prevented mixing of populations of the butterfly *Maniola jurtina* L. separated by them ; and butterflies are, on casual observation, much more prone to apparently haphazard and erratic movements than are the fishes of the Mbuna group which seem to be always either busily engaged among the rocks or to be cruising slowly and unhurriedly from rock to rock.

The Mbuna of the lake do not, therefore, form by any means continuous populations. Each species is broken up into innumerable populations of various sizes which are isolated to a greater or lesser extent. Over long periods of time changes in the lake level and the silting effects of inflowing rivers will result in the removal of barriers and the formation of new ones, with attendant mixing of previously isolated populations and the fragmentation of previously continuous populations.

All the evidence from field studies and from mathematical reasoning points to these conditions as being ideal for speciation of the allopatric kind. Thus Wright (1943) has shown that linear continuity of distribution is much more favourable to differentiation than is areal, and (Wright, 1949) that the most favourable conditions for progressive evolution are to be found where a species is broken up into large numbers of small local populations.

Of variation in nature in different parts of the range of an animal there is abundant proof. Work by Tonolli and others in Italian lakes (summarised by Baldi, 1950) has shown that even within a continuous population of planktonic organisms within a single lake, morphological differences, some of which probably have a genetic basis, can be detected in crustaceans collected from different stations. That the Mbuna vary from place to place can also be demonstrated. For instance the frequency of the genes responsible for the development of the different colour forms of *Pseudotropheus zebra* obviously varies in different parts of the lake (see p. 247). Another striking case concerns the populations of *Cynotilapia afra* at Nkata Bay and at Likoma Island. Members of the Nkata Bay population are very readily recognisable in the field by the presence of a lemon-yellow dorsal fin, the only exceptions noted among literally thousands which have been seen being two juvenile specimens in which, after capture, the dorsal fin was dull grey. At Likoma Island this fin is blue, and not a single yellow fin was noted in the field although many hundreds of individuals were seen. Apart from this the members of the two populations are indistinguishable in structure and habits.

Similarly, at Likoma Island a small percentage of the males of *Pseudotropheus tropheops* had a very striking patch of orange-gold colour on the shoulders and the upper part of the head, but no such patch was ever seen among the thousands of *P. tropheops* seen at Nkata Bay though a similar but smaller and less conspicuous trace of yellow occurred in some males of this species seen and captured at Ruarwe forty miles to the north and was also seen in one male at Kajizinge only about seventeen miles to the north. Examples of this kind could be multiplied,* but the cases mentioned show that genetic variation from place to place is not uncommon in the group.

In the early stages of colonisation of the lake the algal eating ancestors of the Mbuna would begin to colonise the rocky shores. As the niches to be found there would be unoccupied this would presumably be a relatively easy process. As time went on these fishes would gradually become more and more specialised to life among rocks and partly because of this and partly because of the effects of competition with those species of fishes (ancestors of the present-day *Haplochromis* etc.) which were colonising the sandy shores, would become more and more restricted to this kind of habitat. Thus would come into being a state of affairs similar to that seen today in which the fauna

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* An example mentioned elsewhere which involves a structural feature is that of slight differences in the tips of the teeth of specimens of *Gephyrochromis lawsi* in populations at Nkata Bay and Florence Bay (Fryer 1957a).

was split up into innumerable isolated populations. These isolated populations would vary in size, some being large, others small, according to whether they occupied long rocky stretches or isolated outcrops.

Now it has been shown that in small isolated populations, i.e. populations in which the possibilities of panmixy are limited to a few individuals, there is a tendency towards a rapid change in genotype. Some of the cases cited in the literature are attributed to the effects of natural selection, others to the *accidental* concentration of certain genotypes (genetic drift). Dobzhansky (1951) cites a particularly pertinent case studied by Kramer and Mertens in which it was shown that certain islands in the Adriatic Sea whose lizard fauna had been derived from the mainland stock, had recognisably distinct populations and that the populations on small islands had diverged more than had those of large islands of the same geological age. Dobzhansky is of the opinion that such phenomena " can most plausibly be accounted for by genetic drift."

The period of time during which genetic changes can take place in small populations is sometimes remarkably small. Thus Dowdeswell & Ford (1953) found that on the small island of Tean in the Scilly Islands the period involved for " a significant change in spot distribution " on the wings of the butterfly *Maniola jurtina* was only five years ! Dowdeswell & Ford believe that the population was too large for genetic drift to be the responsible agent and attribute the change to natural selection. Similarly, in a population of the moth *Panaxia dominula* L. the frequency of a single gene changed from about 10 per cent to 3 per cent over a period of only about seven years (Sheppard, 1953). Here opinion is divided as to whether drift or selection is responsible.

Irrespective of whether drift or selection is the causal agent, the cases cited demonstrate quite clearly that changes in genotype can occur very quickly in isolated populations.

So far as the Mbuna are concerned it is conceivable that drift has been responsible for some of the minor differences to be seen in isolated populations, but in the last analysis it must be conceded that natural selection has undoubtedly played the more important part in their evolution, for the remarkable array of specialised adaptations to be seen in these fishes can scarcely be conceived as having come into being through the agency of drift.

There is also plenty of evidence to show that populations separated by only short distances may be quite distinct (e.g. see Dobzhansky, 1951, Blair, 1950).

A further fact also needs to be borne in mind. Fluctuations in numerical abundance occur in all populations which have been adequately studied and no doubt during their long history the Mbuna populations have been subjected to similar fluctuations. The effects of such fluctuations on small populations, such as exist and presumably always have existed among the Mbuna, have important evolutionary implications as was shown by the remarkable study of Ford & Ford (1930) on an isolated population of the butterfly *Euphydryas* [*Melitaea*] *aurinia* (Rottemburg) (see also Ford, 1945). Within a period of a few years the genotype of this colony changed quite noticeably after a period during which its numbers were greatly reduced. The evolutionary importance of this kind of process has been emphasised by Tschetverikov (cited by Timofeeff-Ressovsky, 1940) and by Elton in a series of papers from 1924 onwards.

At this point the tropical location of Lake Nyasa can also be emphasised, particularly as Manton (1953), as a result of cytological studies on the fern floras of Britain and Ceylon has stated that " the first conclusion which seems to me to be inescapable is that evolution must be proceeding faster in the tropics than in temperate latitudes ". Although some of the reasons which she puts forward to explain this greater rapidity of evolution in the tropics are applicable particularly to plants, some would apply to all organisms. Tropical conditions also have effects other than those described by Manton, particularly in aquatic environments. Most temperate zone fishes breed only once a year, while the Mbuna produce several broods per year. Even if they produced only two broods per year a genetical change could, theoretically, spread through a population twice as fast as through a similar population breeding once a year.

Moreover, the Mbuna are examples of fishes which exhibit parental care. Dobzhansky (1951) develops the thesis that those animals (particularly mammals, birds and hymenopterous insects) in which parental care is most highly developed are just those groups in which evolution is proceeding most rapidly. His reasoning can well be extended to include the fishes of the family Cichlidae.

The breeding behaviour of the Mbuna involves a distinct courtship before the gametes are shed. It is possible that, during periods of isolation, peculiarities of courtship behaviour, perhaps even imposed by the environment, could be acquired which became characteristic for members of that population and could prevent interbreeding should two potentially inter-fertile populations become mixed. It seems probable that such a mechanism could be more easily acquired than a cytological sterility barrier. As Dobzhansky points out (1951), the minimum number of genes that can form a workable isolating mechanism is two. It is not claimed that the number is anywhere near this in the Mbuna—and it seems very unlikely that it is—but the undoubtedly rapid evolution undergone by cichlid fishes perhaps indicates that interbreeding in nature is more readily prevented than in certain other groups.

The situation probably was, then, that the early Mbuna were distributed in the proto-Lake Nyasa under conditions which were as near to the ideal for evolutionary divergence of the allopatric kind as might reasonably be expected in nature, and that they possessed certain characteristics which, potentially at least, could facilitate rapid speciation.

Reference to the means whereby mixing of previously isolated populations could take place has already been made, but two further possibilities merit consideration as both may have been of great importance. Although the Mbuna are stenotopic and show a marked avoidance of non-rocky shores it is not to be doubted that there must have been occasional migration across barriers, some perhaps accidental and, more important, some deliberate, e.g. when a successful form began to overpopulate a given habitat. The importance of such " population-breakers " is emphasised by Timofeeff-Ressovsky (1940). See also Spurway (1953).

Again, during its history the lake basin has been subjected to many changes and, particularly during such periods as the lake spread to new areas (which happened on at least four occasions according to Dixey (1926)), there could become opportunities for colonisation on a grand scale as is seldom the case in stable habitats. The importance of vacant niches during the early stages of colonisation of a lake was emphasised by Worthington (1940) and it is interesting to note that Manton (1953) believes that many of the newer species and polyploid races of European plants resulted from a similar opportunity for colonisation when the retreating ice of the last glaciation laid bare large areas of unoccupied ground. Increases in the size of the lake with its attendant opportunities for colonisation would give new forms an unprecedented chance of becoming established, perhaps even more so than in the very early stages of the lake's existence as by this time the fishes already present would have acquired certain specialisations which would enable them to exploit all the more readily the new areas to which they gained access.

So far we have considered only in general terms the evolution of new types. It is now necessary to see if we can discern the means whereby fundamentally new ways of life such as plankton-feeding and scale-eating could be evolved and also how species with similar habits could take on a sympatric distribution and yet remain distinct. The evolution of plankton feeding will be considered first.

All rocky shores, while fundamentally alike, are not identical, some being gently shelving, others being precipitous. Imagine then, a population of fishes rather like *Pseudotropheus zebra* which, as a result of some environmental change, became isolated on a precipitous rocky shore. The amount of food produced on the rocks would be limited and necessity would cause them to exploit the other available source of food—plankton—or perish. After prolonged isolation the habit of plankton feeding could become so much a part of the make-up of the organism that adaptations towards its perfection would be selected and could become genetically fixed—so much so that the species, for such it would then be, could persist in this habit and remain distinct if it later succeeded in colonising rocky shores where plankton feeding was not obligatory.

Scale-eating may well have arisen under conditions of food scarcity when the scales of its fellows were one of the few sources of nourishment available to the species which began to adopt this habit. The evolution of such a habit can be more readily visualised as taking place subsequent to the acquisition of genetic uniqueness than as the result of a change in habits of part of a sympatric population. As pointed out elsewhere (Fryer, *et al.* 1955), there is no great difficulty in visualising a change in habits from rasping algae from rocks to rasping scales from fishes, and no great morphological changes are involved.

Topographical differences in rocky shores also probably helped to determine the micro-habitat preferences of certain species such as *Pseudotropheus fuscus* which, at Nkata Bay, is virtually confined to a very narrow strip only a few metres in width along the margin of the shore, although very similar conditions exist over a much wider zone. Such habits could have been evolved on a steeply shelving shore where only a very narrow zone at the lake margin offered a sufficiency of food. On colonising other shores after a period of isolation, the form evolved under such conditions would tend to seek out such a niche although wider possibilities existed. This tendency would be reinforced by the ever increasing competition between species, and a species such as *P. fuscus* which had become specially adapted to life in the most inshore strip may have been unable to compete successfully with other species living in slightly deeper water. As a result mutations leading to a better exploitation of the microhabitat in which it was already successful would be selected.

Competition may well have been very important in influencing the choice of habitat by *Cyathochromis obliquidens* and *Pseudotropheus lucerna.* Their present-day habitat "preferences" may have arisen as a result of a period of isolation on a shore on which rocks occurred among sand during which they became adapted to such conditions. It seems equally probable, however, that, as suggested on pp. 228 and 229 their present-day habitats are frequented less from choice than from necessity, and that they may have been driven from the true rocky shores by other species occurring there and have succeeded in establishing themselves in a niche where the effects of competition are less severe.

A similar state of affairs exists in the case of *Pseudotropheus williamsi.* This species, while very rare on the shore most carefully studied, is not particularly rare in the area as a whole, and several specimens have been observed in rather quiet " pools " on other shores. Restriction of this kind could be due to having acquired special habits in isolation, or to the effects of competition.

As genetically distinct populations came together no doubt some species were forced into those niches to which they were best adapted, and others probably became extinct. However, among the herbivorous members of the group there can be found today several species whose general habits are all very similar, whose horizontal and vertical ranges in no wise differ, and which, although they collect it by different means, eat identical food. The failure to find any differences in ecology between these species does not mean that they do not exist, but it can be fairly claimed that sufficient has been learned about them to indicate that if such differences do exist they must be exceedingly small. In this respect some of the Mbuna do not conform to the so-called Gaussian hypothesis that closely allied species cannot co-exist in the same niche. Indeed they present a much more marked example of co-existence than for instance do the endemic species of *Tilapia* studied in Lake Nyasa by Bertram, Borley & Trewavas (1942), Trewavas (1947) and Lowe (1952, 1953) where distinct differences in habits can be discerned. In this respect too they differ markedly from Darwin's finches, with which they otherwise show many remarkable parallels. In passerine birds closely related species usually occupy different habitats or, if they co-exist in the habitat, they take different foods and/or are different in size. (Lack, 1944, 1949). (Latter paper summarises several studies). In Darwin's finches some species live side by side but differ in size of beak and apparently take different foods, and therefore occupy different niches. This is not so in certain cases among the Mbuna.

The co-existence of so many closely related species which have similar habits appears all the more remarkable when the competitive relationships of species with similar ecological requirements elsewhere are considered. Thus a similarity in ecology between representatives of even different genera is sometimes sufficient to render them mutually exclusive, as is the case of the birds referred to in common speech as flycatchers in the Tonga Islands. Here, according to Mayr (1933), each island has one, and only one, species of flycatcher which may be a member of either the genus *Clytorhynchus* or of the genus *Pachycephala*. No island has representatives of both genera. This state of affairs is quite different from that prevailing on rocky shores in Lake Nyasa.

Co-existence among the Mbuna seems to be possible for two reasons—the existence of a superabundance of food and the effects of predation. On rocky shores there is a superabundance of algal food so that any reasonably efficient species utilising this source of food can obtain sufficient of it without having to compete with its neighbours (see p. 226). Such a state of affairs, however, seems to be dependent upon the presence of predators. Worthington (1937, 1940, 1954) has postulated that the presence of active predators has had a restrictive effect on adaptive radiation in African lakes. My studies on the Mbuna have led me to an entirely different conclusion. Piscivorous fishes are extremely common in Lake Nyasa (Fryer & Iles, 1955) and, like the other habitats, rocky shores have their quota. Now the fish fauna of rocky shores is almost unbelievably dense (p. 164) and, as the food supply of the non-predacious species is not limited, it seems that they could increase in numbers even more but for the predators. Increase in numbers would lead to increased competition and the possible elimination of certain species. The predators, however, by controlling the population density, will limit such competition and therefore favour the survival of certain species.

The obvious weakness in this argument is that predation is theoretically selective and that some species will more easily fall victim to predators than others. This may be so, but the fish fauna among the rocks is so dense and the various species present are so much alike in general habits that a predator will almost always tend to eat the fish which it encounters most often. In other words the most abundant species will furnish the major portion of the diet of the predators, and this will thus facilitate the survival of those species whose ability to increase is less. However unorthodox my stand I firmly believe, therefore, that in this case the presence of predators is one of the main reasons why so many species are able to co-exist and persist.

A comparable case is that described by Sokoloff (1955) who attributes the ability of two very closely related species of *Drosophila* larvae to co-exist in the slime fluxes of trees to the effects of predation on ovipositing adult females, and to the interference with ovipositing females by other insects, which keeps the fly population at a reasonably low level and thus obviates competition.

The idea that two species with similar demands on the environment might be able to live in the same habitat without competing if their numbers were controlled by predators or parasites was put forward by Lack (1949) in a paper which I had not seen until my conclusions were reached. It is interesting to see that Lack regarded his suggestion as purely theoretical and in fact says that " this situation seems to be rare or non-existent in birds ". It seems probable, however, that such a state of affairs does indeed exist among the Mbuna.

A different effect of predation, but one which nevertheless " becomes a major factor in the survival of the species " is cited from the work of Cartwright on the effects of predation on game-birds in Canada in the book by Allee, Emerson, Park, Park & Schmidt (1949) (p. 376) to which reference should be made for details.

There is thus no reason to call on sympatric speciation to explain the evolution of the Mbuna. Indeed, if sympatric speciation took place then it is very difficult to see why or how several different specialisations towards a single way of life—scraping algae from rocks—were evolved ; yet this can easily be imagined to have taken place in isolated populations which would utilise whatever mutations presented themselves for the exploitation of the most obvious means of survival.*

The overlap of formerly isolated, related species without interbreeding has numerous parallels in other groups e.g. see the interesting case of co-existing subspecies of the mayfly *Stenonema interpunctatum* studied by Spieth and cited by Mayr (1947), the only difference being that the isolation in these cases has usually been macrogeographical whereas in Lake Nyasa it was microgeographical. Brooks' (1950) concept of intralacustrine geographical barriers has shown itself to be no mere abstraction during the recent field work. There is some evidence, still incomplete, that some species have evolved in certain parts of the lake and have not yet been able to colonise all available habitats, this seemingly being the case in the genus *Melanochromis* whose virtual absence from the Nkata Bay area is rather striking.

It seems probable that closely related species living together are isolated at least in part by ethological factors, and it is most striking that, in three cases of pairs of very closely related species, the members of a pair differ markedly in coloration. Thus *Pseudotropheus fuscus* and *P. auratus* which, although they have rather different horizontal ranges, must often meet, differ most strikingly in coloration, *P. fuscus* being, even in breeding dress, rather sombrely coloured while *P. auratus* has the very distinctive coloration (black on gold in the female ; blue on black in the male) described on p. 243. The same is equally true for the not very strikingly coloured *Labidochromis vellicans* and the remarkable cobalt blue and black *L. caeruleus* (Fryer, 1956 a). The third case is that of *Pseudotropheus zebra* and *P. livingstonii*. The three males of *P. livingstonii* captured were all bright golden orange in colour with indistinct dark vertical bars ; this coloration differing markedly from that of any of the three types of male coloration found in the very closely related *P. zebra* (p. 245).

This state of affairs seems to be a parallel to the remarkable cases of co-existence of numerous species of butterflies of the genus *Lycaena* studied by Peterson and crabs of the genus *Uca* studied by Crane both of which are quoted by Mayr (1942). " Selective mating " probably plays an important part in keeping the various species distinct, but its usual method of operation is to maintain distinction when once acquired and not to promote it.

Of particular interest in this connection is a case which, at first sight,

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* It is only fair to mention that this conclusion is diametrically opposed to that reached by Stanković (1955) who has recently assessed the evidence appertaining to speciation in L. Ohrid whose fauna is one of the best studied of all those of the world's ancient lakes. Nevertheless, the information now to hand concerning the ecology of the Mbuna seems still best interpreted in terms of allopatric speciation.

appears to be at variance with the above suggestion ; namely that of the two extremely closely related species of *Labeotropheus* which do not appear to be separated by colour differences in this way. Here, however, there is a difference in the incidence of the OB pattern in the female, at least in the populations sampled. Fifty per cent of the small sample of available females of *L. trewavasae* exhibit this pattern as opposed to none or, if the " peppered " pattern be regarded as the same as the OB pattern, about 3 per cent of the females of *L. fuelleborni* (Fryer, 1956 d). It is very tempting to suggest that here, where specific distinction has obviously been only recently acquired, a tendency towards fixation of different colour types is beginning to exert itself and that the OB pattern is being utilised by *L. trewavasae* for this purpose. The facts are not opposed to this view but bigger samples of *L. trewavasae* are needed to establish it.

In addition to separation by colour differences the possibility that closely related species are prevented from interbreeding by the production of different chemical secretions which attract like and frighten unlike species, as was suggested at an infraspecific level by Steinmann (1953), must be borne in mind. The Mbuna would lend themselves particularly well to aquarium studies whereby this possibility could be tested.

Mayr's concept of multiple colonisation (1942, 1947), while unacceptable in its original form so far as the Mbuna are concerned, if considered at a different level provides a picture of what is believed to have taken place during the evolution of the group. If one thinks of a rocky shore as an island being successively invaded from other islands instead of visualising the lake as a whole being a single unit successively colonised from rivers, then one has the story of the Mbuna in a nutshell.

SUMMARY OF PART II

An account is given of the biology, ecology and evolution of a group of closely related fishes which inhabit rocky shores of Lake Nyasa, to which lake they are confined. The group, which is believed to be monophyletic in origin, and which is spoken of as the " Mbuna ", is defined.

Some species are structurally stable ; others are very variable. Although there is a basic colour pattern the actual coloration is very variable both between, and sometimes within specific units. This colour variation, sexual dimorphism and colour polymorphism are discussed.

Notes are given on the distribution, general ecology, habits and food preferences of the group as a whole and of individual species. All species are to a greater or lesser degree bound to rocky shores; sandy beaches constituting very effective barriers to inter-habitat migrations.

Males become territorial during the breeding periods. There is a definite courtship behaviour before laying and fertilisation of the eggs which are subsequently carried in the mouth of the female, which continues to brood the resulting young at least until the yolk sac is absorbed.

There is no definite evidence to indicate the existence of intraspecific homogamy.

Competition for breeding grounds (territories) seems to be obviated by

" continuous " breeding throughout the year, only a small percentage of the population requiring territories at any one time.

The adaptive radiation of the group is summarised and an attempt is made to trace the origin of the Mbuna, the phylogenetic relationships of the various species, and the evolutionary history of the group as a whole.

From the known geological history of Lake Nyasa the history and distribution of environments populated by Mbuna is reconstructed. Against this background the probable sequence of events during the evolution of the various species of Mbuna is reconstructed from the knowledge of the structure, ecology and habits of the present-day species. The evidence is wholly compatible with the theory of allopatric speciation, and there is no occasion to to have recourse to the theory of sympatric speciation to explain the evolution of the group.

The effects of predation on the maintenance of dynamic balance is pointed out. Predation, by keeping a check on the numerical density of populations, obviates interspecific competition and favours the survival of individual species.

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* Original not seen.

APPENDIX 1

Distribution of Mbuna around Lake Nyasa. North end refers to specimens from North of latitude of Ruarwe ; South end to South of Cape Maclear. (Based on Trewavas (1935) and personal records).

	North End	Eastern shore	Western shore	South End
Labeotropheus fuelleborni	x	x	x	x
Labeotropheus trewavasae			x	
Labidochromis vellicans		x	x	x
Labidochromis caeruleus			x	
Petrotilapia tridentiger		x	x	x
Pseudotropheus tropheops	x	x	x	x
Pseudotropheus novemfasciatus	x			x
Pseudotropheus auratus		x	x	
Pseudotropheus fuscus			x	
Pseudotropheus fuscoides			x	
Pseudotropheus elongatus		x	x	
Pseudotropheus minutus			x	
Pseudotropheus zebra	x	x	x	x
Pseudotropheus williamsi			x	
Pseudotropheus livingstonii			x	x
Pseudotropheus elegans	x			
Pseudotropheus lucerna	x		x	
Cyathochromis obliquidens	x	x	x	x
Cynotilapia afra		x	x	
Melanochromis melanopterus			x	x
Melanochromis vermivorus				x
Melanochromis brevis				x
Melanochromis perspicax	x			
Melanochromis labrosus	x			
Genyochromis mento			x	x
Gephyrochromis moorii	x	x		
Gephyrochromis lawsi	x		x	

APPENDIX 2

Number of eggs or young brooded by females of some species of Mbuna. (Only specimens captured by stunning, which retain the full complement of eggs or young, are considered).

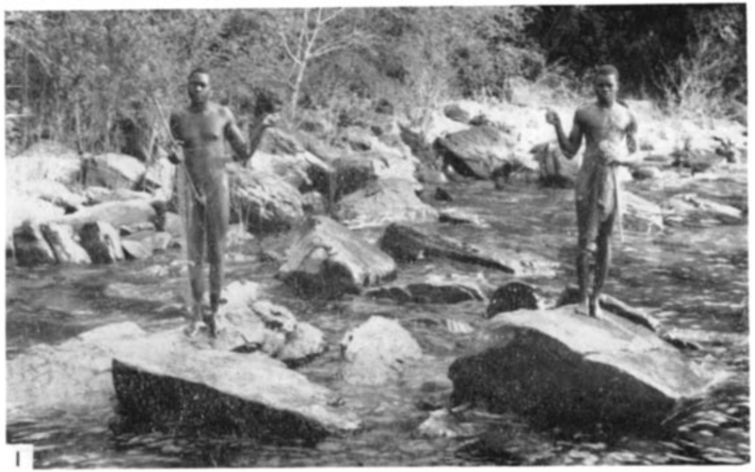
Species	Total length (cm.)	No. of eggs	No. of young	Approximate Length of young (mm.)
Pseudotropheus tropheops	10·7		26	12
,, ,,	10·0	28		
,, ,,	9·2		15	8
,, ,,	10·2		15	14–15
,, ,,	9·5	27		
Pseudotropheus fuscus	10·1		46	11
,, ,,	9·1		32	10
Genyochromis mento	10·5		34	12
Labeotropheus fuelleborni	11·3		18	8
,, ,,	12·1	22 (occluding)		
,, ,,	12·3		23	12
Labeotropheus trewavasae	9·9	10		
,, ,,	10·6		22	15–16
Labidochromis vellicans	6·2		10	8

ADDENDUM

Since the above was written Moreau & Southern (1958) have given an account of polymorphism among birds in what possibly represents a single species of Shrike of the genus *Chlorophoneus*, which bears so many striking similarities to the state of affairs existing in *Pseudotropheus zebra* that the parallelisms are worthy of emphasis. As in the case of the cichlid fish "the occurrence of the various colour phases and the proportions in which they appear in the various local populations vary without apparent correlation." Again, as in *P. zebra*, "the extent to which neighbouring populations differ in regard to the phases represented bears no relation to the distance or to the severity of the ecological barriers between them." Moreau & Southern found it impossible to suggest any adaptive significance in the differences between the various populations.

REFERENCE

Moreau, R. E. & Southern, H. N. (1958). Geographical variation and polymorphism in *Chlorophoneus* shrikes. *Proc. zool. Soc. Lond.* **130** : 301–328.



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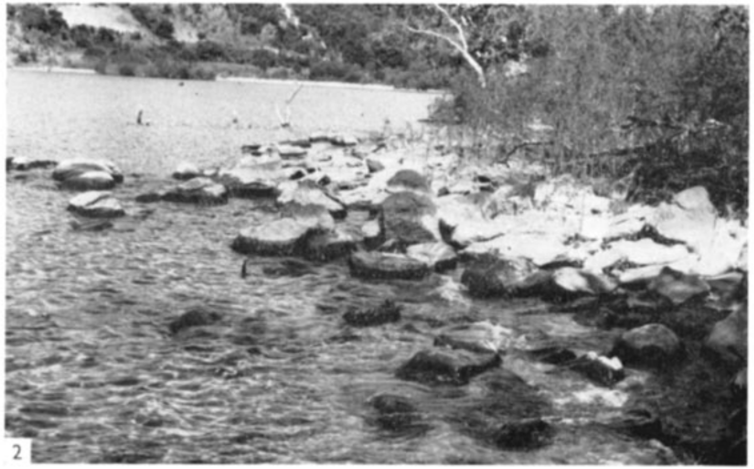

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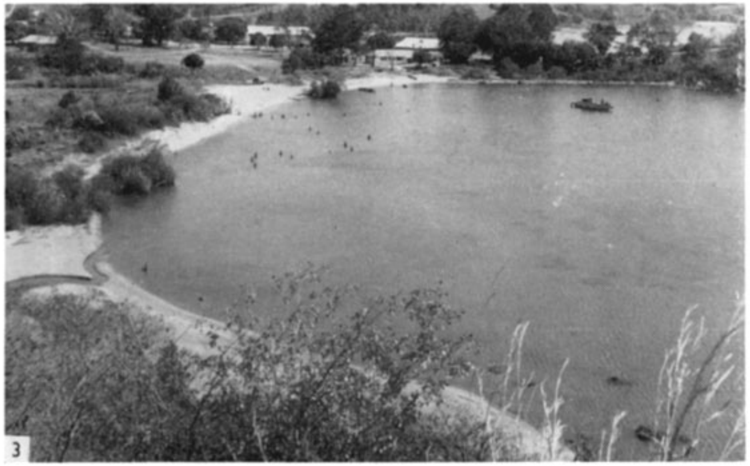
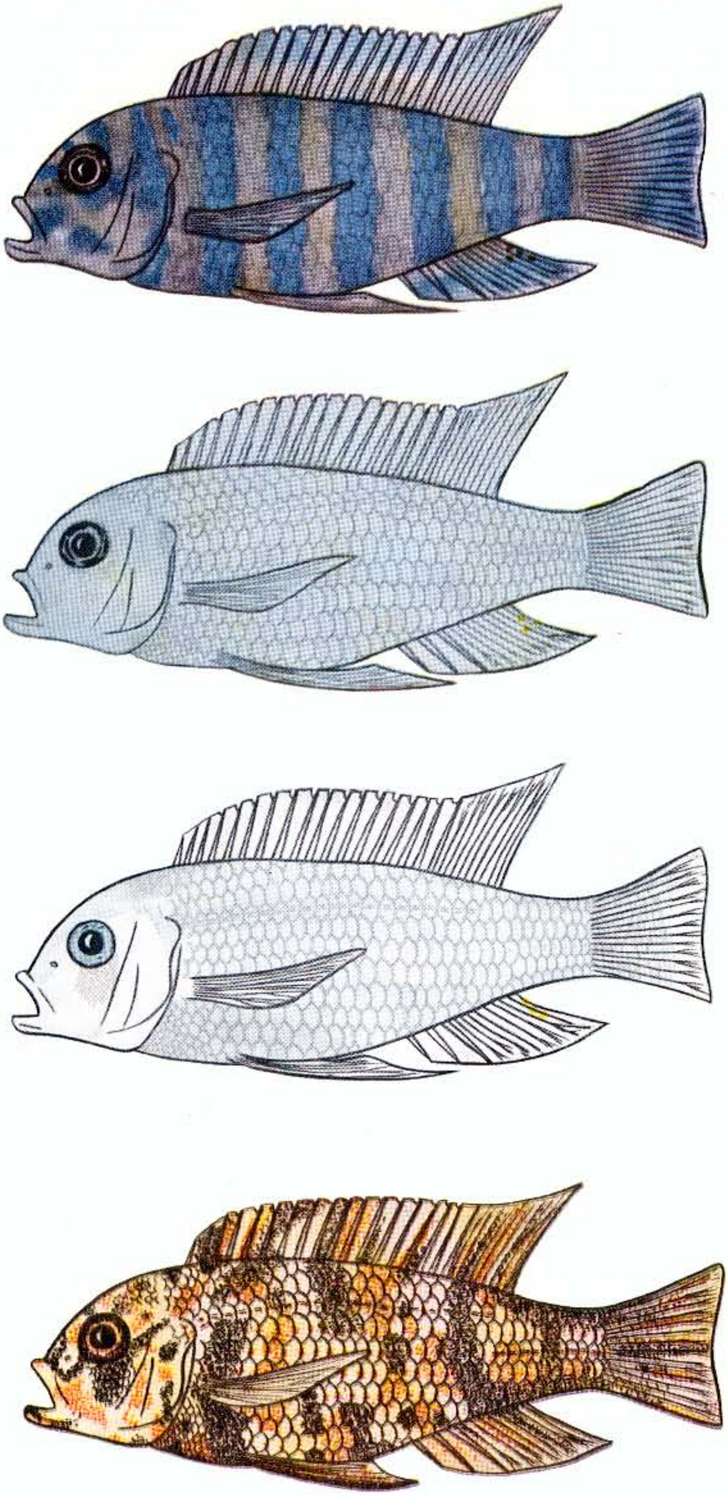


3

4

Physiographic features of the area studied.

Figs. 1-2. The rocky shore.
Fig. 3. The sandy shore.
Fig. 4. The intermediate zone.



The four colour-forms of *Pseudotropheus zebra* (Boulenger)

EXPLANATION OF THE PLATES

PLATE 1

Fig. 1.—The rocky shore. This photograph gives a good impression of the general configuration of the rocky shore. The net held by the two youths is that used for the capture of fishes among the rocks described in the text.

Fig. 2.—The rocky shore, with the sandy shore in the background. The clarity of the water can be appreciated in this and the preceeding photograph.

Fig. 3.—The sandy shore. The outlet of Crocodile Creek can be seen in the foreground, and the intermediate zone in the distance, immediately behind the boat. The dark patches to be seen in the water are beds of *Vallisneria.*

Fig. 4.—The intermediate zone. The large outcrop of rock marks the commencement of the rocky shore.

PLATE 2.

The four colour-forms of *Pseudotropheus zebra* (Boulenger).