Observations on Fishery Management in Africa¹

KENNETH D. CARLANDER²

Abstract. Fisheries personnel in Liberia, Nigeria, Ghana, Sudan, Uganda and Egypt were visited in March and April 1965. Harvest of fish from the sea, lakes and rivers is being improved through improved boats, motors, and docking marketing facilities. High dams on the Nile and Volta Rivers are providing new fishery resources which will require research and development of new techniques. Flooded vegetation has caused oxygen depletion in the Volta Reservoir. The dams will also interfere with spawning of fish and clams downstream, and the Nile dam has already reduced the catch of sardines in the Mediterranean. Fish culture is hindered by lack of experience and research and by shortage of supplemental foods. Africanization of the fisheries depart-ments has often displaced trained biologists before their counterparts could be trained. Attention is being given in each country to the training of fisheries personnel, but out-side help will be needed for many years.

A 2-month visit in eight African countries does not qualify me as an expert, but my opportunities to meet fishery biologists gave me an insight into some of the fishery problems. In March and April 1965, my wife and I visited fishery laboratories and personnel in Liberia, Nigeria, Ghana, Sudan and Uganda. We also visited Ethiopia, Kenya and Tanzania but saw little of their fisheries. Then we were in Egypt for 7 months to develop a university program for training fishery biologists.

In each of these countries fish have been harvested for centuries by techniques that are still being used. The catch per fisherman is usually small, but in some localities the number of fishermen is so high as to harvest all the fish that could be taken

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with more efficient gear. The yield might be increased if there were less intensive harvest, but is it difficult to limit the fishing pressure because there is no other profitable employment available for the displaced fishermen. Furthermore, there are not adequate data on the fisheries to prove the value of less intensive fishing, nor the degree to which the effort should be reduced. That most of the fish are caught before they reach adult size suggests overfishing in some areas.

Protein is deficient in the diets of most of the poorer people in all of these counties, and improved fisheries could provide high quality protein. Improvement of the fisheries must usually be accompanied by improvements in agriculture, education, industry and other aspects of the economy.

Lack of freezers and ice means that the fish must be sold locally and quickly. The quality of the fish in the markets is usually very good because of the necessity of selling the fish within hours of their capture. The small sizes of the catches and selling of most fish in small lots facilitate maintenance of quality. In areas some distance from sources of fresh fish, the people are not used to fish and have to be educated in their use when supplies are brought in.

MARINE FISHERIES

Marine fisheries along the coasts of the West African countries have expanded significantly in recent years, through introduction of larger boats and of techniques for deep-water fishing. Since fisheries require significant capital, most of the advance has come through governmental help through a few large companies. Much of the offshore fishing is done by non-African vessels. Canoes made from large hollow logs are still widely used even in the sea, however.

The Fishery Department of Ghana has provided many facilities at the new fishing port in Tema. There is a boat-building facility where 40 and 60-foot trawlers are built of native lumber and sold under favorable terms and prices to commercial fishermen, and a shop where fishermen's motors are repaired free, except for the cost of parts. The trainees from this shop are then helped to establish repair shops in other ports. There is also a fisheries laboratory where biological data and catch statistics are collected to guide future management. Department biologists also collect fishery statistics at two of the six other marine fishing ports.

LAKES AND RIVERS

There are few natural lakes in West Africa, but East Africa has many fisheries on their Great Lakes. We saw only Lake

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Victoria, some parts of which show signs of being over-fished. The main body of the lake is too dangerous for small boats and has fishery resources not now being utilized. The Uganda Department of Fisheries has been experimenting with a catamaran, made by lashing two fishing boats to a frame, for greater safety in fishing the open waters. They have also developed an improved boat for Lake Victoria. The large trees used for dugout canoes are becoming quite scarce in the area. The new boats are being built of mahogany and are sold to the fishermen below cost. The carpenters, upon certification after 5 years of training, are helped to establish boat-building shops in other areas.

On these larger lakes the fish cannot all be sold fresh locally. Hickling (1961, pp. 186-192) described the large processing plants, for drying and for freezing fish and for producing fish meal at Lake George, established in 1949 by The Uganda Fish Marketing Corporation (TUFMAC). We did not see these but saw fish drying on racks at Entebbe and the pilot project for canning the abundant but small *Haplochromus* spp.

The East Africa Freshwater Fisheries Research Organization in 1947 established a laboratory at Jinja, Uganda, where the White Nile leaves Lake Victoria (Hiatt, 1963). The British Commonwealth supports the laboratory as a "Common Services" contribution to Uganda, Kenya, and Tanzania. Two of the five biologists we met were Ugandans, recent graduates of Makerere College.

Rivers are the principal natural freshwater fishing area in West Africa. Rivers are difficult to manage, and not much has been done to improve their fishery resources. The largest river fishery we saw was on the Nile at Khartoum. An improved fish market has been provided by the fishery department here. Where production is greater than the local fresh fish market can consume, fish are sundried or preserved with salt.

IMPOUNDMENTS

Several large dams are planned or are under construction to provide electrical power for industrialization. We visited the Volta River Project in Ghana and the High Dam at Aswan, Egypt, where two of the largest man-made lakes in the world are beginning to fill. Studies are started on each lake to aid in developing and improving the fishing. Fish show the fast growth typical in new impoundments. The fishermen, however, have to learn new techniques to fish the large lakes and need safer boats and new types of gear. Access roads, docks and storage facilities are needed for proper development of the fisheries on these reservoirs. The Volta River Reservoir floods a tropical

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jungle area, and the inundated vegetation has already caused serious oxygen depletion and fish-kill. The flooded forests will also interfere with many types of fishing gear. A few small areas have been cleared before inundation so that they can more readily seined. The Aswan Reservoir floods a desolate desert area with only a narrow band of vegetation along the river channel.

Many villages have had to be resettled to clear the area for the lakes (about 70,000 people in Ghana and 40,000 in Egypt). Many of these people fished the river and know little about fishing in lakes. As the lakes become established new villages will develop along the lake shore, where fishery facilities may be constructed. The dams also affect the fisheries below. Many of the river fishes spawn in the shallow areas following floods. Control of the floods may greatly reduce reproduction of these fishes. It is known that the Nile River floods are an important source of nutrients in the Mediterranean Sea and that the sardines concentrate in the enriched areas each year after the floods. This last year, when the Nile flood was controlled by the Aswan Dam, the sardine fishery was very poor. In Ghana, there is an extensive freshwater clam fishery that will probably be eliminated by the Volta River Dam, because the clams, Egeria radiata, spawn in the delta area during the floods, which will now be controlled. This clam fishery and others on the lower Volta are also threatened by a large tannery which expects to put its untreated wastes into the river. Increased industrialization will greatly increase the dangers of pollution in many waters in these countries. As yet, little attention has been given to pollution control.

FISH CULTURE

The raising of fish in small ponds would seem to have the greatest promise for increasing fish production in areas where more protein is needed in human diets. Locally produced fish do not need extensive storage and transportation facilities. In general, fish farming has not been particularly successful in Africa. We did learn of the Panyan fish farm in Nigeria where an Austrian fish culturist, Mr. Zwelling, has successfully reared carp and other fishes in 80 acres of ponds. Isolated ponds elsewhere have been quite successful, but much more research and public demonstration are needed. The most extensive research program we saw at the Kagansi Fishery Station near Entebbe, Uganda, where Yoel Pruginin from the F.A.O. is experimenting with hybrid Tilapia, and with Nile perch as predators to keep Tilpia from becoming overabundant. We also visited the brackish water fish culture station at Bugumo, Nigeria, established with help from the F.A.O.

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AFRICAN FISHERIES

Several fish culturists believe that supplemental feeding is needed to raise enough fish to pay the costs of constructing ponds. Most of the African areas lack excess food products which can be economically fed to fish. In Liberia, Peter Youn has shown that rubber tree seed, a surplus product in Liberia, can be used as a fish food, but efficient methods of harvesting and preparing the seeds have not yet been developed. One pond owner was using brewery wastes, which seemed to give good growth but which are probably too expensive for general use. In Ghana we saw ponds where Chinese fish culturists were feeding fish coconut meats from which oil had been extracted.

The best opportunities for successful fish farming are in areas where ponds can be constructed as part of the agricultural land use program. Near the Agricultural Station in Liberia, storage of water in ponds permits a second crop of vegetables or rice, with irrigation during the dry season. The cost of pond construction can thus be justified by the additional farm crop as well as the fish crop.

FISHERY PERSONNEL

Fishery biologists and administrators in these countries are handicapped by the lack of information needed for adequate management and improvement of the fisheries. Basic life history data are unknown for many common species, and there are few keys or handbooks for identifying the aquatic flora and fauna. There are practically no scientific journals and few contacts between the biologists for exchange of information.

The demands for Africanization in these new nations have often meant the displacement of trained European biologists before their African counterparts could be adequately trained. Even at the best there were few fishery biologists in these countries. The British colonies each had a fishery officer, perhaps with a small staff. In Uganda and Nigeria, the British fishery officers were retained by the new nations, but each had an African assistant who was expected to take over the position before long. All the fishery staff in Ghana were Africans except for a Japanese biologist working on the sardine fishery. Two of the Ghanaians were graduates of the University of Washington and a third of the University of British Columbia. The fishery staff in Khartoum were all Sudanese. The chief fishery inspector was a graduate of St. Andrew University, where many of the British fishery officers were trained. The chief of inland fishery research was Mahmoud Mahdi, a graduate of Iowa State University. Peter Youn, another Iowa State graduate, is in charge of the inland fisheries program in Liberia.

Programs for training more fishery biologists are getting

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started but need more staff, libraries, and research. In Liberia, Peter Youn is teaching one course in the biology department at Cuttington College as an introduction to fisheries work. At the University of Eastern Nigeria in Nsukka, the Zwelling College of fisheries was established, but the only biologist who taught the courses returned to the United States this year and has not been replaced. At the time of our visit, the Federal Fishery Office in Lagos was preparing a 2-week short course in marine biology and fisheries for biology students during their spring vacations from various Nigerian colleges. The University of Khartoum has some aquatic biology and fisheries but no extensive program.

In Ghana, students graduating from the university in biology and wishing to go into fisheries were given an additional year of training in the school of business administration before taking governmental positions. It was hoped that after a few years of work the best biologist would be sent to the United States or Europe for graduate study in fisheries.

In Uganda, Makerere Collegé has trained several biologist who have gone into fisheries in recent years. The Assistant Fishery Officer, Mr. Soul Semakule, took a Master of Science degree from the University of British Columbia after graduation from Makerere, and three other biologists are now in the United States doing graduate work in fisheries. The Uganda Fisheries Department has recently raised entrance levels for their staff. Technicians for the collection of fishery statistics and other field work must now have completed Grade 12, whereas in the past some had completed only Grade 6. The Fisheries Office has also received an appropriation for a training school, where 2-year courses in fish biology and management will be given to classes of 20 staff members. The present field staff includes about 100 men who should complete the 2-year course. They also plan short-courses for about 30 fishermen at a time.

Dr. Hugh Lamprey, of the East Africa Wildlife School at Mewki, Tanzania, pointed out that fishery and wildlife management are not fields in which Africans are apt to seek an education. With their newly acquired education they want to leave the village and country life. Before they can be trained as conservation biologists, they must have an understanding of the importance of preservation and management of their natural resources. They must be instilled with a sense of mission and vocation.

Although real progress is being made in training Africans for work in fishery biology, a great deal of help will be needed for many years. In our travels we saw programs assisted by the United Nations (FAO, UNESCO and UNICEF), and by techni-

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cal assistance programs of the United States, Russia, China, Great Britain, Canada and some other countries.

The future of our civilization depends to a great extent upon closing the gap between the "developing" and the "rich" nations. U. Thant, Secretary General of the United Nations stated (1965 p. 31), "No single idea has more profoundly shaped the modern economy than the belief that all citizens have the right to share in its resources and opportunities." Improvement of fisheries in these African countries is part of the development needed to close the gap. We, of the richer countries, must help in the development and must recognize that progress will not be as rapid as the Africans or we would like. Change is coming rapidly though compared with the development to our present condition in the Western world.

Acknowledgments

It is not possible to list all the persons to whom we are indebted for time and effort spent in showing us the fisheries in their countries. We make special mention of only a few: Peter Youn of Liberia; Dr. Elizabeth Babbott, Samuel Wokoma and Donald Niven in Nigeria; E. D. Heinen, Dr. A. Meschkat and John Adjety in Ghana; Mahmoud Mahdi in Sudan; Peter Proud, Soul Seminacole and Youl Pruginin in Uganda. The following agencies should also be given especial thanks: the Departments of Fisheries of Ghana, Liberia, Nigeria, Sudan, Uganda, the Volta River Authority, the East Africa Freshwater Fisheries Research Organization, Legon University, and University of Eastern Nigeria.

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Washington, D.C. Hickling, C. F. 1961. Inland tropical fisheries. Longmans. London.

Thant, U. 1965. Turning point. UNESCO Courier 18(Oct.):4-5, 8-9, 30-34.

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FISH CULTURE IN CENTRAL EAST AFRICA

without coming to harm, because fresh water passes through all the time. Their value as a high priced food is their main importance. Abundant cold, clear water is required for their culture. Breeding of the trout is generally done artificially by extracting the eggs from the female and mixing them with the milt of the male.

Other types of fish culture of some economic importance but not as food production are the breeding and culture of various kinds of ornamental fish for aquariums. This is a flourishing industry in many parts of the world.

Types of fish used for fish culture in central east Africa

CICHLID FAMILY

The fish of the greatest value in fish culture in central east Africa are all members of the Cichlid family and the most important belong to the genus *Tilapia*. For the following reasons *Tilapia* are highly desirable for use in intensive culture:

- a. They are efficient converters of waste foodstuffs.
- b. They have a short food chain.
- c. They can be readily adapted to crowded conditions in artificial culture.
- d. They can be easily bred.
- e. They are generally free from parasites.

1. outopopulation.

2. small size of T. zillii - not suitath for toble fish

It is important to be able to identify the species of fish used for culture because some of the related species are not of value.

Each fish has two names, a generic and a specific. The generic name, for example, *Tilapia*, is written with a capital letter, while the specific name, e.g., *melanopleura*, is written with a small letter. Fish of the same species are almost identical and form a group which interbreeds freely. Fish of the same genus have certain characteristics in common in their anatomy.

The main genera (plural of genus) used in fish culture are Tilapia, Serranochromis, and Haplochromis. One of the best of the Cichlid fan teethlike projection up the gill cover

- a. If the gill rat the mouth lar the anal fin, a is Serranochre
- b. If the gill rak are no spots
- c. If the gill rak, on the anal

Tilapia

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FISH CULTURE PRACTICES IN PONDS

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One of the best ways of deciding to which of these genera a fish of the Cichlid family belongs is to examine the gill rakers, i.e., the teethlike projections on the gill arch, which may be seen by lifting up the gill cover or cutting it away.

- a. If the gill rakers are thick and partly T-shaped or knoblike, the mouth large, set at an angle to the horizontal, spots on the anal fin, and bodies long in proportion to depth, the genus is *Serranochromis* (Figure 30).
- b. If the gill rakers are fine, the mouth usually small, and there are no spots on the anal fin, the genus is *Tilapia* (Figure 31).c. If the gill rakers are short and stout and there are orange spots
 - on the anal fin, the genus is Haplochromis.

Tilapia

This is a widespread group. Five species are of importance (*T. melanopleura*, *T. sparrmanii*, *T. andersonii*, *T. mossambica* and *T. macrochir*). In various countries in central east Africa there has been and is being introduced *Tilapia zillii*. The *Tilapia* are relatively easily separated into species by counting the gill rakers and by identifying other features:

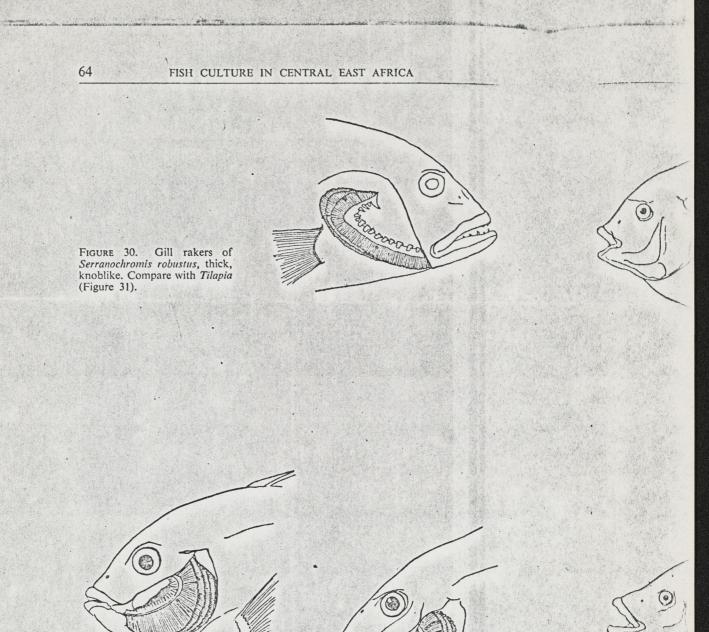
a. 8 to 12 rakers on lower part of first gill arch:

T. melanopleura: Usually with a pink or red chest and five or six dark vertical bars on the body. The tail fin is speckled and darker in the upper half than in the lower. Widespread from Upper Congo to South Africa (Figure 32).

T. sparrmanii: The color varies but there is never a pink chest, the number of dark bars is seven to nine and the tail is uniform. Widespread in occurrence.

b. 14 to 20 gill rakers:

T. mossambica: The snout is often longish and the profile is concave. Does not occur in Upper Zambesi, but is widespread from Rhodesia southward and in tributaries of the middle and lower Zambesi (Figure 33).



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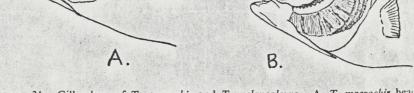
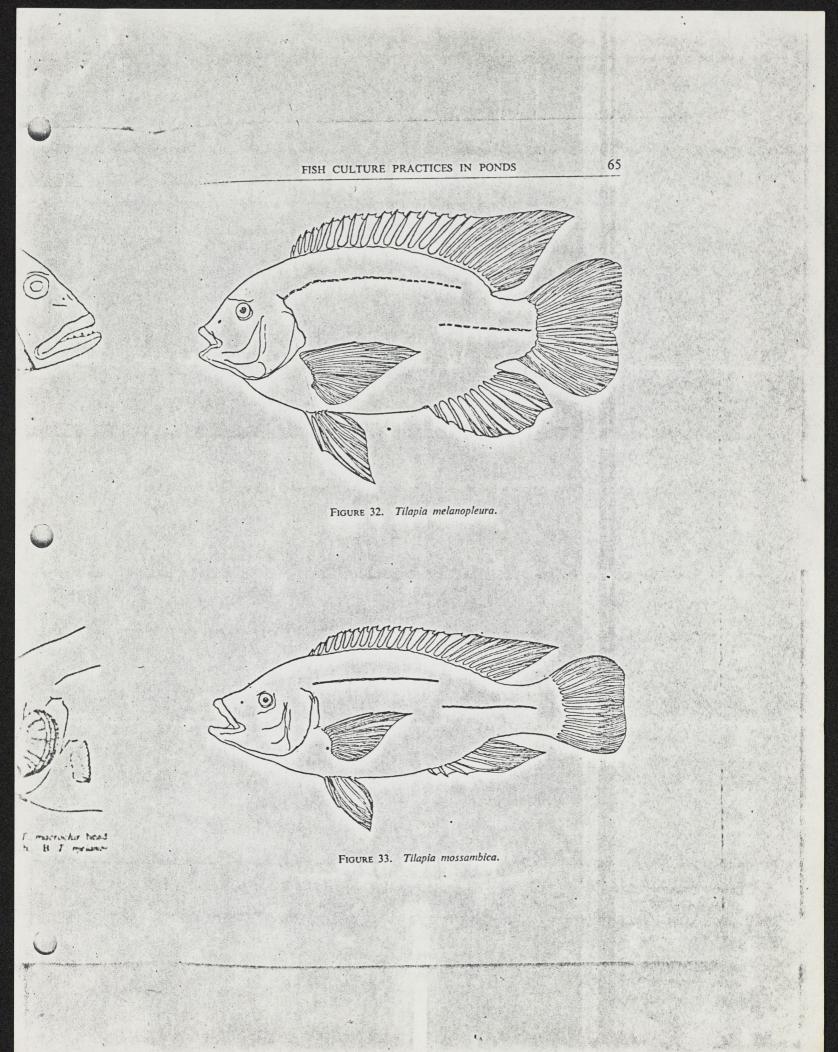


FIGURE 31. Gill rakers of *T. macrochir* and *T. melanopleura*. A. *T. macrochir* head with gill cover removed to show 23 gill rakers on lower part of arch. B. *T. melanopleura* head showing 10 gill rakers on lower part of arch.



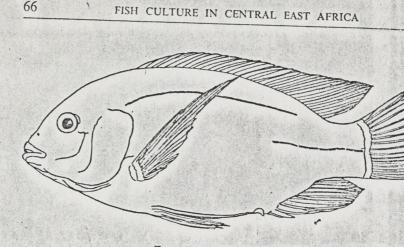


FIGURE 34. Tilapia macrochir.

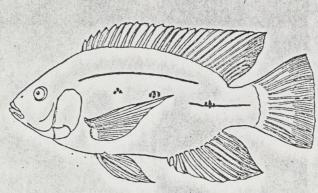


FIGURE 35. Tilapia andersonii.

20 to 26 gill rakers: с.

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T. macrochir: Sides of head speckled, body greenish and always with a rounded or convex snout. There is often a red rim round the eye. Occurs in Congo, Upper Zambesi, Kafue and Okavango river systems (Figure 34).

T. andersonii: Profile of head sloping, silvery in color. Often has three black spots along the side of the body. Occurring in the Kafue, Upper Zambesi and Okavango river systems. generally found only in large rivers or swamps (Figure 35).

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FISH CULTURE PRACTICES IN PONDS

Serranochromis

There are four species which occur in the Kafue River in Zambia, in the Upper Zambesi and the Okavango, and some of these are also found in the Congo River system.

The teeth in the upper jaw are used as a guide in separating the species (Figure 36).



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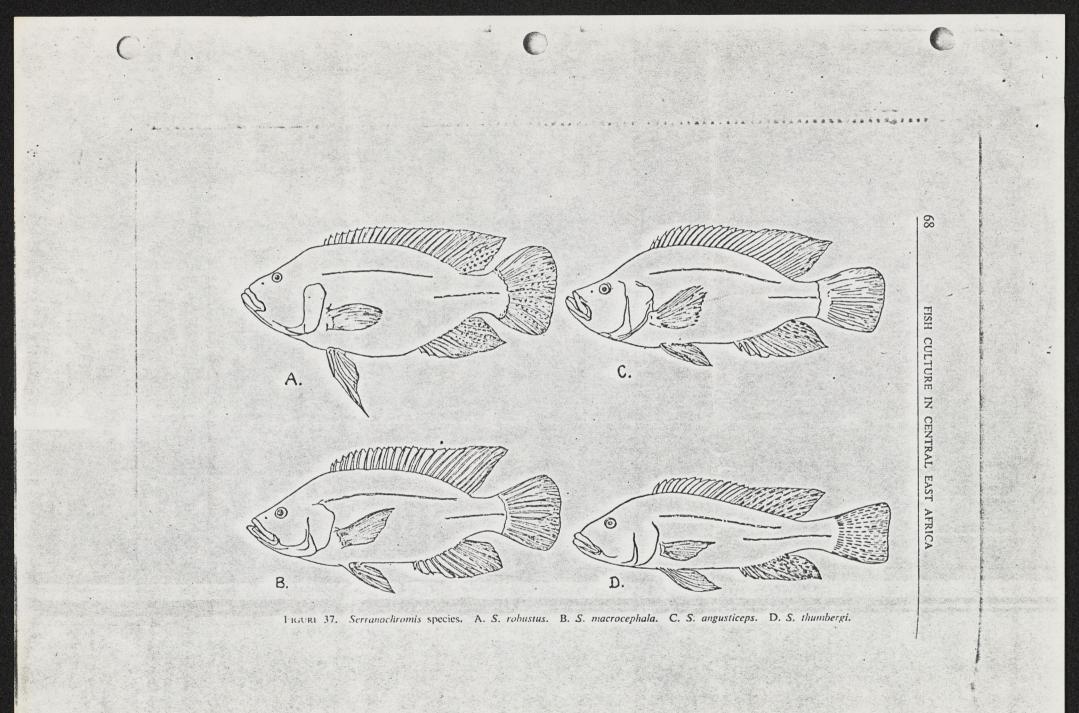
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olor. Often Occurring er systems, gure 35).

FIGURE 36. Teeth of Serranochromis. Left: More than 3 rows of teeth in upper jaw. Top S. angusticeps. Bottom: S. thumbergi. Right: 2-3 rows of teeth in upper jaw. Top S. macrocephala. Bottom: S. rcbustus.



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a. 2 to 3 rows of widely spaced teeth in the upper jaw.

S. robustus: Body color green above the lateral line and yellow to white below. Profile often concave (Figure 37A).

S. macrocephala: Body dark blue to purple above the lateral line. Profile of head usually straight or slightly concave (Figure 37B).

b. More than three rows of teeth close together in upper jaw.

S. angusticeps: Variable body color. Head narrow with eyes placed close together and profile concave. Deeper bodies than most. Mouth is able to be pushed out somewhat (protractile) (Figure 37C).

S. thumbergi: Body color light green above lateral line and whitish below. Broad head with eyes wide apart. Profile convex. Body slender. Caudal fin truncate (Figure 37D).

Haplochromis

anguaticep

macrocephala.

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ruhustus

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Fish suitable for fish culture are included in the *Haplochromis* group, as well as fish which rarely grow to a size of more than a few inches. Identification of the larger growing species is difficult and reference should be made to fisheries departments.

The main features are a short snout, gill rakers usually less than 12, a large mouth with small teeth in three or four rows and orange spotted anal fins, noticeably in the two smaller species.

The most common small species are:

5 species

H. philander: rounded tail fin.

II. darlingi: square-cut tail fin and usually slender body as compared with the former,

There are five other larger species of which three are of interest in fish culture and which feed on water snails:

H. mellandi H. carlottae Pelmatochromis robustus VEVERS, H. G. See ASHTON, E. H.

WAYRE, P. L. The Gyr-Falcon in Iceland. (Exhibition-title only) 149

WILLIAMS, M. C. See MARSHALL, A. J.

WILLIAMSON, D. I. See PIKE, R. B.

1959 - Ploc. Zook. Soc. London, 132:1-20

BREEDING BEHAVIOUR PATTERNS AND ECOLOGICAL DIFFERENCES BETWEEN *TILAPIA* SPECIES AND THEIR SIGNIFICANCE FOR EVOLUTION WITHIN THE GENUS *TILAPIA* (PISCES : CICHLIDAE)

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I. SOURCES OF INFORMATION

In recent years cichlid fish have been much used for experimental work in aquaria on various aspects of breeding behaviour, but as yet there is little published information relating differences in behaviour to ecological differences between species. The aim of this paper is to collate data from field studies

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on many species of *Tilapia* in the waters of East and Central Africa, to relate the types of breeding behaviour to the ecological background, and to try to assess the evolutionary significance of the patterns of breeding behaviour and ecological differences which emerge. Behaviour and ecological studies present complementary pictures of the interaction between the fish and its environment, and an attempt is made here to piece these together to examine the evolutionary effects of their reciprocal and complex interaction.

The data considered in this paper are drawn from my own observations made in natural waters in East and Central Africa from 1945 to 1956 on the following species of *Tilapia*:

Lake Nyasa species, T. squamipinnis Günther, T. lidole Trewavas, 1941, T. karongae Trewavas, 1941, T. saka Lowe, 1953, T. shirana Boulenger, and T. melanopleura Dumeril; L. Victoria species, T. variabilis Boulenger and T. esculenta Graham, 1929; T. nilotica Linné from many East African lakes together with T. leucosticta Trewavas, 1933, T. galilaea Linné and T. zillii Gervais in Western Uganda; Tanganyika species, T. karomo Poll, 1948 and T. tanganicae (Günther); the eastward-flowing river system species, T.pangani Lowe 1955, T. girigan Lowe, 1955 and T. jipe Lowe, 1955, together with some observations on T. mossambica Peters, T. hunteri Günther and T.nigra Günther; Central African species, T. sparrmani A. Smith, T. macrochir Boulenger and T. andersonii Castelneau.

Detailed observations on some aspects of the biology of these species have been published elsewhere (Lowe, 1952, 1953, 1955 a, b and c, 1956 a and b, 1957 and 1958). Identifications were checked at the British Museum Natural History with the kind assistance of Dr E. Trewavas.

Tilapia have been studied extensively as they are of great economic importance as food fish, and additional information on the biology of various species has been culled from the following sources :

Lake Nyasa species, Bertram, Borley & Trewavas, 1942; Trewavas, 1941; Lake Victoria species, Graham 1928 and 1929; Fish, 1951; Greenwood, 1953; T. nilotica and associated species, Boulenger, 1908; Capart, 1955; Daget, 1954; Fish, 1955; Liebman, 1933; Poll, 1932, 1939 a and b; Trewavas, 1933; Worthington, 1929, 1932; Worthington & Ricardo, 1936; and Annual Reports of the Game and Fisheries Department Uganda Protectorate; Tanganyika species, Poll, 1946, 1948, 1956;

Belgian Congo species (mainly *T. macrochir* and *T. melanopleura*), de Bont, 1950; de Bont, Halain, Huet & Hulot, 1948;

T. melanopleura and other species in West Africa, Daget, 1954; Svensson, 1933; Irvine, 1947; Welman, 1948;

T. zillii, Daget, 1952; El Zarka, 1956;

South African and Rhodesian species (mainly T. mossambica, T. melanopleura and T. sparrmani), Barnard, 1949; Hey, 1952; Jubb, 1952; du Plessis, 1946; du Plessis & Groenewald, 1953; Ricardo, 1939 a; also reports of the Northern Rhodesia Game, Tsetse Control & Fisheries Department; T. mossambica, Vaas & Hofstede, 1952;

T. nigra, Brown & van Someren, 1953; Annual Reports of the Kenya Game & Fisheries Department;

T. rukwaensis Hilgendorf & Pappenheim, Ricardo, 1939 a and b ; Swynnerton (unpublished report).

Among the most intensive studies of *Tilapia* breeding behaviour in aquaria so far published are those carried out in America by Aronson (1945, 1949, 1951, 1957) on the West African species T. macrocephala (Bleeker) (synonymous with T. heudeloti Dumeril, vide Trewavas, 1947 a), and in Europe by Baerends and Baerends-van Roon (1950) on T. natalensis M. Weber (synonymous with T. mossambica Peters, vide Trewavas, 1937). Seitz (1948) has also made intensive studies on "T. heudeloti" and "T. natalensis" but there appears to be some doubt about the identification of the species used in his experiments (Aronson, 1949), and Trewavas (personal communication) has reason to believe that they were both forms of T. mossambica Peters. Many species of Tilapiaare morphologically very alike, and there has been considerable confusion over the naming of material used in experimental work.

T. macrocephala studied by Aronson is a mouth-brooder in which the male normally broods the eggs and young in his mouth, hereafter referred to as a "paternal-brooder". Of the twenty-five Tilapia species studied personally and by the above listed authors T. sparrmani, T. melanopleura and T. zillii are "substratum-spawners" in which the eggs and young are guarded by both parents but not brooded in the mouth. In all the other species except T. macrocephala the female normally broods the eggs and young in her mouth ("maternal-brooders"). Only one other species, T. guinasana Trewavas, 1936, from South-west Africa and apparently very closely related to T. sparrmani, is known from aquarium studies to be a substratum-spawner (Aronson, 1949 quoting Roloff, 1938 & 1939). T. macrocephala stands out as an exception in showing the paternal-brooding pattern of behaviour, and it is unfortunate that generalisations have been made from the behaviour of this species which is in many ways different from that of the majority of Tilapia. While it is likely that further investigations, particularly in West Africa and the Congo, may show other species to be paternal-brooders, enough is now known of the *Tilapia* fauna of East and Central Africa to say that the maternal-brooding habit is the general rule among Tilapia species in these waters. Aronson (1949) lists three other species, T. dolloi, T. microcephala and T. simonis in addition to T. macrocephala and T. heudeloti in which the male is credited with caring for the eggs, and the following in which both sexes have been reputed by some authors to care for the eggs, T. simonis, T. galilaea, T. microcephala, T. nilotica and T. zillii. There is conflicting evidence concerning the habits or systematic status of most of these species ; more recent work has made it clear that T. zillii is a substratum-spawner (Daget, 1952; El Zarka, 1956); T. simonis is now referred to a different genus (Aronson, 1949 footnote p. 134), and T. microcephala, T. heudeloti and T. macrocephala now appear to be synonymous (Boulenger, 1915, Trewavas 1947a). As nothing is on record concerning the ecology of T. dolloi Boulenger,* a Congo species studied by Asch, 1939 (referred to by Aronson, 1949), the behaviour of T. macrocephala (T. heudeloti) is here taken as the type behaviour for paternalbrooders.

* Also = T. heudeloti according to Trewavas, personal communication.

Tilapia species also fall into the same three groups on certain basic anatomical characters such as gill raker number. The substratum-spawners all have less than twelve gill rakers on the lower part of the anterior gill arch, whereas the maternal-brooders have more than fifteen (generally more than seventeen) and up to twenty-eight gill rakers on the lower part of the anterior arch, the number varying in different species. T. macrocephala (T. heudeloti) has an intermediate number, fifteen to nineteen, and T. dolloi twelve to fifteen, as do certain other West African and Congo species (Trewavas personal communication) among which other paternal-brooders may be found when more is known of their breeding habits.

II. SUMMARY OF DATA

A. Breeding behaviour differences between the three groups of Tilapia

A comparison of breeding habits of substratum-spawners with those of maternal-brooders in natural waters has shown the following differences in breeding behaviour associated with the two types of habit :

Substratum-spawners

both sexes develop breeding colours and defend spawning territory spawning pairs are generally solitary

both sexes make nest long courtship preceeds spawning

male and female remain together while guarding young

monogamy possible for several broods, sexes remaining together and preparing to spawn again as soon as young become independent

male and female take turns in guarding and feeding

parents guard young near to where eggs were laid

eggs and young remain on substratum for some time so oxygenated bottom water is necessary

Maternal-brooders

male only develops breeding colours and defends spawning territory male spawning territories are in colonies on definite spawning grounds male only makes nest

very little courtship preceeds spawning, which is very rapid

female carrying eggs moves away from spawning grounds, so sexes segregate immediately after spawning

polygamy usual, male fertilising eggs from a succession of females which spawn in his nest

female only broods and does not feed while doing so; male feeds little while actively guarding nest

brooding female seeks shelter of plant beds and may make long movements between spawning and brooding grounds

eggs are only momentarily on the bottom, so poorly oxygenated bottom water may not limit spawning area

Aronson's studies on T. macrocephala suggest that the behaviour of the paternal-brooders is in many ways intermediate between that of the substratumspawners and the maternal-brooders. In paternal-brooders there is little qualitative difference between the colour and behaviour of the sexes, both sexes help to make the nest (though this is primarily made by the female) and both sexes may brood (though this is generally carried out by the male). In T. macrocephala there is a courtship lasting several hours, or more often days, before spawning occurs, and Aronson (1949) points out that this is necessary to ensure exact synchronization of milt production with egg laying as Tilapia eggs water-harden very rapidly after they are laid. In maternal-brooders the male is able to fertilize continuously over a long period (several weeks or months), as the milt production cycle is not interrupted by guarding or brooding duties; maternal-brooders spawn very rapidly with hardly any preliminary courtship (Lowe, 1956 a), this, and the fact that the eggs are picked up immediately by the female, may be a considerable advantage in the deoxygenated water on the bottom of water lily swamps where Tilapia often spawn. In T. macrocephala the male normally picks up the eggs, but should he fail to do so, or to pick up all of the eggs, the female may do so after a time lag of ten to twenty minutes; so both sexes may brood. Paternal-brooders do not seem to have become so thoroughly adapted for mouth-brooding as have the maternal-brooders. For example, once the young are ejected by the male T. macrocephala they are never collected up again, and should they not find cover among the plants they are likely to be eaten by the parent; the brooding fish eats little or nothing while incubating and is cannabilistic after the young are released, at least in aquaria (Aronson, 1949). In the maternal-brooders the young are collected up and brooded again when danger threatens and at night for a considerable period (about a week in many species) after they are first released from the parent's mouth. Again, in Tilapia the number of eggs laid at a time increases with the size of the female (Lowe, 1955 c) and in maternal-brooders the larger females which lay more eggs also have larger mouths in which to brood, whereas among paternal-brooders there is no such relationship between the size of the brooding mouth and the number of eggs produced. Aronson (1949) records that a small male spawning with a large female was not able to pick up all the eggs laid. This was, however, in an aquarium, nothing is yet on record about the relative sizes of the two sexes of T. macrocephala in natural waters and it is possible that the male generally spawns with a smaller female, as in the T. mossambica group of Tilapia mentioned on page 15. In T. macrocephala by the time the young are released the female is often prepared to spawn again; in aquaria the interval between successive broods varies from eight days to a year with a mode at fifteen days (Aronson, 1945), and the presence of the male influences the spawning frequency of the female. In nature the male and female of paternal-brooders may not be so closely associated as they are in substratum-spawners in which both parents stay with the young.

B. Ecological data

The following differences in general ecology were noted between the three groups of *Tilapia*:

Substratum-spawners

Lplants Habitat : restricted to shallow water where plants can grow

Movements : restricted to plant areas for food and shelter so little movement about lake ; young live in shelter of plants near original territory found in open lakes some distance from shore as well as in shallow waters of swamps and rivers considerable movements occur between feeding and breeding grounds; young are left in shelter of weeds and later move to open water

Very little is yet on record concerning the ecology of T. macrocephala but like the substratum-spawners this species appears to be restricted to shallow water areas where there are vascular plants which provide cover for the young and possibly food; there are no very large lakes in West Africa and this species is said to inhabit brackish lagoons along the coast and the swampy deltas of the rivers (Aronson, 1949). Irvine (1947) says that the probable diet of this species is fine vegetable matter.

Thus all known *Tilapia* are primarily vegetable feeders, feeding on algae or aquatic plants, though occasionally zooplankters and insect larvae picked up with bottom debris are eaten. In L. Kivu *T. nilotica* feed on a large planktonic *Spirillum* for much of the year (Capart quoted by Fish, 1955), and in the Malagarasi swamps Protozoa in the thick bottom deposits may be an important source of food for *T. karomo* and *T. nilotica*. The substratumspawning *T. melanopleura* and *T. zillii* appear to be the only *Tilapia* species in East and Central Africa which have become specialised for feeding on aquatic vascular plants. This uniformly vegetable diet in the genus *Tilapia* is in marked contrast with the very varied diet in the associated cichlid genus *Haplochromis* in which an extensive adaptive radiation has occurred and vegetarian, insectivorous, mollusc-eating, zooplankton-feeding and predatory species have evolved; the significance of this difference between the two genera is discussed below.

Fish (1951 and 1955) drew attention to the fact that of the algae eaten by *Tilapia* the blue-green and green algae generally pass right through the fish undigested, and diatoms form the main usable food. Greenwood (1953) showed the roles of the mucus produced in the buccal cavity and the pharyngeal teeth in the feeding mechanism, and Gosse (1956) has shown that microgillrakers present on the inside of the gill arches also have an important role in the feeding mechanism of *Tilapia*.

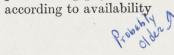
Where several species of 1 implu occur in one together and then generally contain the same food. This appears to be a contradiction of Gause's principle that two species with the same ecology cannot persist in the same region. Possibly phytoplankton is exceptional in being able to support closely related species* (factors other than food supply limiting the numbers of the fish), but these different species generally predominate in slightly different, though widely overlapping, zones, and they separate to breed (see below page 19). Thus in L. Nyasa the five species found at the southern end of the lake inhabit increasingly offshore openwater zones, from the substratum-spawning T. melanopleura which is restricted to lagoons and swampy areas round the lake, T. shirana which keeps to inshore water and does not make long movements, to three members of the T. squamipinnis complex, T. saka, T. squamipinnis and T. lidole, which occupy increasingly openwater zones and make increasingly long movements about the lake (Lowe, 1953). These latter three are often caught together and at these times contain phytoplankton, but when phytoplankton is scarce T. lidole make long movements to other areas, whereas the other two species may take to bottom feeding. The equilibrium between the relative numbers of these different species appears to depend on the fluctuating lake levels (Lowe, 1953). Similarly in L. Victoria T. esculenta and T. variabilis are caught together throughout the year in certain parts of the lake, and then contain phytoplankton; but T. esculenta predominates in areas where the water is opaque and there are soft flocculent bottom deposits of algae, and T. variabilis predominates where the water is clearer and the bottom harder, off sandy and rocky shores, in rivers and in swamps around the lake (Lowe, 1956 b).

In L. Albert where four species of Tilapia, none of them endemic, are present there appears to be more variation in the food used by the different species. The substratum-spawning T. zillii feeds on aquatic plants around the margins of the lake; T. *leucosticta* is found mainly in lagoons where it feeds on algae in bottom deposits; T. *nilotica*, the largest-growing species, is the most ubiquitous and is found in lagoons in the estuaries of inflowing rivers and around the edges of the main lake, and it varies its food with the habitat, taking bottom deposits from the lagoons, epiphytic diatoms in the estuaries and epiphytic diatoms and plankton in the lake; T. *galilaea* is found in the main lake off sandy shores and appears to be primarily a phytoplankton-feeder.

In the more uniform waters of L. George T. nilotica and T. leucosticta are the only *Tilapia* species, they are often caught together and then contain the same algal food (Fish, 1955) over most of the lake at any time of year. In this lake there is some indication that the numbers of T. leucosticta have increased since the selective fishery for the larger, and seemingly dominant, T. nilotica has been in operation (Lowe, 1958).

With the exception of the vascular plant-feeders which generally feed on algae when very small (de Bont, Deceuinck & Detaille, 1950 and personal

* Cf. observations by Fryer (1957, J. Anim. Ecol. 26, 263) on the food of freshwater copepods; herbivorous species do not appear to obey the 'Gausian hypothesis' which may be associated with superabundance of algal food.



Maternal-brooders

Mostly algal-feeders, using phyto-

plankton, epiphytic or bottom algae

observations), there appears to be little change in food eaten as the *Tilapia* grow, the small Tilapia feeding on small particles, algae and some small zooplankters, in the water where they are living. However, Le Roux (1956) found that in ponds in South Africa T. mossambica, T. melanopleura, T. sparrmani and T. andersonii less than 5 cm. total length all preferred zooplankton, from 5-8 cm. long they ate almost all available food, and above 8 cm. long took mainly the same food as the adult stages, T. mossambica and T. andersonii mainly phytoplankton, T. melanopleura plant material, and T. sparrmani was omnivorous with particular preference for bottom food; (all these fish were evidently dwarfed by pond conditions). Algae occur in all the different zones occupied by Tilapia during the course of their life histories, and although some species are more specialised to take algae in one particular form (for example the phytoplankton-feeders have large mouths and very fine pharyngeal teeth) the morphological differences between species are very slight, and on the whole Tilapia are adaptable and will use whatever algae are most readily available, whether in bottom deposit, epiphytic or phytoplankton form.

The substratum-spawners are tied to plant zones as they both feed and breed among plants and show little movement from place to place. Among the maternal-brooders the more openwater-living species make the longest movements about the lake; this is particularly clear in L. Nyasa (Lowe. 1952). In L. Victoria marking experiments have shown that both T. esculenta and T. variabilis make long, often surprisingly rapid, movements; fish of both species marked in the Kavirondo Gulf have been caught up to 150 miles away in Tanganyika waters of the lake, and other marked fish have shown movements of up to four miles (T. esculenta) and ten miles (T. variabilis) respectively in one day (Lowe, 1956 b). The reasons for these very rapid and long movements, and how often they occur, are not known. In all the maternal-brooding . Tilapia in the Great Lakes regular movements are generally made (a) from feeding to spawning grounds, (b) by brooding females from spawning to brooding grounds, and (c) from zone to zone as the fish grow.

The most marked movements between spawning and brooding grounds occur in L. Nyasa, the greatest extreme being shown by T. *lidole* in which brooding females carrying eggs may move several miles from spawning to brooding areas, taking the young into relatively sheltered water along the shore (Lowe, 1952); these Nyasa species appear to have one, or at most two, batches of young in a restricted annual breeding season. In Victoria, on the other hand, females have several batches of young in succession (this seems to be the more usual course among *Tilapia*); brooding females are found with gonads starting to ripen again and such females probably do not move far from the spawning ground. The configuration of L. Victoria is such that there is generally a suitable shoreline nearby to which to take the young, so the distinction between spawning and brooding grounds is not as clear as in Nyasa and movements from one to the other are not so well-defined.

In both Nyasa and Victoria and in many other lakes the young *Tilapia* are left in the plant zone around the margin of the lake by the female; they move out as they grow and are found in shoals along sandy shores when about 7-12 cm. in total length, and at 12-15 cm. are found in surface waters at some

distance from the shore. As they approach maturity $(20-27 \text{ cm}. \log \text{depend-ing} \text{ on the species})$ they frequent the bottom rather than the surface waters. This same pattern is followed by different species of maternal-brooding *Tilapia* in many of the Great Lakes. However, in Lake Albert (and possibly also in Lake Rudolf and Lake Tanganyika) 12-18 cm. long *Tilapia* are found inshore and some *Tilapia* remain inshore and in lagoons round the lake for all or most of their lives ; this appears to be associated with the presence of the predators *Lates* and *Hydrocyon* in these lakes (see below, page 16). In Lake Victoria 12-18 cm. long *T. esculenta* visit certain beaches at definite times each year (Lowe, 1956 b), these fish are still immature and the reason for this seasonal inshore visit of immature fish is not yet known.

Thus in the Great Lakes the maternal-brooding *Tilapia* inhabit many different zones, moving as they grow from swampy inshore areas, to waters off sandy shores, to open surface waters and then bottom waters some distance from the shore; once mature they move from opaque waters where they feed to clearer water where they spawn, and to the shelter of plant beds to brood young; there the fry are left by the female. Thus these *Tilapia* are not confined to distinct ecological zones. This and the long movements about the lake recently discovered by marking mean that there is little ecological or geographical isolation within a lake. The evolutionary effects of this lack of ecological and geographical isolation are considered below.

III. DISCUSSION

A. The evolutionary significance of breeding behaviour and ecological differences between the three groups of Tilapia

It is only among the maternal-brooders that extensive speciation has occurred; all the endemic species of *Tilapia* in the Great Lakes are maternalbrooders. This is in spite of the fact that the substratum-spawners are probably nearer to the basal stock from which the *Tilapia* have evolved, hence more ancient, as both the morphological characters, such as the low gill raker number, and the wide distribution of the few species suggest; also, many of the South American cichlids are substratum-spawners. In *T. sparrmani* the structure, relatively small size and unspecialised omnivorous bottomfeeding habits, suggest that of the present day living *Tilapia* this species is probably nearest to the basal stock from which the *Tilapia* evolved. The wide distribution of *T. melanopleura* and *T. zillii*, right across Africa from the Gambia to the Nile, and south as far as Southern Rhodesia in the case of *T. melanopleura*, also suggests that these are relatively old species. But despite the apparent age of these substratum-spawners they do not appear to have speciated at all in East and Central Africa.

Basal Stock of

Tilupie

Paternal-brooders are, as far as is known, restricted to West Africa and the Congo and have evidently not undergone much speciation. Their behaviour is in some respects intermediate between that of the substratum-spawners and the maternal brooders, as mentioned above, also their gill raker number is intermediate. Two possibilities are presented concerning the relationship between the paternal- and maternal-brooders, either (1) the maternal-brooders originated from paternal-brooding species in or near West Africa or the Congo, and the paternal-brooders could not compete with the more specialised and efficient maternal-brooders in colonising new areas, or (2) the paternal-brooding and maternal-brooding habits have arisen independently from the substratumspawning habit; if so, they may be of comparable antiquity, or the paternalbrooding habit may have arisen more recently which might account for its more limited distribution. Data are as yet insufficient to decide which surmise is correct; the intermediate gill raker number of the paternal-brooders would appear to be in favour of the first alternative, but on the whole the differences in behaviour suggest the independent origin of the two groups from substratumspawners. Substratum-spawners pick up the eggs and young in the mouth when moving them from place to place. Breder (1933) and Myers (1939) when discussing the evolution of oral incubation in fish point out that the habit has arisen many times independently, and in the family Cichlidae this would certainly seem to have occurred.

1. Characters associated with the extensive speciation of maternal-brooders

(a) Preadaptation for life in openwater

Maternal-brooders both by their ability to use planktonic algae and by their habit of brooding young are independent of the shoreline for much of their life and so are preadapted to exploit more openwater conditions. In Africa the formation of large lakes and alternation of arid and pluvial periods has presented unpopulated openwaters to the fish which could take advantage of them, as Worthington (1937) and Trewavas (1949) have pointed out, and the maternal-brooders were pre-eminently suited to do this. All the endemic *Tilapia* of the large lakes are maternal-brooders, as are also the other species such as *T. nilotica* and *T. galilaea* living offshore in the Great Lakes, as well as all the other cichlids in the Great Lakes whose breeding habits are known.

The ability to cross openwater combined with the necessity of moving inshore in a deep lake to find bottom suitable for spawning might, provided the openwater was not crossed very often-and in the early days of adaptation to openwater crossings would probably have occurred less frequently-lead to the establishment of discontinuous populations. Also, the female does not feed while brooding and might then cross more openwater, poor in phytoplankton, than that visited by the fish at other times. Thus the female's wandering movements from spawning to brooding grounds might lead her into new arms or bays where she would leave her young and the area would be colonised by young of one stock, partially isolated from other populations. The effectiveness of this isolation would depend on how frequently fish crossed to the new area and whether the fish within it remained there to breed. Close inbreeding would lead to the more rapid establishment of any mutations throughout the population. Such movements may have been important in the evolution of endemic Tilapia species within Lake Nyasa, as is discussed below (page 25). Recent introductions of Tilapia into new areas in many parts of the world have shown how very rapidly whole new areas become populated from very few fry, provided not too many predators are present.

(b) Polygamy

The maternal-brooders are polygamous whereas among the substratumspawners monogamy, at least for several broods, may be the general rule. The male of the maternal-brooders fertilises as many females as he can lead to his nest, and as many males congregate on the spawning grounds a particularly successful male may spawn more often than other males in the vicinity. Kosswig (1947) suggested that "monogamy" may have been important in the rapid speciation of cichlids in the African lakes, but it is the polygamous species, and not the monogamous ones, which have speciated ; Kosswig assumed that the cichlids of the Great Lakes had the "father-and-mother" type of parental care, i.e. were not mouth-brooders, whereas it is now known that the endemic cichlids of the Great Lakes are all, as far as is known, maternalbrooders. The ability of a particularly successful male to fertilise eggs from more females than do other males may have had important effects in spreading characters in a population. The presence of many males together on the spawning grounds presents ideal conditions for sexual selection to operate, and this would appear to have contributed to the development of the very striking breeding colours shown by the males of the maternal-brooders. A female normally spawns one batch of eggs all in one nest ; whether she ever moves on to another nest if interrupted while spawning, and then rears a brood fertilised by more than one male, needs further investigation.

2. Characters of substratum-spawners which may have inhibited speciation

The Cichlidae appear to be a relatively young family of fish-in East Africa the earliest fossils are probably those of Miocene age studied by Greenwood (1951 b)-and still in a very plastic state, speciating freely whenever conditions are suitable. It is therefore perhaps important to consider what characters may have inhibited speciation in the substratum spawners. These would seem to include the fact that they are limited to shallow waters by food and spawning requirements; they have little incentive to more long distances as feeding and breeding grounds are close together, so that extensions of range will take place along shore lines and through swamps (which will account for their wide distribution). Under such conditions the new breeding populations will be contiguous with the parent population. Although it has been argued that distance and the presence of intervening populations along a shore line would promote isolation and speciation if the fish did not move much, the fact remains that those Tilapia which are restricted to inshore areas-both the substratum-spawners and the maternal-brooding Tilapia in lakes where these are restricted to inshore waters by predators (see page 16)-have not speciated. Local differences between populations do arise among substratum-spawners, but do not attain specific rank significance, perhaps because in the shallow waters in which these species live environmental changes, such as fluctuations in water level, are likely to be more rapid than in deeper bodies of water, and are unlikely to allow time for the development of new species. The substratumspawners are likely to be monogamous at least for several broods ; the effect of this is difficult to see, as discussed above Kosswig (1947) thought that this would promote speciation, but it is just the monogamous species which have not speciated.

In the substratum-spawners both the type of food eaten and the absence of brooding habit bear a close relationship to the low number of gill rakers. The few widely spaced gill rakers, together with the course pharyngeal teeth which allow the consumption of relatively large food particles, have led away from the plankton-feeding habit in these species. Substratum-spawners lay smaller eggs than do maternal-brooders (Lowe, 1955 c). Although the eggs and young, which are also very small, are on occasion moved from place to place in the parent's mouth, trials have shown that the small eggs pass quite easily through the widely-spaced gill rakers. This combination of few gill rakers and small eggs makes mouth brooding impossible and the loss of eggs and young through the gill rakers would presumably militate against the evolution of the brooding habit in these species. Although the evolution of lakes is, in general, towards less openwater conditions as the lake matures, these African Great Lakes have offered greater opportunities to fish which could exploit more openwater conditions. In the substratum-spawners the interrelationships of gill raker density, food and spawning habits have evidently prevented these species from taking advantage of these more openwater conditions.

3. The significance of breeding colours and associated characters

Experimental work by Baerends & Baerends-van Roon (1950) on T. mossambica in aquaria suggested that the colour of the breeding male is very important for successful spawning in these maternal-brooding Tilapia, and it was of great interest to find that the two morphologically almost identical Tilapia in Lake Nyasa, T. saka and T. squamipinnis, developed different coloured breeding males (pitch black sometimes with white edges to the dorsal and caudal fins in T. saka and light blue with a white head in T. squamipinnis (Lowe, 1953)). This suggested that the male breeding colour was important for species recognition by the female and perhaps an important part of the isolating mechanism between closely related sympatric species. Since then much more has become known about breeding colours in other Tilapia species. These data suggest that there are certain trends in breeding colours which may in some cases be a guide to systematic relationships, and that the possession of such different breeding colours in two such closely related species as T. saka and T. squamipinnis is quite exceptional. Before discussing these breeding colour trends it is necessary to consider the possible functions of the breeding colours and whether these functions are the same in all three groups of Tilapia.

Breeding colours and their functions in the three groups of Tilapia. The paternal-brooder T. macrocephala does not develop any special breeding colours in the ripening fish; in most populations there is, however, a secondary sexual difference in the presence or absence of pigment in the operculum of the uncastrated fish (Aronson, 1951). In the substratum-spawners the ripening fish of both sexes develop similar breeding colours and guard territory; their colours vary very much with the activity of the fish (and they generally fade on death), they become intensified when they are driving away other fish, indicating that they have a function of territory advertisement, and they also assist courtship in the synchronisation of the male and female cycles. In the maternal-brooders only the ripening male develops breeding colours and establishes and guards a territory, and these colours are lost again by the spent fish. The female retains the drab colours of the non-breeding fish which are presumably of protective value (in association with her habit of swimming inconspicuously with her dorsal fin down) when hiding among weeds brooding young, though in some species, such as T. leucosticta, the branchio-stegal membrane may become deeper in colour and the pelvic fins darker.

The male breeding colours of the maternal brooders serve for advertisement of spawning grounds, an effect which is enhanced by the habit of many males congregating together in certain places to spawn. This advertisement effect is most marked among the species endemic to Lake Nyasa where the breeding season is restricted; in this lake the males congregate on well-defined spawning grounds and have very definite breeding colours (black in several species) which show little variation in intensity throughout the short breeding season (and are retained in the dead fish). In Lake Victoria where some ripe *Tilapia* are found at all times of year breeding places are not so well-defined and male breeding colours are not so intense; in aquaria the colours of the Victoria *Tilapia* show great variations in intensity with the activity of the fish (and half-fade on the death of the fish).

Advertisement of spawning grounds is particularly necessary in Nyasa as, in addition to the restricted breeding season, the spawning grounds may be some way from the feeding grounds inhabited by the fish at times of year when they are not breeding. This is because each species tends to spawn in the most clear water zone of its range, where the sandy bottom provides a good substratum for nest making, and to feed in the most eutrophic part of its range as this carries the best phytoplankton (Lowe, 1953). In Lake Victoria there are not such sharp distinctions between feeding and breeding areas, possibly because the water inhabited by the *Tilapia* in this relatively shallow lake is more uniform than in Nyasa.

In the maternal-brooders male breeding colours may also have an important role in species recognition and in stimulating the female to lay. In these species the pre-spawning courtship is very short, the ripe females wander from nest to nest then suddenly spawn in one nest, sometimes without any preliminary courtship. (In *T. variabilis* which has two colour forms the atypical piebald-and-orange form is almost limited to the females (occurring in over 30 per cent of females but in less than 5 per cent of the males) and no ripe males of the atypical colour form were ever found (Lowe, 1956 b).

It should be mentioned in passing that in the maternal-brooders nest forms as well as breeding colours and associated behaviour may also be important for species recognition and release of egg laying, as the nests often have a characteristic form in different species, although the form may vary somewhat with the substratum. In *T. karomo* the nest is a small plaque on a high mound (Lowe, 1956 a), in *T. macrochir* the nest has radiating grooves leading out from a central crater (figured by de Bont, 1950), and the nests of Pangani species and *T. variabilis* have small pits around the central crater (Lowe, 1955; 1956 b). (In the substratum-spawners an area of rock or stick is cleared for the adhesion of the eggs, and holes are prepared into which the minute young, which have adhesive head glands are transferred).

Thus in both substratum-spawners and maternal-brooders the breeding dress, assumed by both sexes in the former and by the male only in the latter, advertises the spawning territory, and among the maternal-brooders the congregation of many males on the spawning grounds enhances this effect. In substratum-spawners breeding colours may also aid courtship in synchronising milt production with egg deposition (though this synchronisation is achieved without breeding colours by the paternal-brooders), whereas in the maternalbrooders milt is produced over a long period, courtship is extremely short and male breeding colours, possibly in conjunction with nest form, may be important for the recognition of the species by the female and in stimulating the female to lay.

Breeding colour trends. In certain maternal-brooding Tilapia it seems that breeding colours may indicate systematic relationships. In Nyasa, despite the apparent and probable importance of the different male breeding colours for species recognition in T. saka and T. squamipinnis mentioned above, most of the Tilapia species have black breeding males. T. lidole and T. karongae, like T. saka, have black breeding males, sometimes with white tips to the dorsal and caudal fins, and these species seem to depend on other morphological differences and differences in spawning place to keep separate. Thus black seems to be the basic colour pattern for breeding male Tilapia in Nyasa and in this the Tilapia are distinguished from other cichlid genera in the lake (including Corematodus shiranus Boulenger which mimics and lives with the shoals of Tilapia and appears to feed by rasping scales from their tails (Trewavas, 1947 c) but which develops a blue and old gold breeding dress). In the Pangani river system the males of the two species endemic to Lake Jipe and T. pangani from the river, all closely related species, have very similar male breeding colours (Lowe, 1955 a). T. esculenta which replaces T. nilotica in the Nile system above the Murchison Falls, and T. nilotica both have a black and red male breeding dress, unlike that of any other known Tilapia, which is almost identical in the two species (Lowe 1958) and supports the view that these geographical replacement species are closely related, as well as ecological counterparts in their respective waters.

There is, however, a common form of male breeding dress, with a greenishblue body and strongly contrasting bright orange edges to dorsal and caudal fins and sometimes with an orange or white genital papilla or tassel, which is found in many species of *Tilapia* in widely separated parts of East and Central Africa, and it is not yet clear whether bearers of this dress form one group of closely related species or whether this breeding dress has arisen independently several times. The breeding colours of *T. variabilis* in Lake Victoria, *T. karomo* in the Malagarasi, the Lake Jipe and Pangani river species, and *T. andersonii* in Southern Rhodesia all approximate to this pattern. This is a highly functional colour pattern, the orange edges to the fins when the fins are extended making the male look larger and more conspicuous when guarding his spawning territory (Lowe, 1956 a)—a function which the white edges on the fins of the Nyasa species may also serve—whereas the blue-green body colour renders the fish relatively inconspicuous as he flees from his territory with fins down if suddenly disturbed (Lowe, 1956 a).

Increasing the apparent size may be important as Baerends & Baerends-van Roon (1950) found that in T. mossambica in aquaria the size of the male was important in allowing him to stake and keep a spawning territory. In nature space is not so limited, but in some places the nature of the bottom and deoxygenation of the bottom water may limit the area of suitable spawning ground (Lowe, 1956 a). In Tilapia of the T. mossambica group, T. mossambica, T. nigra and some Pangani river species, the males are nearly always bigger than the associated females; these are species which have evolved in rivers, where suitable bottom for spawning may be limited and the size of the male at a premium for successful spawning. Experimental work in ponds has shown that the males of these species actually grow faster than the females (Vaas & Hofstede, 1952, Brown & van Someren, 1953 ; Lowe, 1955 a), and in these species the mature male develops a characteristic enlarged mouth and concave upper profile, so the growth characteristics and the appearance of the adult fish are considerably different in the two sexes. In the Tilapia species endemic to the Great Lakes the males and females grow to, and mature at, comparable sizes and retain the same general head shape, and pond experiments have shown that they grow at the same rate. Though the full significance of this differential growth rate in the two sexes is not yet clear, this character seems to be genetically determined and of significance for the study of the systematic relationships between different groups of Tilapia.

4. Environmental influences on speciation

Thorpe (1945) in a paper considering the evolutionary significance of habitat selection has stressed the importance of imprinting in the young of birds and insects in determining where they will return to breed. In the maternalbrooding *Tilapia* the female carries the eggs away from spawning to brooding grounds and the first impression of the young fish will be of quite a different ecological zone than that to which they will later go to spawn ; also the young will not see the breeding male. Hence it seems that under natural conditions knowledge of the nature of the spawning grounds, and of the colour of the breeding male, cannot be due to imprinting in these species, though in the substratum-spawners, in which the young follow both parents in the same environment in which they will later spawn, the learning mechanism may be different.

The environmental factors most concerned in speciation are those which present barriers, physical or temporal, between breeding populations, whether in different waters or within one body of water. The differences between Lakes Nyasa and Victoria discussed in a later section (page 21) illustrate some of the barriers which may operate within one body of water and these are therefore considered in this later section. A *Tilapia* changes its environmental niche many times as it grows and different factors may operate at the various stages of its life-history. In addition to environmental and behaviour barriers which may allow an incipient species to become a new species, biotic factors such as predation pressure have been thought to influence speciation by affecting the numbers of the incipient species which survive.

Worthington (1937, 1940, 1954) maintained that predator pressure was an important factor in controlling speciation, since incompletely adjusted forms would be selected against when predator pressure was high. Worthington was greatly impressed by, and recent work has confirmed, the striking differences between the faunas of Lakes Albert and Rudolf, which have the predatory Lates and Hydrocyon and hardly any endemic cichlids, and those of Lakes Victoria, Edward-George and Nyasa, which are without these predators and have numerous endemic cichlids. Lake Tanganyika presents rather a special case since it has these predators and a higher proportion of endemic cichlid genera than any other lake ; the probably greater age of this very deep lake has been invoked to explain this (Worthington, 1940; Trewavas, 1949). Worthington (1932) used as evidence of differential predator pressure his observation that fish with abnormalities were not found in lakes with these predators, Albert and Rudolf, whereas they are quite commonly found in the other lakes, Victoria and Edward-George, an observation confirmed by more recent study; from this Worthington inferred that such abnormal fish could not survive in lakes where the predator pressure was high.

Fryer & Isles (1955) suggested that the restrictive effect of predators on evolution has not been so important as Worthington believed as Nyasa, though lacking *Lates* and *Hydrocyon*, has a large number of predatory cichlids and several predatory non-cichlids (species of *Bagrus*, *Clarias*, *Barilius* and *Barbus*). Predatory *Bagrus* and *Clarias* are also found in other lakes without *Lates*, such as Victoria and Edward-George, in which extensive speciation has occurred. Most of the predatory cichlids in Nyasa are, however, small, and, *Bagrus* and *Clarias* appear to be "lurking" rather than "swift" predators compared with *Hydrocyon*. Much remains to be learnt of the relationships between the various predators and prey in all these lakes before it is possible to draw conclusions regarding the role of predators in speciation.

Pole tis

Recent work has, however, stressed that in Lakes Albert and Rudolf the fish of many genera are much larger than their counterparts in the other lakes and the *Tilapia* tend to have longer stronger spines (personal observations). Also, the distribution of the *Tilapia* is different, the *Tilapia* being restricted to the edges of the lake throughout all or most of their lives in the lakes with *Lates* and *Hydrocyon* and having openwater-living phases in the other lakes ; this also applies to Lake Tanganyika where *T. tanganicae* is the only really lacustrine species but even this species is restricted to the littoral zone, to water less than 10 metres deep along sandy shores (Poll, 1956). Thus the particular predators *Lates* and *Hydrocyon*, or some associated factor, do seem to have had a marked effect on the fish, and they might conceivably have had effects on evolution by controlling the distribution of the fish within the lake. In the case of Lake Tanganyika, which though evidently an older lake than Nyasa has no species flock of *Tilapia*, these predators may have restricted evolution within this genus.

It is, however, among the Haplochromis and not among the Tilapia that the difference between lakes with and without Lates is most marked. Tilapia provide little evidence as there is little difference in the number of species between lakes with and without Lates, as the following Table 1 shows. Also as is discussed in a later section, Nyasa is the only lake with a genuine species flock of Tilapia, and predators are likely to have most effect on the sympatric development of species flocks as these involve the greatest changes in the habits and habitats of the fish.

TABLE 1

The numbers of *Tilapia* species in lakes with (+) and without (-) the predators *Lates* and *Hudrocuon*

		Tilapia species		
Lake	Lates and Hydrocyon	No. present	No. endemic	
Rudolf	+	3	0	
Albert	+	4	0	
Tanganyika	+	4	2	
Edward-George		5 2	0	
Victoria	· · · ·	2	2	
Nyasa		6	5	
Rukwa		1	1	
Jipe		2	2	

Lakes which already have several species of *Tilapia* do not develop endemic species unless the *Tilapia* can exploit more openwater (as they have done in the case of Nyasa); this is probably bound up with *Tilapia's* restriction to a vegetarian, mainly algal, diet, and suggests that interspecific competition in inshore waters, as well as presence or absence of openwater predators, may play a part in controlling the distribution and further evolution of *Tilapia* species.

Can interspecific competition between different species of Tilapia have affected their further evolution ? Data summarised above concerning the food habits suggest that competition for food is not often a limiting factor in these algal-feeding fish under natural conditions, even though several species may use the same source of food for much of the year. It is, however, possible that there is competition for spawning grounds in lakes such as Victoria where suitable hard bottom appears to be limited, and for nursery zones, as so much of the shallow water in the swampy areas at the edge of the lake, used as a nursery zone by the 3-10 cm. long fish of both Victoria species, is unavailable because it is deoxygenated. The distributions of T. esculenta and T. variabilis in Lake Victoria, and of T. nilotica and T. leucosticta in Lake Edward-George suggest that inter-specific competition exists, the larger-growing T. esculenta and T. nilotica dominating the other two species and affecting their distribution in their respective lakes (Lowe, 1956 b and 1958); such a situation could presumably have effects on the future evolution of the fish by governing their distribution within the lake.

B. The significance of the Lake Nyasa Tilapia species flock

Several lakes, Nyasa, Victoria, Tanganyika and Jipe, have more than one endemic species of *Tilapia*, but Nyasa is unique in having more than two endemic species (Table 1). Endemic fish species arise either by gradual change

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in a population isolated from other water systems (allopatric speciation) or by speciation within a lake (sympatric speciation). In Nyasa four species form a genuine "species flock" in the sense defined by Brooks (1950) as a flock of species in a lake all more closely related to one another than to any population existing outside the lake. No similar Tilapia species flock is found in any other of the lakes, despite the fact that large Haplochromis species flocks also occur in Lakes Victoria and Edward showing that conditions were suitable for the extensive speciation of some cichlids in these lakes too. The unique Nyasa species flock presents an opportunity to examine the ecological conditions, and their counterparts in the behaviour of the fish, which may have led to the evolution of a species flock in Nyasa and not in these other lakes.

1. The sympatric speciation controversy

Much has been written on the subject of whether sympatric speciation has occurred among cichlids in the African lakes by Worthington (1937, 1940, 1954), Mayr (1942, 1947), Trewavas (1941, 1947 b, 1949), Brooks (1950), and for Haplochromis species by Greenwood (1951 a). The gist of the controversy is that Worthington after extensive field studies in East Africa held that fish species in the Great Lakes had arisen by adaptive radiation within the lakes. Mayr (1942) maintained, largely from his work on birds, that geographical isolation was always necessary for the formation of new species and that new fish species could not arise sympatrically (then taken to mean within the same lake), and he suggested that multiple invasions had been more frequent in the African lakes than realised by those who had worked there. Much turned on the exact meaning of the word "sympatric" and in later papers Mayr (1947) somewhat modified his view on the scale of isolation necessary, evidently partly as a result of Thorpe's work (Mayr, 1947, page 266) as Thorpe (1954) pointed out, primarily from work on insects, that changes of ecological preferences often preceed geographical isolation. In recent years it has become evident that ecological isolation may entail microgeographical isolation (see Poll, 1952; Worthington, 1954), and that many of the species present in a large lake, and thereby "sympatric" according to Mayr's earlier (1942) view are in fact ecologically and microgeographically isolated. This applies, however, particularly to species which remain in one ecological zone throughout life, as do many of the Haplochromis species, but not so much to Tilapia species which move from zone to zone as they grow.

The Tilapia species flock has figured prominently in this controversy and the position concerning these species has been admirably summarized by Trewavas (1949). In Nyasa there are six species of Tilapia, the nonendemic T. melanopleura, the endemic T. shirana which is most closely related to T. mossambica found in the Shiré river flowing from the lake, and a species flock of four endemic species, T. squamipinnis, T. saka, T. lidole and T. karongae, which are all more closely related to one another than to any species outside the lake. These four species differ from one another largely in the degree to which they are adapted for openwater conditions, indicating that they have evolved under such conditions. All the evidence from morphological, ecological and behaviour studies, and from studies of the history of the lake, leads to the conclusion that these four species have evolved within the lake. Trewavas (1949) pointed out that lake level changes may have added to the possibility of isolation in bays and creeks as suggested by Mayr (1947), but she concluded that in Nyasa geographical isolation appears to be supplemented by "minutely specialised breeding habits, induced or selected by environmental change". Brooks (1950) when reviewing the question of speciation in ancient lakes concluded that in the unparalleled evolution of cichlids in the African Great Lakes there is little doubt that biological factors are acting to reinforce the initial isolation controlled by intralacustrine geography; he referred to Kosswig's (1947) suggestion (without, however, realising that Kosswig's assumption that the Great Lakes cichlids are monogamous was wrong, see page 11) that specialised breeding behaviour may be important in restricting genetic interchange, and he concluded that any genetic divergence in a population isolated for only a relatively short time might, particularly if the colour pattern were altered, lead to inbreeding and more or less complete reproductive isolation even when the geographical barriers are no longer effective.

BREEDING BEHAVIOUR AND ECOLOGICAL DIFFERENCES IN TILA

The question now is how much have geographical and ecological isolation the did breeding did breeding diverge? hin the lake been concerned and how much have other factors such as breed-habits contributed to speciation within Lake Numer and the special diverge? within the lake been concerned and how much have other factors such as breeding habits contributed to speciation within Lake Nyasa. The widely overlapping zones occupied by the three species of the Tilapia complex which live at the southern end of the lake, where they live in mixed shoals for much of the year, have been considered above (page 7). Apart from T. karongae, which appears to be restricted to the northern half of the lake where it is found together with the other species, there is no evidence of any present-day geographical isolation, or of any complete ecological isolation among the present day Tilapia species.

Conditions for the formation of a new species demand (a) colonisation of new areas, and (b) isolation, or semi-isolation until the genetic characters become fixed. _ Ecological isolation need not, however, be complete throughout life, provided that the different populations are isolated from one another when the fish are breeding. This principle is particularly well demonstrated in the Nyasa Tilapia and does not seem to have been generally appreciated ; (it is very relevant for the many studies of the operation of Gause's principle (see page 7) as this is generally interpreted in terms of competition for food). In Nyasa shoals of different Tilapia, T. saka, T. squamipinnis, and T. lidole are caught together, all feeding on phytoplankton, for much of the year, but differences in depth and place at which the different species spawn ensure spatial isolation when spawning. This spatial difference is reinforced by temporal isolation as there are well-defined breeding seasons, and differences in colour of the breeding male (see page 12); this Nyasa species flock will be considered further (page 24) after more detailed examination of some of the factors which may have affected speciation in Lake Nyasa.

2. The uniqueness of the Nyasa Tilapia species flock

Reconsideration of the Nyasa Tilapia species flock in the light of further knowledge of the ecology and behaviour of cichlids in East African lakes 2*

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stresses that Nyasa is unique in having a Tilapia species flock and that this species flock is very small compared with the Haplochromis species flocks in this and other lakes. In Nyasa there are only six species of Tilapia compared with over a hundred recorded species of Haplochromis and many other cichlids of different genera (Bertram, Borley & Trewavas, 1942). In Victoria there are only two species of Tilapia compared with over seventy closely-related species of Haplochromis (Greenwood, 1954). This paucity of Tilapia species compared with Haplochromis species is probably connected with (a) Tilapia's restriction to algal food, whereas among the Haplochromis there has been an extensive adaptive radiation exploiting every available kind of food (see page 6), and (b) Tilapia's habit of moving from zone to zone in the lake as the fish grow and also making long movements in the lake. Thus there is little ecological or geographical isolation between populations of Tilapia. This is in direct contrast with Haplochromis species, which are all smaller than the Tilapia and tend to remain in one zone (for example over a hard substrate, or over mud, or sand, or in plant beds, or where the shoreline is rocky), throughout life (Greenwood, 1954), and are therefore, unlike the Tilapia, split up into populations which are subject to a high degree of isolation.

The only other lakes at present known to have more than one endemic species of *Tilapia* are Tanganyika, Victoria, and Lake Jipe (a small lake on the Pangani River), which each have two endemic species (Table 1). In Tanganyika the two endemic species, *T. tanganicae* and *T. karomo*, appear to have evolved under very different conditions and in different areas, the former in the main lake and the latter in the Malagarasi swamps flowing into the the lake ; the two species only meet in the Malagarasi delta so there is geographical as well as ecological isolation. In addition, these two species appear to have come from different stocks, *T. karomo* from the *T. mossambica* group, and *T. tanganicae* from the *T. galilaea* group of *Tilapia*. In Lake Jipe and Lake Victoria the two endemic species concerned are found together in each case, but it appears probable that in Lake Jipe two invasions have occurred and that in Lake Victoria the two species may have come from different stocks of *Tilapia*.

Lake Jipe is a shallow lake, probably not more than ten metres deep at the present day. With the well-known fluctuations in rainfall in East Africa this lake must have fluctuated greatly in extent and must have more or less dried out several times and then been recolonised from the Pangani River. Of the two endemic species T. girigan is very little different from T. pangani now found in the Pangani River, and T. jipe, which is more distinct, may represent the result of an earlier invasion from the river. This interpretation is supported by the similar male breeding colours and nest forms found in these two endemic species and in T. pangani (Lowe, 1955 a). The mechanism whereby these two sympatric species keep distinct is not yet known.

Trewavas (1949) and Worthington (1954) considered that T. esculenta and T. variabilis in Lake Victoria might be a species pair, but more recent field studies on *Tilapia* in East Africa lead to the conclusion that these two Victoria species are more distinct than was formerly believed. Certainly they are more distinct than are the members of the Nyasa species flock, and in the field T. variabilis gives the impression of being closer to the Tilapia of the eastward-flowing rivers allied to T. mossambica, and T. esculenta to T. nilotica, although Trewavas (1949) considered that they both could have evolved from one Tilapia not very different from the population named by Günther T. spilurus, now existing in the eastward-flowing Tana River in Kenya. Greenwood (1951 b) considered that Miocene fossils from Lake Victoria appeared to be most closely related to T. mossambica Peters. Greenwood (1951 a) has summarised ideas concerning the history of Lake Victoria and postulated that the fish retreated into the east-west river systems as the lake more or less dried up in the interpluvial periods, and then recolonised the lake as it expanded again during the pluvials, and it seems possible that the two present-day Tilapia may have originated from stocks entering the lake at different times or from different rivers.

3. The contrast between Tilapia speciation in Lakes Nyasa and Victoria

(a) The effects of depth and age of the lake

There is no evidence of any complete geographical isolation in Nyasa and the configuration of the present shoreline would make this seem improbable. However, the Nyasa Tilapia although adapted for "openwater-living" are rarely found over water more than fifty metres deep, probably because phytoplankton is less abundant there, and such deep water may form a barrier which is infrequently crossed. In Nyasa deep water comes right inshore at several critical places, for example between the south-east and south-west arms of the lake. The frequency with which such barriers are crossed is likely to be of significance. Also, as suggested above, such barriers may be crossed by brooding females, which are then not feeding, moving to inshore areas with their young. In the shallower Lake Victoria, conditions are more uniform and there is less necessity for the fish to move right inshore to find shallower water for spawning, so breeding populations are less likely to be discontinuous than in the deeper Lake Nyasa. In Victoria the Tilapia disappear from the catches at the time when phytoplankton is blooming in the main lake and it is possible that there are some seasonal movements into the open lake although very few Tilapia are caught out there ; marking experiments mentioned above (page 8) have shown that some Victoria Tilapia make long movements about the lake. The only exception noted to the lack of geographical isolation in Lake Victoria was the collection of a few rather atypical T. variabilis from near Godziba Island right out in the centre of the lake ; possibly this Godziba population has not been isolated, or sufficiently isolated, for long enough, to have become specifically distinct. The fluctuations in level known to have occurred in all these African Great Lakes would lead to greater mixing of populations when the level was low in the more uniform and shallower waters of Victoria than in the deeper waters of Lake Nyasa.

Lake Nyasa is thought to be a much older lake than Victoria so there has probably been longer for semi-isolated populations to become specifically distinct. The coefficient time x degree of isolation is undoubtedly important. Carter (1951, page 190) summarized work by Wright and others or the

- Deep water Barrier to all but Brosding Females,

mathematical effects of isolation in populations of various sizes, and concluded that conditions for evolution are most favourable in medium-sized local populations partially isolated from similar populations of the same species. In Lake Victoria there has been time for the evolution of a large *Haplochromis* species flock, but speciation in this genus is likely to have been more rapid than in *Tilapia* owing to the high degree of ecological and microgeographical isolation in the former genus, as discussed above (page 20). This emphasises that the degree of isolation, largely determined by the habits of the fish, has evidently been of far greater importance in the evolution of new cichlid species than the age of the lake *per se*.

(b) The effects of defined breeding seasons

In Lake Victoria some ripe *Tilapia* are found at all times of year. In Nyasa the *Tilapia* have well-defined breeding seasons and different species breed at somewhat different times of year. This means that temporal isolation is added to spatial isolation between species. The most marked difference is between *T. saka* which breeds in the hot weather before the rains, August to November, in water 2–4 metres deep, and *T. squamipinnis* which breeds during the rains from December to April, in water 16–20 metres deep (Lowe, 1952). The presence or absence of defined breeding seasons among *Tilapia* depends

on the hydrological conditions and these are primarily dependent on the geographical latitude. Lake Nyasa lies between 9° and 15° south and has a well-defined annual hydrological cycle in accordance with annual wind and rainfall cycles (Beauchamp, 1940). In the equatorial Lake Victoria the hydrological cycle is less definite and differs in the main lake and the Gulfs (Fish, 1957), and the Tilapia can escape an annual though ill-defined cycle in one part of the lake by moving about the lake, as marking experiments have shown that they do. The effect of latitude and hydrological conditions on Tilapia breeding seasons is clearly shown in those species found over a wide latitudinal range. Thus T. nilotica in Northern Nigeria (about 10° to 13° north) have a restricted breeding season, breeding only in the rains, whereas in equatorial waters breeding fish are found at all times of year (Lowe, 1958). Similarly T. mossambica in South Africa and Rhodesia breed only in the warm season (du Plessis & Groenewald, 1953; Jubb, 1952; Maar, personal communication) but in Indonesia (introduced) breed throughout the year (Vaas & Hofstede, 1952). Among many Tilapia most ripe fish are found in the rainy seasons, for example among T. macrochir and T. melanopleura in ponds in the Congo (de Bont, 1950), T. rukwaensis in Lake Rukwa (Ricardo, 1939 b, Swynnerton unpublished report), and Lake Victoria species (Lowe, 1956 b), but Aronson (1957 p. 274) records that in T. macrocephala in West Africa there was a marked drop in the spawning frequency during the period of heavy rains, coupled in some areas with retrogression of the gonads. How the effect of the rain operates is not clear; Aronson (1957) suggests that intensity of illumination may be a controlling factor. In Nyasa T. saka and T. lidole both breed before the rains and T. squamipinnis during the rains (is it significant that the latter species, which spawns deeper, spawns after a longer period of light increase ?); T. karongae at the northern end of the lake and T. shirana which lives inshore both appear to have more extended breeding seasons.

The Nyasa species have more restricted breeding seasons than species on a nearly comparable latitude in Rhodesia, where *T. mossambica*, *T. macrochir* and *T. andersonii* start to breed as soon as the "weather becomes warmer" about September and continue to spawn throughout the warm weather until about March, having many successive broods. The very restricted breeding seasons in Nyasa appear to be exceptional and are probably related to the hydrological conditions in this large lake, Meyen (1944) suggested that in species with long drawn-out breeding seasons divisions into "early" and "late" spawning groups might initiate speciation. Can this have happened in the case of *T. saka* and *T. squamipinnis* in Nyasa ? In Nyasa differences in hydrological conditions prevailing at different times of year may have been responsible for changes in spawning places following changes in place; the evidence is not yet sufficient to say which is most likely. Frost (1956) has found that in the Windermere Char, *Salvelinus willughbii* Günther, differences in spawning season and the depth at which two populations spawn appear to be contributing to speciation.

The very restricted breeding seasons in Nyasa mean that relatively few batches of young are produced a year compared with most other *Tilapia*. Also, the Nyasa *Tilapia* have larger eggs and fewer eggs are laid at a time than in other *Tilapia* species (Lowe, 1955 c). In the Nyasa species the young are, however, brooded to a large size than in other species, which may lead to greater survival of the young. In Victoria *Tilapia* fry seem to have a critical stage and suffer a high mortality when about 15 mm. long, which is also the size at which these fry become independent ; in Nyasa *T. saka* fry are brooded until 24 mm. long, *T. squamipinnis* fry until 30 mm. long, and *T. lidole* fry until 52 mm. long, this may help them over a critical stage and appears to be an adaptation associated with more openwater conditions.

The possession of definite breeding seasons, and associated with these definite breeding places, means that waters away from the breeding grounds can be exploited at other times of year, the fish congregating at a well-defined and advertised rendezvous in the spawning season. This may have been an important factor in the colonisation of openwater in Nyasa by species which have to return inshore to spawn, such as T. lidole among the *Tilapia* and the zooplankton-feeding "Utaka" group of *Haplochromis*, some species of which return to the same areas to spawn for a month or six weeks every year (Lowe, 1952). (Indeed, the absence of definite seasons and places for breeding may be one of the reasons why Lake Victoria has not developed a comparable group of openwater zooplankton-feeding *Haplochromis*, as without such a rendezvous for spawning it is difficult to see how species occupying this openwater niche could evolve).

Thus to sum up, in Victoria, which is a relatively shallow lake, conditions are more uniform and the *Tilapia* move from zone to zone as they grow and make long movements about the lake, so there is no ecological or geographical

isolation; neither is there any temporal isolation as the Tilapia breed throughout the year. Nyasa, on the other hand, is a deep lake so conditions are more varied ; although the Nyasa Tilapia are adapted for more openwater-living, water more than fifty metres deep presents an infrequently crossed barrier; there is no direct evidence that the movements of the fish about this lake are as long as those in Victoria, but the brooding female makes quite long movements to inshore areas with family broods of young ; the presence of definite breeding seasons means that temporal as well as spatial isolation may have helped to keep new populations apart.

4. Possible lines of evolution within Lake Nyasa

The salient facts bearing on the relationships of members of the Nyasa Tilapia species complex appear to be: (1) T. saka and T. squamipinnis are morphologically most alike and appear to be the most recently separated species, (2) T. lidole is a specialised form for more openwater conditions which could most easily have arisen from a T. saka-like form, (3) The main mystery remains in the north, and in particular the relationship between T. saka and T. karongae. Very little is yet known about the biology of the Tilapia at the north end of the lake. T. karongae may be restricted to the northern end as this is the only part of the lake with permanent inflowing rivers ; this species appears to have a protracted breeding season, as is more usual for Tilapia at this latitude, but further work may show that all the species have a more protracted breeding season at the north end of the lake (which is, of course, nearer the equator) than they do further south.

Geological evidence suggests that the north is the oldest part of the lake (Dixey, 1941) and it would appear to be the cradle of the species flock, the . ancestral Tilapia, thought to belong to the T. galilaea group of the genus (Trewavas, 1947 b), gaining access from the rivers to the new and deepening lake. This Tilapia would probably have had rather estuarine and inshoredwelling habits at first, the young were probably not brooded to a large size, there would be a protracted breeding season as among Tilapia in the rivers of Rhodesia, and a dark, probably not very black, breeding male. As the lake deepened and with fluctuations in lake level this form may have become split into populations, becoming T. karongae, possibly in the estuary of one of the permament rivers, and a T. saka-like form, possibly in the main lake. The enlarged pharyngeal bones of T. karongae may have developed gradually in association with the silt burden of the river estuaries as suggested by Trewavas (1941), a suggestion supported by the enlarged pharyngeal bones noted in some T. squamipinnis from this area (Lowe, 1952, page 8).

The species T. lidole and T. squamipinnis would both appear to have evolved from a T. saka-like form after fluctuations and general increases in lake level brought more openwater conditions closer inshore ; deep water, only very infrequently crossed by the Tilapia, probably helped to isolate the populations of the incipient Tilapia species. The well-defined breeding seasons probably developed as the lake and Tilapia populations extended southwards and as the lake increased in depth and developed a regular hydrological cycle.

T. lidole shows greater morphological differences from T. saka than does T. squamipinnis which suggests that T. lidole originated earlier from a T. sakalike form, though many of the differences are adaptations associated with the more openwater habit of T. lidole. The possession of more or less the same breeding season in T. lidole and T. saka at the south end of the lake (Lowe, 1953) might suggest that the split came after the restriction of the breeding season, but this may be a parallel development in the two species, as T. squamipinnis, believed on morphological grounds to have evolved more recently than T. lidole, may have split off from a T. saka-like form before this restriction of breeding season. T. lidole retained the dark male breeding colour similar to that of T. saka and T. karongae. It is possible that the movements of the brooding females of the incipient T. lidole may have had a vital role in the evolution of this species (see page 10).

At another time and place, probably after some rise in lake level and perhaps further south where and when hydrological conditions facilitated the development of breeding seasons, the T. saka-like population appears to have divided, those fish breeding before the rains in very shallow water and retaining the dark breeding male becoming T. saka, and those breeding later, during the rains, in deeper water and developing a blue and white male becoming T. squamipinnis. Whether changes in breeding season or place came first is not known. Hydrological differences such as wave action might account for the later-breeding T. squamipinnis breeding in somewhat deeper water; alternatively changes in depth of breeding places due to changes in lake level might, particularly if light is a controlling factor in determining spawning frequency as suggested by Aronson (1957), lead to later spawning in the deeper spawning populations (though this does not appear to have happened in the case of the deeper-spawning T. lidole). How much geographical barriers within the lake, such as barriers of deep water, aided this split is not known, and this remains the crux of this sympatric speciation controversy. The most probable sequence of events would seem to be that the lake rose and those fish which could spawn in deeper water stayed in these deepened areas and gradually delayed their spawning, then in some population semi-isolated by barriers of deep water a mutation occurred leading to a change in male breeding colour, after which selective breeding between fish with this colour and the later and deeper spawning habit enabled this population to keep distinct when the geographical isolating barriers were no longer effective. Such barriers would become less effective as the numbers of fish increased.

Throughout the ages fluctuations in lake level have probably helped to keep the different populations of the Nyasa Tilapia complex in balance, the more openwater-living forms increasing during periods of high lake level and the inshore-dwelling forms becoming relatively abundant in years of low water.

IV. SUMMARY OF CONCLUSIONS

IV. SUMMARY OF CONCLUSIONS 1. Within the genus *Tilapia* three distinct types of breeding behaviour occur, the fish in the three groups being designated substratum-spawners, paternal-brooders and maternal-brooders. Structural and ecological differences are associated with behaviour differences between these three groups. 3 Jistinc T Types of breeding Behaviour are associated with behaviour differences between these three groups.

2. Substratum-spawners comprise only four known species, which are of wide distribution in Africa; paternal-brooders are also few in number and appear to be confined to West Africa and the Congo. The numerous *Tilapia*-species found in the waters of East and Central Africa, including all the species endemic to the Great Lakes, are maternal-brooders.

3. Breeding behaviour and ecological differences between the three groups are summarised.

4. The significance of these differences for evolution within the genus is discussed. Despite the probably greater antiquity of substratum-spawners, it is only among maternal-brooders that extensive speciation has occurred. Characters which may have accounted for the extensive speciation of the maternal-brooders include (a) preadaptation for more openwater conditions, both by ability to feed on phytoplankton and by brooding the eggs and young, and (b) the polygamous habit combined with the congregation of males on certain spawning grounds; this may have had effects in the spread of mutations and also presents ideal conditions for sexual selection to operate and has probably contributed to the development of the striking male breeding colours. These breeding-colours advertise the spawning grounds so there is a well-marked rendezvous for spawning; this effect is particularly noticeable in Lake Nyasa where there are well-defined breeding seasons, and permits the fish to exploit feeding grounds away from the spawning grounds at other times of year. The ability of the male mouth-brooder to fertilize continuously over long periods allows rapid spawning as pre-spawning courtship is reduced to a minimum.

5. Fish of the family Cichlidae speciate readily; in the substratumspawners speciation may have been inhibited by their restriction, both by food and spawning habits, to inshore waters where plants can grow; thus populations can only spread contiguously along a shore line.

6. The uniform predominently vegetarian diet, found in all species of *Tilapia*, and the *Tilapia*'s habit of moving from zone to zone as the fish grow (in contrast with the *Haplochromis* species which tend to remain in one particular ecological zone throughout life), and their long movements about a lake, would appear to have militated against the formation of *Tilapia* species flocks comparable with those of *Haplochromis* in Victoria and other lakes.

7. Nyasa appears unique in having a *Tilapia* species flock, evolved within the lake; Lakes Tanganyika, Victoria and Jipe all have two endemic species of *Tilapia*, but in Tanganyika there is geographical as well as ecological isolation between the two species, and these may also have come from different stocks; in Victoria the two species appear to have come from different stocks of *Tilapia*, and in Jipe the two species appear to have arisen by invasions at different times from the Pangani River.

8. In Nyasa the colonisation of new areas was probably promoted by the ability of the phytoplankton-feeding *Tilapia* to cross openwater combined with the necessity for them to move inshore to find suitable bottom for spawning; the movements of the brooding females may have played a special part. In Lake Nyasa incomplete geographical isolation, brought about mainly

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and superseded by ecological isolation, the *Tilapia* species separating to spawn at different depths, and temporal isolation, the species having well-defined breeding seasons which differ in the two most closely similar species, T. saka and T. squamipinnis, and a difference in colour of the breeding male between these two species. T. saka appears to be nearest the basal stock from which T, karongae, T. lidole and T. squamipinnis have been derived.

ACKNOWLEDGMENTS

I am most grateful to Dr E. Trewavas of the British Museum (Natural History) for her very great interest and assistance in many ways throughout these studies of *Tilapia*, and I would especially like to thank her and Dr M. E. Brown (Mrs G. C. Varley) for reading and criticizing the manuscript. The Director of the East African Fisheries Research Organization Mr R. S. A. Beauchamp and my colleagues, particularly Mr P. H. Greenwood, together with Dr E. B. Worthington have all contributed by many stimulating discussions during the course of this work.

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SOME ASPECTS OF EVOLUTION IN LAKE NYASA

GEOFFREY FRYER

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Received December 12th 1958

As a result of some two years' field beaches, predominate. Some of the sandy work on the fauna of Lake Nyasa, and shores are reed-fringed, others bare. This, gained, a number of points relevant to the majority of sandy shore species. Other evolutionary phenomena shown by that major littoral habitats are few, and estuafauna have emerged. Some of these have rine regions, occasional areas of local been mentioned in previous papers, par- swamp, and even rarer shingly beaches ticularly in one dealing with the ecology cover all the other main types. Littoral and evolution of some of the littoral fishes macrophytic vegetation is very sparse; it (Fryer, 1959), but several points, albeit is represented over much of the lake aldisconnected, but none the less pertinent, most entirely by Vallisneria, and even this remain to be presented. It is the purpose is absent from some exposed sandy of the present paper to draw attention to these points.

(1) THE NON-DIVERSITY OF HABITATS

The fact that some of the great lakes of Africa are large and deep has led to the assumption that they provide a great diversity of habitats (de Beaufort, 1951). That this is not so in certain cases was. however, pointed out by Worthington (1954), who referred to the monotony of the shorelines of Lakes Rudolf and Kioga, and to the absence of dissolved oxygen at depths of 60-200 meters in certain other lakes. More recently, when referring to Lake Nyasa, Jackson (1955) suggested that "sufficient stress has not been laid ... on the large variety of habitats present in a big lake such as Nyasa." With this I cannot agree, for, in spite of its great size, Lake Nyasa seems to provide a remarkably small assortment of habitats.

As in all lakes, save the very smallest and shallowest, Lake Nyasa is divisible into littoral, sublittoral and profundal regions and there is the usual pelagial zone -here of enormous extent and of typical uniformity. In spite of the great length of its shoreline the number of major littoral habitats in the lake is remarkably few; two types, rocky shores and sandy bottom is very nearly in this deoxygen-

subsequent analysis of the information however, is of scant importance to the beaches, and is completely absent from rocky shores, which support no higher plants whatsoever. Habitat differences related to the zonation of plants at different depths, which are so prominent a feature of many lakes, are scarcely recognizable in Lake Nyasa. The only vegetational change with increasing depth is usually the disappearance of Vallisneria.

Within each major littoral habitat there are of course microhabitats and/or niches (depending on the usage of these terms), but there is nothing to suggest that the number of microhabitats is any greater than in other lakes; in fact, the uniformity of conditions within each major habitat suggests that such microhabitats are relatively few (see also remarks on the restricted number of available feeding niches, p. 442).

The great maximum depth of Lake Nyasa (over 700 meters) suggests the existence of a series of habitats in the profundal region. However, at least 45% of the bottom area of the lake cannot be inhabited by aerobic organisms because it is completely and apparently permanently oxygenless, and, at least in parts, contains hydrogen sulphide. A considerable percentage of the remainder of the

which dissolved oxygen has been detected times when thermal stratification is most is about 250 meters and here the percentage saturation is always too low to permit tween the upper layers of water and that most animals to survive. At a depth of at 200 meters is only about 6° C., and 150 meters the amount of dissolved oxy- frequently the habitable zone is more or gen not infrequently falls below 1 part less homothermal. per million (Beauchamp, 1953).

down to say 100 meters, a series of niches exists for exploitation. However, notwithstanding the presence of a few deepwater species of Bathyclarias (caught at depths as great as 70 meters) (Jackson, 1959), which in any case must eat to live and are therefore precluded from living at the greater depths which their tolerance of low oxygen tensions to some extent permits, it is true to say that if all the water below a depth of say 30 meters be discounted from consideration, the picture of the fauna of Lake Nyasa would scarcely differ from that which it presents in its entirety.

Even if a distinct "deep-water" fauna (at depths of say 70-120 meters) should be discovered in Lake Nyasa, as one has been in Lake Tanganyika (Poll, 1956a and b), the argument would in no way be altered insofar as the already known fauna and its habitats are concerned.

uniformity of conditions in Lake Nyasa, as compared with many other lakes, are the relatively slight change in temperamilitates against the development of seasonal faunas, and, more important, the tion is reinforced, at least during the 1959). summer months, when most animals are active, by marked differences in temperature (a difference of 15° or 20° C. bemeters is by no means unusual). Such of foods at their disposal. striking thermal gradients exist also in champ's data such temperature gradients oboride apparently of

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It is therefore apparent that Lake It is not denied, however, that in water Nyasa does not offer the diversity of habitats that some have supposed.

(2) QUALITATIVE AND QUANTITATIVE POVERTY OF CERTAIN ANIMAL AND PLANT GROUPS

Of the Nyasan fauna only the fishes and one or two other groups have been studied in detail by systematists. However, ecological studies in the littoral zone have shown that the number of species of invertebrates in certain groups is surprisingly low, thus to a large extent bearing out Moore's statement made as long ago as 1903 that the fauna of Lake Nyasa consists of "fishes and molluscs." Even molluscs are by no means everywhere plentiful, and on rocky shores in the northern part of the lake they appear to be completely absent. Of the Crustacea the order Cladocera is almost entirely absent from the littoral zone, at least in the northern part of the lake. The num-Further points in connection with the ber of species of the larger insects is also surprisingly low, and the species that do occur are by no means so abundantly represented as in many lakes. The paucity ture throughout the year, which perhaps of the higher plants has been referred to above. On the other hand, a few groups, such as lithophilic chironomid larvae and small thermal gradient with increasing ostracods, may occur in enormous numdepth. In temperate lakes vertical zona- bers in certain microhabitats (Fryer,

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Further points in connection with the uniformity of conditions in Lake Nyasa, as compared with many other lakes, are the relatively slight change in temperature throughout the year, which perhaps militates against the development of seasonal faunas, and, more important, the small thermal gradient with increasing depth. In temperate lakes vertical zonation is reinforced, at least during the summer months, when most animals are active, by marked differences in temperature (a difference of 15° or 20° C. between water at depths of 1 meter and 30 meters is by no means unusual). Such striking thermal gradients exist also in warm monomictic (subtropical) lakes (Yoshimura, cited by Hutchinson, 1957). In Lake Nyasa, as revealed by Beauchamp's data, such temperature gradients

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Thus it is apparent that the fishes, which exhibit the most remarkable speciation of all the groups in Lake Nyasa, have not had a particularly diverse assortment of foods at their disposal.

It is relevant to record here that the "lake flies" which often emerge in vast swarms from Lake Nyasa are not, as is generally assumed, chironomids, but chaoborids, apparently of one species only,

Corethra edulis Edwards. They were referred to as chironomids by Beauchamp (1940) whose statement was utilized as the basis of a supposition by Brooks (1950) in a well-known review. As the larval habits of these two groups differ fundamentally, the one being benthic and conveys a completely wrong impression of the hydrological and biological regimes of the deeper layers of Lake Nyasa, and a new species possibly referable to Haplocalls for correction.

(3) PROOF OF STATEMENTS (1) AND (2) AND THEIR EVOLUTIONARY SIGNIFICANCE

Since many species of fishes are present in Lake Nyasa (particularly in the family Cichlidae, of which more than 180 species are now known), the occurrence of many species per habitat should follow if, as has been suggested in (1), there vision of a great diversity of habitats as are few major habitats in the lake. This is indeed true. Further, if, as suggested in (2), the number of available foods is few, then the utilization of the same kind of food by several species is to be ex- the great depth of Lake Nyasa enabled pected. Again this is true. (Details of the basin to retain water, and with it an ' the co-existence of many species in the aquatic fauna, during the arid interpluvial major littoral habitats, and of their feed- periods of the Pleistocene that resulted in ing habits, are given in Fryer, 1959.)

evolutionary biologist is that one cannot per se has also been of importance. attribute the remarkable speciation of the . As is pointed out elsewhere (Fryer,

ability of a diversity of habitats for colonization, nor to the availability of a diverse series of foods that would allow each species to fill a different feeding niche.

Perhaps, as a corollary to the second conclusion, attention may be drawn to the remarkable habit of feeding on the scales the other planktonic, this erroneous idea of other fishes that has arisen at least three times among the Nyasan cichlidsin Corematodus, in Genvochromis, and in chromis or perhaps meriting the erection of a new genus. This habit may have arisen partly as a result of the availability of only a few different types of food and partly because so many other fishes were available for exploitation.

(4) THE TRUE IMPORTANCE OF SIZE

Although the great size and depth of Lake Nyasa have not resulted in the prosome have supposed, these factors have not been without importance in evolution. First, as was pointed out by Worthington (1937) and is now generally accepted, the dessication of shallower lakes else-The significance of these fact to the where in the continent. In addition size

cichlid fishes of Lake Nyasa to the avail- 1959), the relatively few major habitats

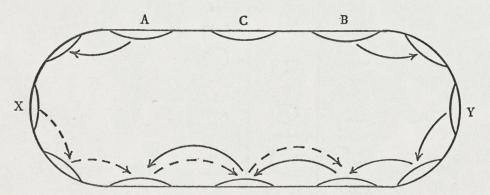


FIG. 1. Diagrammatic representation of Lake Nyasa showing how one type of habitat (e.g. rocky shore) is reproduced many times to give a series of similar but isolated habitats. Arrows indicate movements of fishes from original centers. For details see text.

are fragmented: rocky shores and sandy organisms, which han easily be dispersed beaches alternate. Now consider a given by currents, can be isolated in this way stock of an organism that in the past be- suggests that these animals that are came distributed around the whole or capable of resisting such chance dispersal part of the lake in suitable habitats as a are even more likely to be isolated as a result of the various changes, some of them possibly cataclysmic, that have taken place during the history of the basin. Representatives of this stock may have begun to specialize in different directions in areas remote from (or near to) one another, e.g. at X and Y (or A and B) in figure 1. Both specializations, although perhaps different, may have been successful. Now the time taken to overcome the holds this view (254). His suggestion various barriers between the two and to that prefation is slight in Lake Nyasa cover the distance involved would, it was ques oned by Fryer and Iles (1955), is postulated, sometimes be sufficient to who showed that predacious fishes are allow the two populations to become sufficiently distinct to prevent interbreeding it was suggested that the predators, by when they (e.g. populations X and Y in retarding the growth of populations of figure 1) eventually met. Such a state of non-pressiony success, help to prevent affairs is comparable with the Lesser competition between them for the avail-Black-Backed-Herring Gull circumpolar able foot and perhaps in some cases for cline in the northern hemisphere. Even living space, and consequently assist in in cases such as A and B where "swamp- the survival of large numbers of species ing" could take place at C, the outwardly in a giver habitat (Fryer, 1959). It remigrating mutants could become more mains to be seen thich of these diametriand more distinct and separated by ever cally opposed views will prove to be corincreasing distances until they eventually rect. Here some further aspects of predaoverlapped. Evolution of this type could tion that appear to support the second not take place so easily in a smaller lake view are put forward. where the time required to cover the smaller distances and surmount the less littoral zine, a given species of fish usunumerous barriers would be less.

planktonic organisms can be isolated in from say a rocks shore should attempt different regions, although the pelagial to cross # strip ? sand or vice versa it waters in which they live extend through- would, as a result of its coloration and out the lake with no apparent barriers. ill-adapted escape feaction in that habitat. The fact that this is probably a reflection be particularly easy prey for a predatory of different types of lake morphometry fish. Vorthinging (1954) said exactly acting via the trophic regime in different the same thing. iz., "Where predators areas in no way alters the fact that size are continually of the prowl, the lesser is ultimately the governing factor. Thus forms, dapted to heir particular ecologithe endemic copepod Diaptomus (Ther- cal niche can deart from them to colomodiabtomus) mixtus Sars and the non- nise new micro-attironments or to breed endemic cladoceran Daphnia lumholtzi with the personers only on pain of Sars have been found in abundance at the death," but used this as evidence that southern end of the lake but not in the predation has had marked retarding in-

result of the great size of the lake.

(5) THE ROLE OF PREDATION-PURTHER SUGGESTIONS

The suggestion that lakes whose cichlid fish fautas are subject to considerable predation show less speciation than those in which predation is slight was put forward by Worthington (1937), who still particularly numerous in this lake. Later

(a) I has been emphasized how, in the ally is agorously restricted to a given The size of the lake is such that even habitat. Now, if for any reason, a fish north (Fryer, 1957). The fact that such fluence on specifion. This is surely a

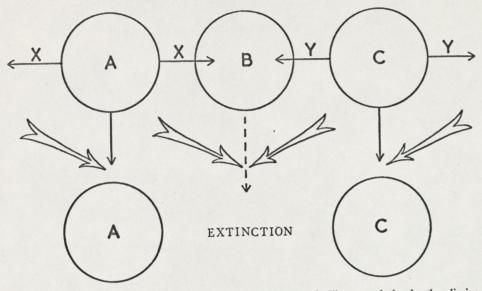


FIG. 2. Diagrammatic representation of how predation can facilitate speciation by the elimination of hybrid populations. A and C are the original populations specializing in directions X and Y respectively. The vertical arrows represent the passage of time and the broad arrows predation. For further explanation see text.

wrong interpretation. By restricting species to particular habitats the predators in fact assist in keeping them isolated in numerous discontinuous populations and assist in the process of speciation can be therefore undoubtedly favor rather than restrict speciation. If this be so, then one can readily understand why the presence could be more) populations as at A and of the large number of predacious species shown by Fryer and Iles (1955) to occur in Lake Nyasa is not incompatible with the existence there of the greatest total of cichlid fishes of any African lake.

(b) It must be generally agreed, and is agreed to by Worthington (1954), that ill-adapted mutants of the fishes of the various habitats will more readily fall victims to predators than their betteradapted brethren. Such a belief is indeed implicit in the concept of natural selection. In the absence of predators some production of ill-adapted offspring could of these ill-adapted mutants would survive (though others would be eliminated population would be more easily elimiby other means), and this would lead to nated by predation and competition than a reduction in efficiency of the species concerned, and thus enhance the likelihood elimination would prevent the swamping of elimination by competition. Predatory activity of this kind therefore surely as-

sists in the survival of species rather than in their elimination.

(c) Another way in which predation can understood by reference to figure 2. Consider a stock of fishes split into two (it C. Now suppose that population A begins to specialize in a certain direction X and population C begins to specialize in a different direction Y. Members of each of these populations would eventually move outwards from their centers of origin as shown in the figure. Now, if genetical or behavioral differentiation had not proceeded to such a stage as would prevent interbreeding of these stocks, a hybrid population in which the antagonistic X and Y tendencies resulted in the arise at B. Such an ill-adapted hybrid either of the parent stocks, and such and mixing of the X and Y tendencies which could then continue to increase of distinct species between which gene hibited both by the various members of a flow was impossible. Here again, therefore, the role of predation, which acts as a selective sieve, would be to favor rather than to restrict speciation.

forward elsewhere, point to the conclusion that the presence of predacious fishes in Lake Nyasa, and in other lakes, has probably hastened and assisted the speciation of the non-predatory species.

(6) THE RESTRICTED RADIATION PATTERNS OF THE CICHLID FISHES

The overall picture of the adaptive radiation shown by the cichlid fishes of Lake Nyasa is one of completeness. Every available niche appears to have been filled. The means whereby this filling of niches has been accomplished, however, seems, at least in part, to be somewhat different from that generally accepted as explaining the ecological evolution of related species. Thus, analysis of the ecological data reveals the existence of a number of morphological types, some of generic and one of suprageneric standing, each of which has its own ecological preferences. Radiation of each of these particular types tends to be restricted within certain rather narrow limits. The outstanding example of this is that of an assemblage of 9 genera comprising some 27 species that form a compact morphological group whose members are more closely related to each other than to the species of any other genus in the lake. Although the members of this group show some very striking trophic adaptations, many of which are described elsewhere (Fryer, 1959), adaptive radiation has in fact been rather restricted in that all these species are to a greater or lesser extent confined to rocky shores, most of them rigorously so, and very many of them take exactly the same kind of food, namely, algae scraped from the rocks.

Among these rock-frequenting species

until ultimately they became characteristic identical food preferences are often exsingle genus and by the members of several genera. For example, within this group is one genus, Pseudotropheus, comprising 12 known species, of which at All these suggestions, like those put least 8 feed exclusively on lithophilic algae, as do members of the genera Labeotropheus and Petrotilapia.

The same phenomenon is exhibited at a generic level by other fishes of the lake. For example the genus Rhamphochromis, with at least 8 species, consists exclusively of active piscivorous species that frequent open water just offshore. Similarly the 24 or more species of Lethrinops, though showing a certain amount of trophic diversity, seem to be confined to sandy shores, where they feed on benthic invertebrates, usually insect larvae. More ecological information on this genus is needed, but it can at least be stated that not a single species was found on a wellstudied rocky shore in the northern part of the lake during a comprehensive survey of its fauna, though several species occurred on an adjoining sandy beach.

The genus Haplochromis, which has given rise to rather more than 100 species in Lake Nyasa does not, at first sight, appear to conform to the pattern described above, for its members have colonized a variety of habitats and have evolved widely differing specializations. However, within this genus, whose limits are at present somewhat vague and certainly wider than those of most if not all other Nyasan genera, a certain amount of group-specialization of the type described above has taken place. This is shown most strikingly by an assemblage of species known collectively as the "utaka," that have taken to feeding on zooplankton and that are so similar morphologically as to render identification of some species distinctly difficult. Mr. T. D. Iles, who is making an intensive study of this group of fishes, has so far been able to recognize at least 16 species with certainty. He tells me that when his studies are comincreased. I am most grateful to Mr. Iles fishes of African lakes before sufficient for this as yet unpublished information.

from that found in many other animal groups where, as in the passerine birds surveyed by Lack (1944), closely related species usually occupy separate habitats or regions or, if they co-exist, tend to take different foods. The latter type of radiation is indeed found even among the cichlid fishes of African lakes, for Greenwood (1958) reported the existence among the 70 species comprising the species flock of in large measure in Lake Tanganyika, Haplochromis in Lake Victoria, of several morphologically similar species-pairs one member of which lives inshore on hard bottoms, the other offshore on soft bottoms, which implies that radiation took place by the colonization of new habitats during specific divergence. Such an evoradiated into a variety of habitats and bebeen tacitly assumed by theorists seeking ample, there are prairie and forest races

plete this total will almost certainly be to explain the evolution of all the cichlid ecological data were available. This, This type of radiation is quite different however, certainly does not apply to some of the rock-frequenting, algal-eating species of Pseudotropheus and allied genera. nor to some of the feeders on chironomid larvae among the sand-loving species of Lethrinops, nor to the numerous openwater plankton feeding "utaka," of Lake Nyasa. It seems probable also that a similar speciation pattern to that shown by these cichlids of Lake Nyasa will apply which is morphometrically similar to Lake Nyasa and has a basically similar cichlid fauna.

The type of radiation described above. while not unknown elsewhere in the animal kingdom, seems to be distinctly unusual and I know of no case so striking lutionary history during which the fishes as the ones described. On the contrary cases are recorded where infraspecific gan to take different foods seems to have taxa frequent different habitats. For ex-

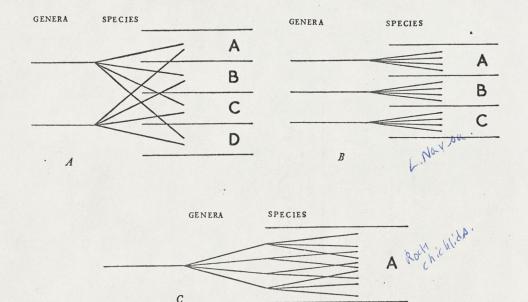


FIG. 3. Patterns of adaptive radiation. In each diagram the bands designated by the capital letters represent habitats: (A) The type of adaptive radiation typical of many groups of animals. (B) Adaptive radiation as exhibited by certain cichlid fishes of Lake Nyasa. (C) Adaptive radiation as exhibited by a group of rock-frequenting cichlid fishes (the "mbuna") of Lake Nyasa.

of the deermouse Peromyscus maniculatus.

(7) THE SIGNIFICANCE OF LAKE LEVEL FLUCTUATIONS

The level of Lake Nyasa is not stable but is subject to annual and longer-term fluctuations. Possible influences of these fluctuations on the evolution of fishes were suggested by Trewavas (1947) and by Lowe (1952), and further points are mentioned by Fryer (1959). A rather important point which has not yet been sufficiently stressed is the influence of these fluctuations on the basic food supply of the littoral zone which is, faunistically, both qualitatively and quantitatively the richest zone of the lake. On sandy shores Vallisneria and its epiphytic algal flora are the most important basic foods, at least in the northern part of the lake. Now sandy shores often shelve quite gently near the shoreline then pitch steeply downward. As was observed on one such sandy beach (Fryer, 1959), a fall in the lake level may result in a serious depletion of this food on the gently sloping part without any possibility of an equally productive flora developing on the steeper slope, because of the limitations imposed by depth on the photosynthetic activities of the plants. Such a state of affairs could lead to an intensification of competition among the fishes utilizing these primary food sources either directly or indirectly; to the elimination of the less successful individuals or species; or to migration, for which, under normal relatively stable conditions there is very little tendency among most species.

(8) PLANKTON FEEDING AND SHOALING IN NYASAN FISHES

The adoption of plankton feeding by Nyasan fishes seems to have gone hand in hand with the habit of shoaling. This is readily seen by a consideration of the plankton-feeding fishes of the lake. The small cyprinid Engraulicypris sardella (Günther), which subsists entirely on plankton (including occasional gluts of H. kiwinge frequents rocky shores and,

pupae of the midge Corethra edulis Edwards), is a good example, for where one specimen is found one usually finds thousands.

Numerous cichlids exhibit the same phenomenon. The most striking case is provided by the complex group of Haplochromis species known in the vernacular as the "utaka." All these appear to be plankton-feeding and shoaling species, yet none of the numerous other species of Haplochromis of the lake, which occupy a diversity of feeding niches, shoal.

A particularly instructive series showing how the degree of assumption of one habit is associated with a corresponding development of the other is that of the Tilapia species of the lake. Neither of the inshore species, T. melanopleura Duméril and the endemic T. shirana Boulenger, is a plankton feeder and neither shoals, but the endemic T. saka Lowe and T. squamipinnis (Günther), which inhabit more open water and feed partly on plankton, show a marked tendency to shoal, while the truly open-water plankton-feeding T. lidole Trewavas shoals throughout life (Lowe, 1952, and personal observations).

A particularly pertinent case is that of Cynotilapia afra (Günther), whose phyletic relationships are clearly with a group of littoral rock-frequenting fishes, none of which shoal. This species has taken to feeding on plankton but is still not emancipated from rocky shores (Fryer, 1959), yet, like the other plankton-feeding fishes of the lake, it shows a marked tendency to shoal.

To some extent this habit might be regarded as an example of ecological neoteny. This can be explained by reference to Haplochromis kiwinge Ahl. In its very early stages this species is brooded in the mouth of the female parent, and a dense shoal of young at this stage of development has been watched in nature feeding on particulate matter, presumably plankton, while guarded by the female (Fryer, 1956). Later in life

largely on zooplankton (Fryer, 1959). when opportunity offers, suggests that At this stage it tends to move around in considerable advantages are conferred on groups, though as its size increases still those species which brood their eggs and more and it becomes more omnivorous it young in the mouth; that is on the cichtends to become solitary.

from plankton to some other food being surviving for more than a few minutes accompanied by a breakdown in shoaling habits is not uncommon among freshwater fishes generally. In some cases the cessation of shoaling is probably imposed by in this habitat, and in fact of the six necessity when the diet is changed, for non-cichlid species that frequent rocky not all habitats could withstand the effects shores in the northern part of the lake of large shoals of fishes demanding the during the whole or part of their life same kind of food. The pelagial zone and history four are either definitely known the plankton which it produces impose no to breed elsewhere or are suspected of such limits and the habits of immaturity doing so. Of the other two Mastacem-

nected with the maintenance of the shoal- and crevices inaccessible to other species ing habit but which, as is shown by the of the habitat, and may well deposit its incipient shoaling behavior of Cynotilapia eggs in such situations. The breeding afra, has probably contributed but little habits of the other, Labeo cylindricus to its evolution, is the tendency for shoal- Peters, are not yet known, but other speing species to congregate at certain points. cies of this genus both in Lakes Nyasa In Lake Nyasa echo sounding has re- and Victoria ascend rivers and streams vealed the existence of shoals of planktonfeeding Haplochromis in areas where submerged rocks approach the surface and where the African fishermen say there are for certain other habitats such as sandy currents. Similar echo traces involving shores for, as shown in (3), the number plankton-feeding fishes are obtainable in of species per habitat is high, though percomparable situations in other African haps nowhere are the difficulties attendant lakes (e.g. see Capart, 1955). This seek- on "free spawning" so great as on rocky ing out of particular areas where plankton shores. As on rocky shores some of the is presumably obtainable with a minimum of effort will tend to concentrate pelagic mesops Günther, are known to run up fishes and thus reinforce the shoaling impulse.

(9) THE IMPORTANCE OF MOUTH-BROODING AMONG THE CICHLID FISHES

The presence of very dense populations of fishes in the littoral zone of Lake the lake, and can scarcely be considered Nyasa and particularly on rocky shores as truly lacustrine. Even though the (Fryer, 1959), considered in conjunction breeding habits of these species are often with aquarium observations which have unknown one can at least be sure that shown that even the herbivorous members of these communities eagerly devour eggs

while more catholic in its tastes, still feeds and young of their own and other species

lids. Indeed it is difficult to conceive of The phenomenon of a change in diet unprotected eggs shed on a rocky shore unless secreted in inaccessible crannies. Fishes that produce such eggs are therefore virtually precluded from breeding can be retained, as can the feeding habits. belus shirana Günther is a small skulking A factor that is perhaps not uncon- fish of eel-like form that inhabits cracks to spawn (Lowe, 1952; Frver and Whitehead, 1959).

> The same state of affairs holds good non-cichlids of sandy shores, e.g. Labeo rivers to spawn.

> Relevant to this matter is the fact that at present many of the non-endemic species of the Nyasa basin, which are almost always non-cichlids, are, as Jackson (1955) has pointed out, confined to rivers, lagoons, and other situations fringing they are not mouth-brooding fishes.

It is also interesting to note that the

which are not mouth brooders, namely Tilapia melanopleura Duméril and T. sparrmani A. Smith, which, by virtue of their wide distribution in Africa, must be regarded as very successful species, have met with little success in colonizing Lake Nyasa. T. melanopleura occurs only in certain weedy lagoons connected with the lake and in small numbers in a few sheltered regions of the littoral zone, and the parent to feed more than a limited T. sparrmani occurs only in lagoons and rivers and has not been recorded from the lake proper. This of course may be due in large part to the lack of suitable habitats for these two species in the lake, but duce the smallest number of eggs per more significant is the fact that it is not from such egg-guarding species but from those forms which developed mouthbrooding that the cichlids which occupy the various habitats of Lake Nyasa today have been derived.

Such facts as these point to mouthbrooding as having played an important part in the biological success of the cichlids of Lake Nyasa. They also go a long way towards explaining why some of the habitats of the lake can support dense sedentary populations of fishes and why these populations are composed largely of mouth-brooding cichlid fishes.

(10) BROOD SIZE, EGG SIZE, AND HABITAT AMONG THE CICHLIDAE

Data concerning the size of the brood produced by the Nyasan cichlids are still too scanty to permit the making of many deductions, but in view of the interest recently aroused by Lack in the ecological and evolutionary significance of allied phenomena, and particularly in the clutch size of birds and the litter size of mammals (see Lack, 1954, for review), brief mention of one point is merited.

The habitat in which most predation on the very early stages of development is to be expected is that in which the population density is greatest; that is, on rocky shores. Under such conditions selection may be expected to favor those species producing a few large eggs which can be

two cichlid species of the Nyasan area brooded until the young have attained a relatively large size. It is quite conceivable that survival will be greater in small broods that receive prolonged protection than in larger broods that are liberated at an earlier and more vulnerable stage of development-a state of affairs analogous to the often greater survival of young from small than from large clutches of eggs in birds because of the inability of number of chicks. It is interesting therefore that available data suggest that the group of genera of fishes most characteristic of rocky shores (the "mbuna") proclutch of all the Nyasan cichlids and, furthermore, these eggs are both relatively, and apparently absolutely, larger than those produced by the often larger cichlids of other habitats (Fryer, 1959).

Data on the brood size of the cichlids of other habitats, while scanty, indicate that, in general, broods are larger than in the rocky-shore species. For example, the figures given by Lowe (1955) for the number of ripe ovarian eggs produced by three closely related endemic species of Tilapia indicate that in these species, which live under much less crowded conditions than do the rocky-shore species, the number of eggs brooded is, at a conservative estimate, upwards of six times the number brooded by the rocky-shore species.

General observations on cichlids frequenting sandy shores, where populations are less dense than on rocky shores, but where the young are more exposed to predation than are the young of some of the species of Tilapia mentioned above, which brood their young among weeds, suggest that these species produce more eggs than the former but less than the latter, but more details are required.

The above data, while highly suggestive of an adaptive correlation between egg size, brood size and habitat, require further elaboration, particularly where complicating factors have to be considered. For example, in Tilapia lidole Trewavas

. . . .

a few young are retained to a large size, size, Lake Nyasa does not provide either presumably with the shedding of many a great diversity of habitats or of differsmaller individuals-a fact perhaps indicative of a recent change to more openwater brooding conditions than those experienced by its relatives, and of incomplete adaptive changes to these conditions.

(11) THE IMPORTANCE OF SPECIALI-ZATION IN INTRALACUSTRINE SPECIATION

Freshwater fishes are, in general, relatively unspecialized. This can be correlated with the transient nature of most freshwater environments (Larkin, 1956). Two aspects of this lack of specialization are an ability to exist under a wide range of environmental conditions (e.g. see any general work on British freshwater fishes) and the capacity of many species to utilize a wide range of foods (e.g. see Hartley, 1948). By way of contrast, many of the fishes of Lake Nyasa are extremely specialized for life in one particular environment and especially for the collection of one particular kind of food. This specialization seems to be intimately bound up with speciation. The relative permanence of certain environments in elsewhere in the animal kingdom. the lake is an incentive to specialization: the more specialized a species becomes, the more successful it is likely to be in a particular environment. Perhaps even more significant from an evolution- the speciation of the fishes. ary point of view is the fact that the more specialized a species becomes, the more it among the fishes of Lake Nyasa seems becomes restricted to a particular envi- to have been invariably accompanied by ronment and the less likely it is to venture the adoption of the shoaling habit. Exinto habitats to which it is ill-adapted. amples of this, including an incipient case, In other words specialization has led to the state of affairs described in detail that the shoaling habit is an example of elsewhere where most species exist in numerous discrete, isolated populations of various sizes-ideal conditions for the able speciation in the lake are those of operation of allopatric speciation.

SUMMARY

lating to evolutionary phenomena within tant in the evolution of the many endemic the basin of Lake Nyasa are put forward.

ent foods for the fishes that exhibit the most striking speciation of all the groups in the lake. Thus neither the existence of many habitats nor of a wide choice of foods can be called upon as means whereby this speciation could have been accomplished.

The great size of the lake, enabling isolation by distance to become effective, is believed to have played an important part in permitting the evolution of numerous species.

Various aspects of predation, supplementing evidence previously put forward, suggest that, contrary to the view of Worthington, the presence of numerous predators has facilitated and not impeded speciation.

Although the cichlid fishes fill numerous niches, adaptive radiation has been restricted in that groups of related species, or even genera, frequently co-exist in the same habitat and often utilize similar foods. Examples of this type of radiation are given and comparison is made with the adaptive radiation more usually found

Some new considerations, in addition to those already put forward by previous students of the lake, indicate that lakelevel fluctuations have had a bearing on

The evolution of plankton-feeding are given. The suggestion is put forward "ecological neoteny."

The fishes showing the most remarkthe family Cichlidae which, with only two known exceptions, neither endemic, are mouth-brooders. The habit of mouth-A number of facts and speculations re- brooding is believed to have been imporspecies, and in permitting their co-exist-It is shown that, in spite of its great ence in dense multispecific populations.

relation between the size of the eggs produced, the number of young brooded by the female, and the habitat frequented by any given species of cichlid fish. Those species living in the most densely populated habitats produce few large eggs and rear small broods of young to a relatively large size, while species in less densely populated habitats produce larger numbers of relatively smaller young from smaller eggs.

Relatively stable conditions prevailing over a long period of time have apparently provided an incentive to specialization to the fishes of Lake Nyasa such as is absent in most lakes which, geologically speaking, have but a short life span. This specialization had the inevitable consequence of restricting individual species to very definite habitats, thus rendering isolation of populations by even small barriers of unsuitable terrain an easy matter. Such conditions have been conducive to allopatric speciation.

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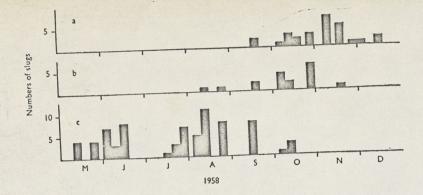
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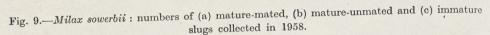
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were beginning to disintegrate showing that the intensity of mating was then starting to wane. Unfortunately the dissections of this species were not started until May, but the young began to be collected in February. Newly hatched specimens were never collected. Only one mated individual was found between May and the end of August. I suggest that this species hatches in early spring, grows throughout the summer to become mature and mates in September, October and November. Egg-laying starts during these three months, after which the adults presumably soon die.

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SOME CONTROVERSIAL ASPECTS OF SPECIATION OF AFRICAN CICHLID FISHES

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A clear distinction must be made between the intralacustrine speciation shown by some groups of African cichlid fishes and the simple specific proliferation shown by others. The former phenomenon is exhibited by several genera but hardly at all by the genus Tilapia.

Inshore dwelling habits and an algal diet have not had restrictive effects on speciation. In fact it is among inshore species that speciation has been most active.

While, partially by exploiting their small size, genera which have given rise to the endemic species flocks of the great lakes have become highly specialized for the exploitation of specific niches, the species of Tilapia have usually remained large and unspecialized and therefore capable of existing in a variety of environments.

Further consideration of the effects of predation supports the idea that it has accelerated rather than retarded the process of speciation.

If certain conditions are fulfilled, closely related species can co-exist throughout life in one habitat, eat the same kind of food and breed in close proximity to each other.

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INTRODUCTION

The existence of remarkable assemblages of cichlid fishes in African lakes has encouraged a number of zoologists to speculate on various aspects of their evolution. Although more and more concrete information on the biology of these fishes is now coming to hand full agreement has not yet been reached on several points. Thus a recent paper by Lowe (McConnell) (1959), which gives a valuable summary of certain aspects of the biology of members of the genus Tilapia also makes a number of suggestions with which other students will be unable to agree. Some of these points are discussed in the following paper which, it should be clearly understood, does not purport to level criticism at Lowe's factual data but only at certain of her conclusions.

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INTRALACUSTRINE SPECIATION AND SIMPLE SPECIFIC PROLIFERATION

It is perhaps unfortunate from the point of view of the student of evolution in African lakes that so much attention should have been directed to the genus Tilapia, for conclusions drawn from the study of this genus can be misleading if applied to other African cichlid fishes. The evolutionary history of the genus Tilapia is in fact quite different from that of Haplochromis and the other genera which constitute the species flocks of the great lakes. Thus although several lakes are inhabited by endemic species of Tilapia in only one, Nyasa, is there any suggestion of that intralacustrine speciation for which several other cichlid genera are so renowned. The occurrence of endemic species with little or no intralacustrine speciation-the almost inevitable result of geographical isolation-is not particularly remarkable and is in fact to be seen in several other genera of African fishes. In Lake Nyasa, where some intralacustrine speciation has taken place in the genus Tilapia, the resulting species flock comprises only four species, a fifth endemic species, T. shirana Boulenger, being obviously of different ancestry. This state of affairs compares strikingly with the situation in Haplochromis which has given rise to about seventy species in Lake Victoria and more than a hundred in Lake Nyasa, and with genera such as Lethrinops with twenty-four Nyasan species and Lamprologus with thirty-four species in Tanganyika. The speciation to which Lowe refers when she speaks of the extensive speciation of the maternal brooding species of the genus Tilapia is surely nothing more than the normal proliferation of species which one expects in a successful and widely distributed genus and is a quite different phenomenon from that which has attracted so much attention to African lakes. Specific proliferation of the type shown by Tilapia is for example exhibited in an equally or more striking manner by several genera of African fishes, such as Gnathonemus, Marcusenius and other mormyrid genera, by Alestes and Distichodus among the characins, by the silurid genus Clarias, and by cyprinid genera such as Labeo, Barilius, and particularly Barbus, none of which incidentally, are mouth brooders. Failure to differentiate clearly between these two types of speciation phenomena makes it difficult to understand the significance of statements to the effect that some groups of Tilapia have undergone " extensive speciation " (p. 9) and that others " have not speciated " (p. 11).

DIET, HABITAT AND SPECIATION

Lowe repeatedly mentions the advantages of open-water habitats to which she thinks that mouth-brooding species are pre-adapted, and suggests that both inshore-dwelling habits and an algal diet have acted as brakes to speciation (pp. 11, 12, 16, 17, 20, 26). So far as the genus *Tilapia* is concerned she to a large extent equates the frequenting of inshore habitats with the habit of substratum spawning (though later, p. 11, she extends this argument to inshore-dwelling mouth-brooders) and believes that because this group is confined by feeding and breeding habits to shallow waters its opportunities for speciation have been restricted. That mouth-brooding has advantages in African lakes and has been important in permitting intralacustrine speciation is not denied, but the reasons for my adherence to this view are not those advanced by Lowe and are recorded elsewhere (Fryer 1959 b). It is quite true, as Lowe points out, that the inshore-dwelling species of *Tilapia*, both substratum spawners and mouth brooders, have not undergone intra-lacustrine speciation in African lakes, but this does not mean that the inshore habit is itself a brake on speciation. On the contrary it is just those species of cichlid fishes of other genera which live in the littoral zones of the great lakes that have undergone intralacustrine speciation to the greatest extent. No one denies the advantages of an open-water habitat—advantages which have been exploited by cichlids other than species of *Tilapia*, e.g. the *Haplochromis* species of the "Utaka" group in Lake Nyasa—but to claim that inshore conditions are less favourable to speciation than are those prevailing in open water is to ignore an overwhelming mass of evidence to the contrary.

The fact that a species is restricted to inshore waters does not necessarily mean, as Lowe seems to imply, that it is not a successful species nor, incidentally, as she infers in the case of T. tanganicae (Günther) in Lake Tanganyika, that it is kept there by predators, of which more anon. It is axiomatic that a species is in most respects well adapted to the habitat in which it occurs, and the fact that some species of *Tilapia* are undoubtedly successful as frequenters of open-water should not be allowed to obscure the fact that other habitats offer alternative advantages, or that the species of *Tilapia* concerned, ecologically euryvalent though they may be, may not possess all the requisite adaptations necessary to permit them to exploit open-water conditions. (See also p. 572.)

The idea that a vegetarian, and more specifically an algal, diet has had restrictive effects on speciation in the genus *Tilapia* is suggested by Lowe. My own studies on a group of endemic rock-frequenting cichlid fishes of Lake Nyasa have shown that such a diet is no disadvantage for no fewer than eleven closely related and co-existing species subsist largely or entirely on algae growing on rock surfaces, as do two other cichlid fishes of the genus *Haplochromis* which occupy the same general habitat (Fryer 1959 a). Neither the inshore habit nor an algal diet has prevented the development of this species flock which is in fact one of the most striking of all known examples of intralacustrine speciation. Data given by Poll (1956) on the gut contents of members of a group of Tanganyikan cichlid fishes with similar habits but with an independent evolutionary history suggest that here too an algal diet has by no means restricted speciation.

Most fishes tend to be carnivorous and the assumption of an algal diet may in fact have been an important evolutionary step in the history of these cichlid fishes and one which opened up a new series of niches for colonization. This seems to be the case in the rock-frequenting species mentioned above (and in the wider sense of the term speciation, in the genus *Tilapia* itself) and in the case of another group of freshwater organisms which shows several interesting parallels to these fishes, namely the cyclopoid copepods whose basic feeding mechanism is obviously that of a carnivore (Fryer 1957 a) but of which many species are now algal feeders (Fryer 1957 b). Although they seem to be in some ways not fully adapted to a vegetarian diet it is those genera which comprise the algal eating species which now contain the largest number of species.

Although the suggested reasons for the lack of intralacustrine speciation in the genus Tilapia adduced by Lowe have been rejected it seems possible to point to an explanation of this phenomenon. The answer would appear to lie in the unspecialized nature of the genus. All species of Tilapia are very much alike, and trophic specializations-so important in the adaptive radiation of African cichlid fishes—seem to be confined to two types, weed chopping and fine particle feeding. The latter habit can enable its possessors to feed on either bottom material or on phytoplankton and some species at least are facultative feeders utilising whichever of these two sources of food is most readily available. The unspecialized nature of several species is revealed by their wide geographical distribution within which they frequent habitats of considerable diversity; the great tolerance of several species in the latter respect being in large measure a reflexion of feeding habits, for few habitats lack organic bottom detritus. Lowe refers to the wide distribution of some of the substratum spawners, but certain mouth-brooding species such as T. galilaea (Artédi), T. nilotica (L.) and T. mossambica (Peters) are also wide ranging species. T. galilaea has a range extending from Senegal and the Gambia, through the Niger and Volta, and much of the Nile system to the Jordan Valley, while T. nilotica covers much the same area but also extends further south into the Congo system. Within this vast range both species frequent both riverine and lacustrine habitats. The adaptability of many species of *Tilapia* to fish-pond conditions and the way in which introduced species often establish themselves in new environments also reveals the unspecialized nature of members of this genus. The importance of specialization in speciation in African lakes has been pointed out elsewhere (Fryer 1959 b) and it is an incontravertible fact that the vast majority of the endemic cichlids of the great lakes are highly specialized for life in one particular environment. One could not, for example, conceive of any of the rock-frequenting species of Lakes Nyasa and Tanganyika existing under the range of ecological conditions tolerated by T. nilotica.

Another difference between the genus *Tilapia* and those genera which have undergone much intralacustrine speciation, and one which to a large extent reflects the unspecialized nature of the former and the specializations of the latter, is size. Almost without exception members of the genus *Tilapia* are larger than are members of the species flocks of other cichlid genera. Now, Hutchinson (1959) has recently demonstrated that small size, by permitting animals to become specialized to the conditions offered by small diversified. elements of the environmental mosaic, permits a degree of diversity quite unknown among groups of larger organisms. (See also Hutchinson & MacArthur 1959). Few groups can provide a more elegant demonstration of this principle than these cichlid fishes.

The larger size of the species of Tilapia which have colonized the lakes must also to a large extent render them immune from the effects of predation which I believe to have been a stimulus and not a brake to speciation in their smaller brethren (see below). Some predation can of course be expected during the growth of *Tilapia esculenta* Graham are at all typical of the genus as a whole and the indications are that some species grow more quickly than this one—then after one year's growth, by which time they have achieved a length of some 15 cm., individuals of this species are already larger than the adults of many other lacustrine cichlids, and after two years, when they have grown to a length of about 19 to 21 cm., they are too large to be eaten by many predators.

During the evolutionary history of the African cichlids therefore it would appear that, in general, the lacustrine forms have specialized for life in certain environments while the genus *Tilapia* has adopted the alternative evolutionary possibility and has remained unspecialized. While the taking of the latter course has necessitated forfeiture of the opportunity of undergoing great adaptive radiation in the lakes it has paid dividends in other ways and has given rise to several adaptable, highly successful, and wide-ranging species.

THE EFFECTS OF PREDATORS-A SUMMARY OF RECENT EVIDENCE

Lowe also enters the controversy regarding the effect of predators and takes her stand alongside Worthington who believes that the existence of predators, particularly *Lates* and *Hydrocyon*, has had a restrictive effect on intralacustrine speciation. Several papers relevant to this controversy were in the press at the same time as that of Lowe and all contain either factual or theoretical evidence, or both, which is opposed to this view.

A mortal blow has been dealt to this theory by the discovery of fossils of *Lates* in Holocene deposits from Lake Edward (Greenwood 1959 b). This means that, contrary to Worthington's view, *Lates* and the speciating *Haplochromis* flock of Lake Edward co-existed until very recent times. Even after taking into account extenuating circumstances, to which Greenwood gives full consideration, such as the fact that the Lake Edward cichlids were apparently derived from partially specialized ancestors from Lake Victoria, the blow to Worthington's hypothesis is a telling one.

Other facts, derived from work in Lake Nyasa, which suggest that predators have hastened rather than retarded speciation, have been given in some detail elsewhere (Fryer 1959 a, 1959 b), and a very similar conclusion, at least in so far as concerns the part played by predacious species in keeping the population density of the prey species at a level low enough to prevent much interspecific competition and, by inference, preventing the elimination of species, has been reached independently by Greenwood (1959 a) as a result of his studies on the *Haplochromis* flock of Lake Victoria. Details of these studies need not be repeated here, but the evidence adduced by Lowe in favour of Worthington's theory must be dealt with.

First she repeats Worthington's idea that "incompletely adjusted forms" will be selected against when predation pressure is high, and that abnormal forms occur more often in the *Lates* and *Hydrocyon*—free lakes, Victoria and Edward, than in Lakes Albert and Rudolf in which these predators occur. As pointed out elsewhere (Fryer 1959 b) the elimination of the unfit is an accepted process of evolution and will favour speciation and not retard it. The removal of malformed individuals, of whose incidence more precise data

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are required before they can be regarded as significant, would have this beneficial effect on speciation.

Lowe then refers to the fact pointed out by Fryer & Iles (1955) that Lake Nyasa, although lacking Lates and Hydrocyon, has many predators, both cichlid and non-cichlid. She rightly points out that the predatory cichlids of the lake tend to be small and that Bagrus and the clariids (some, formerly placed in the genus Clarias, now being referred to the endemic genus Bathyclarias (Jackson 1959)), which are among the most important non-cichlid predators of the lake, appear to be "lurking" rather than "swift" predators. It may appear intuitively obvious that such predators are of less significance than the very obviously piscivorous Lates and Hydrocyon, but consideration of concrete data reveals that the above facts in no way minimise the importance of these fishes as predators. Thus the species of Rhamphochromis, while relatively small, are quite large enough to prey heavily on other cichlids, many species of which never achieve a total length of 20 cm. In the case of Bagrus and the clariids the way in which the food is obtained is quite irrelevant*; the important thing is that members of these, and other genera, do undoubtedly prey heavily on cichlid fishes. Thus a very large body of data concerning the food of some three thousand specimens of Bagrus meridionalis Günther, which conclusively demonstrates its predatory nature, has recently been collected and prepared for publication by Mr T. D. Iles.

The same is true in Lake Victoria where species of Bagrus and Clarias are similarly important predators and from which lake precise data relating to the food of large numbers of these fishes are now available. Thus in this lake Corbet (1959) has shown that of a sample of more than a thousand specimens of Bagrus docmac Forskål more than 78 per cent had fed on cichlid fishes, and that even this total was probably lower than the true figure because a small proportion of fish remains could not be identified with certainty. Similarly over 80 per cent of almost four hundred specimens of Clarias mossambicus Peters were shown to have fed on cichlid fishes. That both these species, and particularly B. docmac, are abundant in the lake is readily shown by examination of figures for fish landings in 1957 recorded by the Lake Victoria Fisheries Service (1958). These figures show that about half a million Bagrus and a smaller number of Clarias passed through the recording stations (which by no means record all landings), and that members of these two genera comprised some 12 per cent of the total recorded commercial catch made in gill nets of 4 inch mesh and above in both the Kenya and Uganda waters of the lake, and that in Tanganyika waters their contribution to the total catch in this range of nets was as high as 85 per cent! Approximate though these figures are and biased as the figures for Tanganyika waters may be by the locations of the sampling stations, it is obvious that to argue that

*One way in which these "lurking" predators may find it possible to capture active prey is by being active at times when the prey is "sleeping". This happened in an ornamental aquarium into which I introduced juvenile specimens of *Tilapia variabilis* Boulenger and a young *Clarias* mossambicus Peters. By day all was well but at night, when the young *Tilapia* rested, have was caused by the *Clarias*. A similar fate befell specimens of *Lebistes* which definitely "sleep" at night, though by day their nimbleness was such as to enable them to evade the young *Clarias*. predation of this order of magnitude is less important than that exercised by fishes which to the popular imagination are better suited to the role of predator is to ignore a mass of concrete data.

Of interest too in the present connexion is the fact that Corbet's figures show that *Bagrus* and *Clarias* prey far more heavily on *Haplochromis* than on *Tilapia* in Lake Victoria yet it is the former and not the latter genus which here exhibits intralacustrine speciation. These data lend support to the idea expressed elsewhere that predation favours and does not retard intralacustrine speciation.

Lowe also refers to the fact that in Lakes Albert and Rudolf, in both of which are found Lates and Hydrocyon, the species of Tilapia present (none of them endemic) frequent inshore waters (as does .T. tanganicae in Lake Tanganyika mentioned above) whereas in lakes lacking these predators they have open-water living phases. Apart from the fact that this is not true for T. nilotica in Lake Edward this explanation cannot be accepted without question. In Lake Edward, which contains neither Lates nor Hydrocyon, Lowe herself (Lowe (McConell) 1958), quoting Worthington who presents data which flatly contradict his theory, states categorically that "the typical habitat [of T. nilotica] is the comparatively shallow inshore water " and that " this species does not occur in the deep water of Lake Edward except occasionally at the surface". A partial explanation of a different kind has been mentioned above (p. 571) but it might be noted further that general ecological conditions reflecting the morphometric characteristics of the lake should not be overlooked as factors influencing intralacustrine distribution. In the southern part of Lake Nyasa Tilapia of the saka-squamipinnis group frequent open waters and feed by preference on phytoplankton (Lowe 1952) but in the north, where more precipitous shores prevail, they are found inshore and feed on material accumulating on the bottom (Fryer 1959 a). These differences in ecological distribution obviously reflect lake morphology and have nothing to do with the presence or absence of Lates and Hydrocyon. There is indeed a world of difference between, for example, Lakes George and Albert, and it would be a very credulous ecologist who would expect that a given species would have the same sort of distribution in each of these basins.

Relevant to this too are some of Lowe's own observations on *T. nilotica*. This fish has been introduced into several small predator-free lakes to which it is not indigenous and in these its distribution, to use Lowe's own words, "depends on the ecological conditions". In some lakes it is evenly distributed, as in Lake George ; in others it occurs in localised areas where there are stands of aquatic plants (Lowe (McConnell) 1958).

Furthermore, one would expect on a priori grounds that phytoplankton feeding fishes would exhibit a preference for inshore rather than offshore waters in African lakes, for it is in inshore waters of all save the smallest and shallowest lakes that the greatest concentrations of phytoplankton are to be found (Ross 1955). It is also important for those unacquainted with African lakes to realise that, no doubt in part as a consequence of the above fact, some of the so-called open-water species are certainly not pelagic in the way in which are fishes of the open seas but are in fact confined essentially to inshore waters.

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This applies, for example, to T. esculenta Graham and T. variabilis Boulenger in Lake Victoria—a lake lacking Lates and Hydrocyon. Work from the time of Graham's survey some thirty years ago to the present has shown that, save in closed gulfs and sheltered regions where offshore islands occur, T. esculenta is seldom found more than five miles off shore and even in the most sheltered regions is seldom or never found more than twenty miles from land. Similarly T. variabilis, while exhibiting rather different ecological preferences, is also concentrated in a relatively narrow belt of inshore water.

It must also be pointed out that those who would argue that predators serve to restrict other species to inshore waters are thereby surely damaging their own case for the restrictive effects of predators on speciation, for it is species which are so ecologically restricted which, in spite of what may have been said to the contrary, have undergone the most abundant speciation in the great lakes.

As a further point held to be evidence of the importance in this connexion of Lates and Hydrocyon Lowe refers to the fact that in Lakes Albert and Rudolf "the fish of many genera are much larger than their counterparts in the other lakes and the Tilapia tend to have longer stronger spines". Of the reasons which could conceivably be responsible for this the effect of predators is only one and the suggestion would appear to be quite incapable of proof. The fact that Lowe refers to genera and not to species also betrays a further weakness in the argument. Thus T. melanopleura Duméril is much larger than T. sparrmani A. Smith but one cannot say why save that the difference is genetical. Even if identical species were involved or implied the argument would be false. This is adequately demonstrated by the widely divergent growth patterns of any of several species of fishes when grown in different types of fish ponds.

As to stout spines, the strongest I have seen in any species of *Tilapia* are those of a species now being studied which inhabits Lake Kitangiri in Tanganyika Territory. If, as I believe, this has nothing to do with predation, then the suggestion made concerning the stout-spined specimens from Lakes Albert and Rudolf loses much of its weight. If, on the other hand, there is a connexion between stout spines and predation, then other predators must exert similar effects, because of predacious species only *Clarias* and *Protopterus* (a "mild" predator) occur in Lake Kitangiri.

REPRODUCTION AND ECOLOGICAL ISOLATION IN RELATED SPECIES

An interesting fact discovered by Lowe is that, in Lake Nyasa, while three very closely related species of *Tilapia* feed together on the same food they breed in different situations and at different times of the year. However, it is misleading to think that this type of behaviour, which to a large extent parallels that of certain birds, is essential in order to permit closely related and frequently meeting species to remain distinct as Lowe suggests. On the contrary it is possible for species to live together and to breed in close proximity to each other at all times of the year and yet remain distinct ; and it is surely in such cases, of which the rock-frequenting Nyasan cichlids are an outstanding example, that differences in breeding behaviour patterns, to our knowledge of which Lowe has herself made significant contributions, become supremely important. Instead of saying, as does Lowe, that "ecological isolation need not, however, be complete throughout life" one is tempted to go so far as to say that ecological isolation need not exist provided that food is superabundant (as seems often to be the case among feeders on both lithophilic and planktonic algae), that the population density is controlled by predators or some other means, and that different species have different patterns of breeding behaviour (particularly courtship, as may be deduced from the striking and specific colour patterns of the males) which assist in the maintenance of interspecific sterility barriers. Here again the small size of some of the cichlids exhibiting these phenomena may have been important in permitting them to split up for breeding purposes one major habitat and to do so to such an extent that it has so far proved virtually impossible to discern differences in the territories selected by the males of closely related and co-existing species.

SUMMARY

Some controversial topics relating to the evolution of cichlid fishes in African lakes are discussed and certain recently published suggestions are refuted. It is shown that a clear distinction must be made between the phenomenon of intralacustrine speciation as shown by several cichlid getera and that of mere specific proliferation as shown, save to some extent in Lake Nyasa, by the genus *Tilapia*. Failure to differentiate clearly between these phenomena has led to considerable confusion in the past.

The recently expressed idea that inshore dwelling habits and an algel diet have had restrictive effects on speciation is shown to be unfounded. It is in fact among the inshore dwelling species that the greatest amount of species has taken place in African lakes.

Different evolutionary routes, each of which has led to success, have been taken by those genera which have given rise to the endemic species flocks of the great lakes, and by the genus *Tilapia*. The former, partially by exploring their small size, have become highly specialized for life in one of several possible environments and usually for the collection of one type of food. By contest the species of *Tilapia* have, with few exceptions, remained large and inspecialized, and this has enabled individual species to exist over wide geographical areas in a variety of environments.

Recent views on the effects of predation on evolution in the great lates are considered and concrete data having a bearing on this question are reviewed. This evidence very strongly suggests that the old idea that predators (of which fishes other than *Lates* and *Hydrocyon* are shown to be important) have had a restrictive effect on speciation, is unfounded. In fact a good case car be made out for the reverse role—that of accelerating speciation—for these fishes.

It is emphasized that closely related species can co-exist throughout life in one habitat, where they may even take the same food and breed in very close proximity to each other, provided certain conditions are fulfilled. The importance under such circumstances of that part of the reproductive behavour leading up to the shedding of gametes is emphasized.

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DENTITION OF THE RIBBON SEAL

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(With 3 plates)

The dental formula of Histriophoca fasciata is : I 3/2, C 1/1, PC 5 (rarely 6) = 34 to 36. The teeth are rather weak, smooth and distantly spaced. The lower incisors are only half the size of the upper ones and are frequently lost. The lower canines point outward at an angle of 45° from the horizontal. In each half of the jaw, upper and lower No. 1 is the smallest of the postcanine series; Nos. 3 and 4 are the largest; Nos. 2 and 5 are nearly equal. On some skulls the gap between upper postcanines Nos. 4 and 5 is distinctly the widest. The upper postcanines may have a small posterior cusp ; the lower ones frequently have both anterior and posterior cusps. In each half of the jaw, upper and lower postcanine No. 1 is single rooted; No. 5 is double rooted; Nos. 2, 3 and 4 are transitional. On one specimen, the third pair of upper postcanines is missing and all of the teeth

are unusually small. This skull may be pathological or it may be evidence of the variation to be expected in a declining evolutionary form.

Male and female are similar in body size and may reach a length of at least 170 cm. and a weight of at least 95 kg. Cranial measurements of five adult males, one adult

female and one adult sex-unknown are given.

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INTRODUCTION

The genus Histriophoca Gill 1873 contains a single species, H. fasciata (Zimmermann) 1783, the ribbon seal. This seal lives among the drift-ice floes of Okhotsk, Bering and Chukchi seas (Scheffer, 1958, map on p. 104). It does not come on land. Its nearest relative is the harp seal, Pagophilus groenlandicus (Erxleben) 1777, of the North Atlantic Ocean and adjacent seas. The genus Histriophoca was the last of twenty genera of pinnipeds to be

distinguished. Even today, few skulls of the ribbon seal are in museum collections. As recently as 1942, Doutt (p. 93) could find only two adult specimens for study ; as recently as 1951, Mohr (p. 192-3) was first to publish photographs of the skull. It was therefore a pleasure to receive in 1959 from Dr Francis H. Fay a well-prepared adult skin and skull. Because of certain odd features of dentition, the Fay skull is referred to as "anomalous BDM

1959. Proc. Zool. Hoc London Vol 132

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

153

BY

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(With 2 plates and 99 figures in the text)

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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 the individual species of animals occupying the various habitats which 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 norther extremity. The selected area included both a rocky and a sandy shore are also a small, swampy, estuarine region. The data obtained from this area have been supplemented by occasional collections and observations made elsewhere

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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 macrobic organisms. Because of this the littoral region is of even greater reportance 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 only well over 90 per cent of the total shoreline ; rocky shores predominating the north and sandy shores in the south. Other types of littoral zones do that and of these swampy regions of relatively small extent, estuarine regions the point of inflow of certain rivers and streams, and one other type described how, probably embrace all those worthy of inclusion in a broad scheme of the sification such as is adopted here.

A few words about the fauna of L. Nyasa are necessary to put the present rey in its correct perspective. Its most outstanding characteristic is the adaptive radiation shown by the fishes which has resulted in the evolution harge numbers of distinct endemic species, particularly in the family blidae, of which more than 180 species are now known to occur in the Such radiation is shown also, but to a lesser extent, by other families as the Clariidae. Some groups of invertebrates such as the parasitic speciation, but on the whole the invertebrates do not appear to have duced endemic species to such an extent as is the case in certain other

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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 $2\frac{1}{2}$ incomes mesh gill net have provided most specimens while a few have been taken traps. In the small estuary a seine net and trap, supplemented by the use 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 hove 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 $\cdot 303$ 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 small number of specimens could be obtained. Even in cases where abundant interial was available it was considered advisable to make a very thorough and 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 a very restricted. Even so well over 1,600 detailed gut analyses were carried at on the fishes alone within the confines of the area under consideration, and any more guts received a cursory examination, while a number from other that were carefully studied for comparative purposes. The food along the ether length of the gut was studied, except in cases such as *Labeo* and *L*

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

PHYSIOGRAPHIC FEATURES OF THE AREA STUDIED

The area studied is shown in the accompanying map. (Fig. 1). Within relatively small area fairly typical examples of rocky and sandy shores represented as is a somewhat swampy miniature river estuary. In addition on the type of major habitat with distinctive faunistic peculiarities gradually one recognisable as the study proceeded, this being a very small area area the rocky and sandy shores, which, because of its intermediate fracter in certain respects, is for convenience henceforth spoken of as the intermediate zone". Because of the presence there of crocodiles, the meany 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.

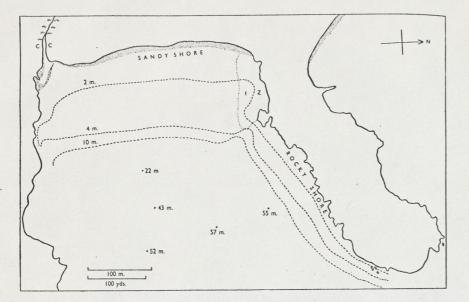


Fig. 1.—Map showing area studied (South Bay, Nkata Bay, Nyasaland) and distribution of major littoral habitats. C.C.=Crocodile Creek. I.Z.=Intermediate Zone.

(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

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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

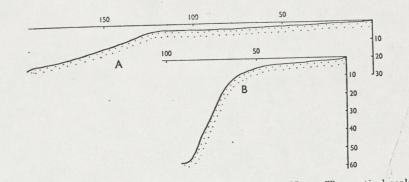


Fig. 2.—Actual sections of A : Sandy shore, B : Rocky shore. Note : The vertical scale is not exaggerated. All figures are in metres.

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.

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

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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

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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 Seechi 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*

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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
	1	19
Nymphal bugs	· 1	19
Afronurus nymphs 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 tare elmid larva, an occasional bug Naucoris flavicollis Sugn., and a few tiny thabdocoele turbellarians. This list is by no means a long one, and of the inder-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 noncichlid 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, *Phala-crocorax 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*

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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 figurés 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		
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 molluse *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 atle 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 *Eucycleps 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

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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 syrinid 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 llydra, 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

* The expression "unable to establish themselves" is used with deliberation as on one occaion 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 enterminated by subsequent wave action and did not survive to maturity.

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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

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SANDY SHORE vridina nilotica Roux pridopsis cunningtoni Sars mocypris sp. icrocyclops nyasae Fryer icrocyclops bitaenia Fryer icrocyclops bitaenia Fryer icrocyclops dubius (Sars) cyclops dubius (Sars) gasilus macrodacylus Sars hizopera consimilis Sars

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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 offen 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 longimostris (O. F. Müller) and Bosmi. nopsis 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.

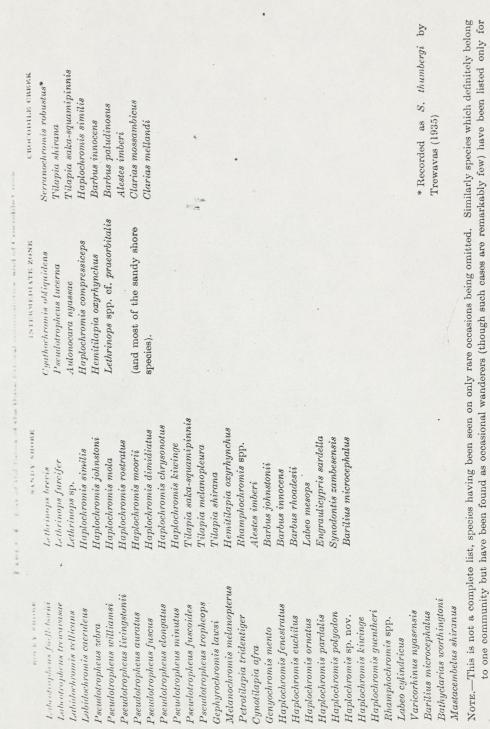
THE FISHES : THEIR ECOLOGY AND ADAPTATIONS

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 lidea 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 fisshes. 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



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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 Nyassan cichlidto 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 common fishes of the rocky shore. It is seldom to be seen more than a few continet from rock surfaces from which it obtains its food. It swims over rocks of a $_{shapes}$, 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" shally take place in quick succession during which time the fish moves forwards try slightly. The effect of a forward movement of the lower jaw and a hanward (backward) movement of the upper jaw (the latter following as an tryitable consequence of the former during the process of closing the mouth) to scrape Aufwuchs from the rock surface and pile it up along each palisade teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken into the buccal teeth. This piled up food material must then be taken

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While Calothrix figures largely in the gut contents of this species it seems at most only partially digested and the fish is by no means dependent 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

striking similarities to those found in the non-cichlid genus Labeo,

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

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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*.

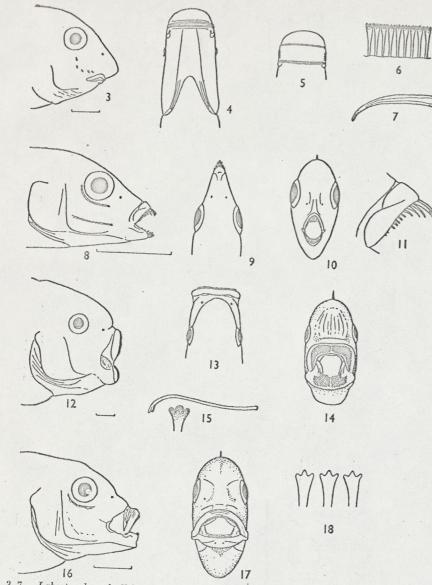
Petrotilapia tridentiger Trewavas. (Figs. 12–15)

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 localized area. For convenience the process is houseforth 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.

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"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

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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 s_{16} 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 tlength 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 pecies 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

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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 pleutitul, 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 locse 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 d 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 alore 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 tricuscul teeth it seems probable that they will not allow filaments of Calothrix to mass easily between them as do the homologous

* As recognised here this species annumaces the forms previously described as : *P. tropheops tropheops* Regard

P. tropheops tropheops Regain	P. microstoma Trewavas
P. tropheops gracilor Trewayas	P. macrophthalmus Ahl.

The reasons for uniting these united 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. Obsertations made further north, at Florence Bay, where this species occurred plentifully among coarse shingle and boulders indicate that such conditions other than truly rocky shores represent the optimal conditions for its occurtance. 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 coninderable 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 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 set rows are shorter and tricuspid. Such a dentition, and particularly the truded oute row of teeth of the lower jaw, will be suitable for scooping material from rock surfaces.

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

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

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

While sometimes occurring fairly close to the shore this species usually about the 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.

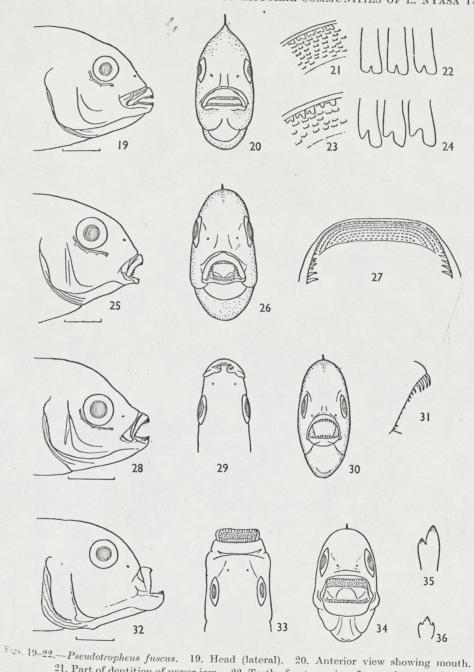
The mouth is similarly constructed to that of P. zebra and is similarly mobile. Here, however, the wide gape which follows as a natural consequence of this mobility, is utilised, not so much for scraping rocks but for the taking in of water from which plankton is sifted. Underwater observations indicate 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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21. Part of dentition of upper jaw. 22. Teeth of outer series of upper jaw.

23-24.—Pseudotropheus fuscoides. 23. Part of dentition of upper jaw. 24. Teeth of outer series of upper jaw.

12: 25-27.—Pseudotropheus tropheops. 25. Head (lateral). 26. Anterior view showing mouth. 27. Dentition of upper jaw.

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

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

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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 molluse. 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 short 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.

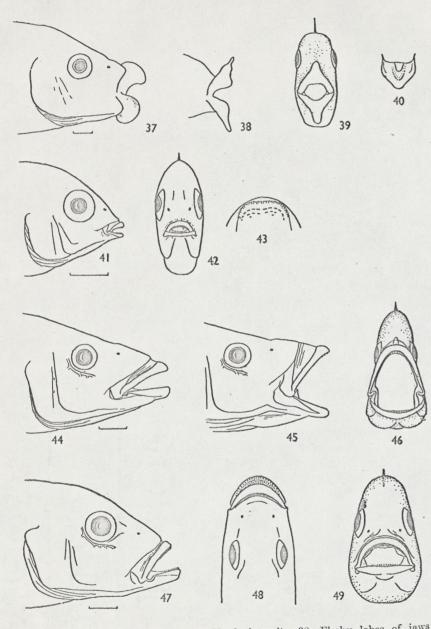
Haplochromis kiwinge Ahl.

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 toplankton, 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 twenile specimens). Larger specimens become wider ranging and, while hartly piscivorous, they appear to be essentially omnivorous. These larger dividuals are by no means so intimately integrated into the rocky shore 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 typearing around anchored boats in quest of garbage.

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

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Figs. 37-40.—Haplochromis euchilus. 37. Head (lateral). 38. Fleshy lobes of jaws drami 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 moutopen to full gape. 46. Anterior view showing mouth open to full gape. TROPHIC INTERRELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 187

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.

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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 backwardlydirected 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 f_{mmon} , 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 is h remains.

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

Haplochromis guentheri Regan. (Figs. 50-51) Underwater observations indicate that, while not very common among the

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 filamen. tous 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 *Haplo* chromis" (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 $2\frac{1}{2}$ 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 $18\cdot1$ to $21\cdot0$ cm. in length and almost all were very ripe or, in a few cases, spent. Of these all save nine had either empty guts contained traces of indeterminate slime. The food present indicated as 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 nymplaand the other contained a few fragmentary insect remains. It seems probable

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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.

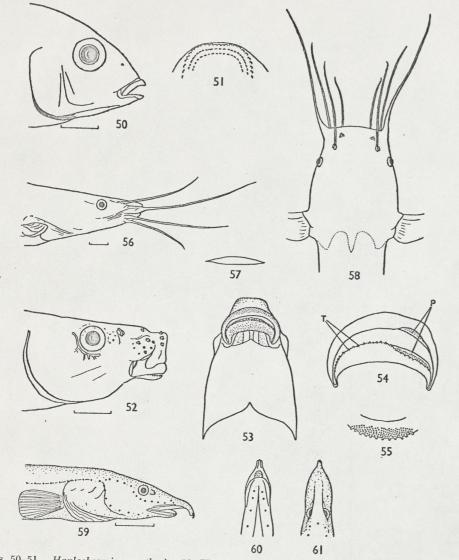
L. cylindricus can very easily be seen feeding in nature though details of the process are difficult to observe. The mouth can be seen moving rapidly as the fish lies over a rock and, as it moves away, a distinct bare area, approximately circular if it remained stationary during the browsing process or more clongate 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 schedular. 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 other face numerous rows of sensory papillae (Fig. 55). The rim of the lower p is also provided with a row of short sensory tentacles. These papillae and interfaces 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 trace, but often they are apparently not pressed firmly against it or they would always remove the omnipresent tufts of *Calothrix*. It seems probable that much of the loose material eaten is actually sucked into the mouth expansion of the buccal cavity, and that the horny pads are not always and for the purpose to which they seem so obviously suited and for which the buccal structures in *Varicorhinus nyasensis* (see below) are most certainly and

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



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).

smong 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 suitedscraping 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 curvvalence 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 kinenge, 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 met, 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 midlges, 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 Correthra, in the gut in addition to other material. Occasional bottom animals such as chironomid larvae and once a hydropsychid larva were also seen cas were chironomid pupae (presumably caught as they rose through the watter), 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 (11933). It is worthy of note that in addition to the specimens about 3 cm. in leangth 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 head been collected in the lake itself. The presence of such small specimens imdicates either that young very quickly come down from the rivers in which scome of them at least are born, or that, and more likely, the story told by Africean fishermen of two "kinds" of "Samilka", one of which spawns in rivers and the other in the lake itself, is true. This seems very likely as there is noo river up which this species is known to run, within many miles of the point that which these tiny specimens were found. It may even be that these "races", if they exist, differ in certain morphological characteristics, and this may impart explain the variation encountered by Worthington in his material.

Baingclarias worthingtoni Jackson (Figs. 556-58)

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 jits life near the shore (though whether the species actually spawns there is not kknown) and moves to deeper water after attaining a length of about 30 cm. If is a very retiring species which lives under stones and is therefore not to bee 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 irequent 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 mains 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 -cales 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 tets 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, adaptations such as this in the Clariidae by the fact that the Nyasan "presentatives 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 the days when fish poisoning was carried out among the rocks it was caught large numbers.

Several specimens have been caught on hooks baited with worms and $\frac{1}{1000}$ among the rocks, and thirteen guts (of specimens 7.5 to 27 cm. in $\frac{1}{1000}$ 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 mayily nymph, a chironomia 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 at "Nguwa", and two unidentified cichlids, both probably new (insect eater and mild predator), and at least one unidentified species of *Barbus* (browset) They also include a very few specimens of *Cyathochromis obliquidens* and 4 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 excludively 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 harvae 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.

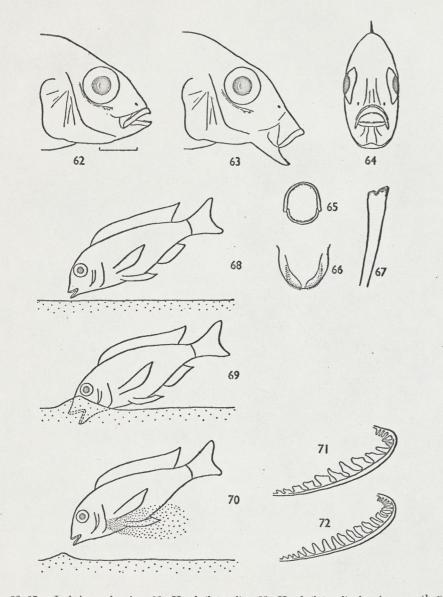
The snout is fairly sharp and the lower jaw is fairly long and pointed and solited to dibbing in the sand when the mouth is protruded as shown in Fig. 63. The teeth are very weak and only those of the outer row are likely to have any functional significance. These are slender and recurved, and it is 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 takers is eminently suited to the process of feeding which takes place in *L*. *farcifer* (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 sambers. 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. length show that, like *L. brevis*, its food consists almost entirely of chironomid are dug from the sand. As in *L. brevis* these chironomid larvae, which are the same size as those eaten by that species, are mixed with coarse sand and indeed typical gut contents of the two species are indistinguishable. It two specimens deviated from this very distinct diet. One had eaten six cichlid fishes each about 1 cm. in length which still retained traces of the sac and were still at a stage of development at which they would receive thaving been spat out by a brooding female during or immediately after stature).

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).



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.

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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 taten 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.

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GEOFFREY FRYER

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 t_0 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 triturition 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.

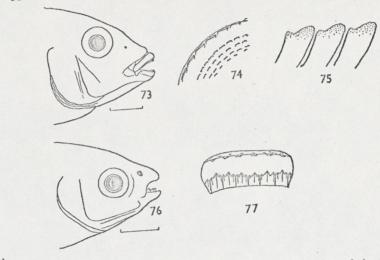
Haplochromis johnstoni (Günther)

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 molluse 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 molluse-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 molluses. 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 molluses 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 molluscfeeding 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,

The single specimen caught on the sandy shore contained five young fishes. 1956 c).

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 botto: detritus, and an even larger specimen from an adjacent sandy shore had eater 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 inshere than most of its near relatives,* and is occasionally to be found on the sanda shore. One such adult had supplemented its diet of plankton with maying 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, includes bottom detritus, centric and naviculoid diatoms, fine threads of filamentoalgae, a few ostracods, and, in one case each, a tiny chironomid larva 55

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

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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 guite 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 disctiminate 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 Gunther) 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 elentified 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 f fresh plant matter and grey over most of its length where this material 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 Clamentous algae among a mass of inorganic particles. Variety was provided by by three specimens which included fragments of Vallisneria among their feel. Specimens from an adjoining sandy beach and the few from the rocks fed likewise. Specimens from Crocodile Creek had similar gut contents but the presence of a more muddy bottom was reflected by their rather different a mistency.

Lowe (1952) found that T. saka and T. squamipinnis tend to feed on open where phytoplankton when this is plentiful but turn to bottom browsing in of phytoplankton scarcity. The fact that at Nkata Bay they seem areas to browse on the bottom may not be unconnected with the fact that the optoplankton in this part of the lake is extremely sparse ; much sparser for stance than in the more eutrophic South East arm of the lake where most of lewe's work was carried out. It is possible that the food may include orgasuch as protozoans which will not be easily detected, for Ross (1954) that in L. Victoria he found heavy populations of these organisms in 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 auch less common than the saka-squamipinnis group of the genus. The gut

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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 *Wallisneria*. Bertram *et al.* (1942) record similar food from the stomachs of six Nyasan specimens of this species and Lowe (1952) records it as eating *Cerateophyllum* in the southern part of the lake. As Bertram *et al.* point out its janws 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 tricus spid teeth. This dentition is very similar to that of *Haplochromis similis* which takes similar food.

Alestes imberi Peters. (Figs. 76-77)

Supecimens 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 some times occurs in Crocodile Creek and has been found in nearby rivers.

Guat 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 Worthhington (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 cassavera washings, and, in one case, fish remains. Many contained maize and cassavera washings resulting from the washing of these materials on the beach by Africa in women.

The striking dentition of this species (Figs. 76-77) is suited to seizing relativity 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 minost members of its genus, a bottom feeder. Nine guts, of specimers 7.5 to 19.9 cm. in length contained a preponderance of vegetable matter, sin of them containing fragments of *Vallisneria*. Filamentous algae and diatoms were alalso present and may have been deliberately scraped from the *Vallisneria* A single chironomid larva, a single mayfly nymph and a few cyclopoid copepois were alalso seen.

Barbus rhoadesii Boulenger.

Whithile the data relating to the movements of this species are few the indications at are that it moves onto the sandy shore in March, April and May. The only suggestion towards explaining these movements that will be made TROPHIC INTERRELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 203

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. lies 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, $6\cdot2$ to $8\cdot6$ 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 precimen of 17.4 cm. in length had its gut crammed with molluses (*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 colluses in the guts of four young specimens. Very large specimens seem to the in the more open waters of the lake.

Labeo mesops Günther

On the sandy shore this species occupies a similar feeding niche to that accupied by L. cylindricus on the rocky shore. While L. cylindricus is always itesent among the rocks, however, L. mesops is not invariably present on the andy shore, but seems to occur mainly from about March to May during which refield it is present in considerable numbers. At such times it comes inshore from deeper water early each morning often making its presence known by exping 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 seewhere, by sucking up the sand from the bottom which it then passes in arre amounts through its enormously elongated alimentary canal presumably suffacting from it such organic matter as is present. The mouth structure is scalar 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, $5 \cdot 0$ to $9 \cdot 9$ 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. obliquiders are for areas in which rocks give way to sand is shown by its occurrence else where in situations similar to those prevailing in the intermediate zone (vizin the north bay at Nkata Bay, at Likoma Island, and at Mbamba Bay).

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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 estracod 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 Valliseria, 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 dentical in the two species, and, as observations both in nature and in aquaria asseal, each species scrapes rock surfaces in an identical manner. The teeth 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 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 its ability to feed on the Aufwuchs growing on the Vallisneria this species ives 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 be confined to the rocky shore, *P. lucerna* exhibits a very well marked ference for the intermediate zone where it appears to be not uncommon. Thas also been taken under similar conditions in the north bay at Nkata Bay. It contrast only a single specimen of this species has been taken on the rocky the during the whole of the time that work was in progress there, and a specimen was taken under rocky shore conditions at Ruarwe, though as that had young in the mouth it was not feeding there.

The gut contents of twenty-eight specimens (including the one from the body 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 prefersituations where both sand and rocks are present.

All five specimens collected in the intermediate zone had eaten insectshydropsychid 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.

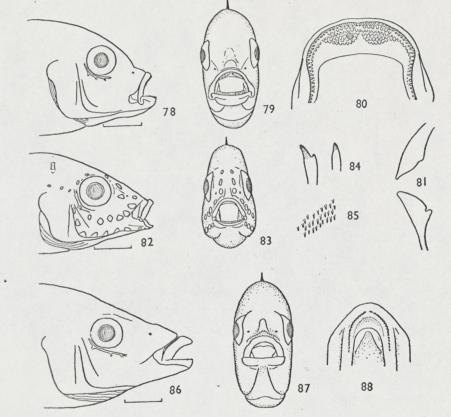
Its adaptations towards this kind of diet are fairly clear but it is less easy to point to adaptive features correlated with its habitat preferences. The mouth is somewhat protrusible and the teeth of the outer row in both jaws are all functionally conical although the median teeth actually have a small 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.

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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.



N.S. M. S. Dentition of upper jaw.
 S. M. S. M.

S2-S5.—Aulonocara nyassae. 82. Head (lateral). 83. Anterior view showing mouth.
 S4. Outer teeth. Left, near centre of jaw; Right, from lateral portion of jaw. 85. Inner teeth.

The \$6-88.—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 there, ranging from 8.7 to 13.9 cm. in length plus two specimens from the survivalent of the intermediate zone in the north bay at Nkata Bay were statistical. Almost all these contained only the Aufwuchs scraped from the states of *Vallisneria*, and fine sand particles. One had in addition picked up a statement of the little lamellibranch *Corbicula* and a mayfly nymph, one had statelowed 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 specimencaught 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. 4 respectively. According to Dr Trewavas, to whom specimens were sent, our 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.

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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. Out 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 harva 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 * ater.

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 the by specimens collected in the lake. Several small specimens 14 to the mm. in length were collected in May 1955. These contained tiny chirotonid larvae, ostracods, cyclopoid and harpacticoid copepods, rhizopod tests, they algae and detritus. The young stages are therefore more selective in finding 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 Crocodile Creek but large adults have not been seen. The guts of several pretimens 6 to 11.2 cm. in length contained very similar material to those of sectimens from the lake proper but reflected the nature of the substratum intering more "muddy".

In March, April and May 1955 several shoals of young *Tilapia* of this the point of the state o

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. *Barbur 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 at 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

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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 *Potamon orbitospinus* Cunnington (Bott, 1955) is very common on the tocky 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 pecimens appear from beneath rocks when bait is being used, the rocks must like a considerable population of this species. While females with large broods of young are sometimes caught in deep water small independent specitions 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 tests 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 intangled 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 has 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 tools no emphasis and consequently no attempt has been made to identify the species encountered. From an ecological point of view however, the and of the species living among the Aufwuchs on the rocks, all of which the of small size, can be regarded as Aufwuchs feeders, for the food in the attentary 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 *Cypridopsis*, both possibly undescribed. As in the case of the chironomid true they can be readily classified as Aufwuchs eaters. The food seems to be readily algal and they show a marked predilection for diatoms, the gut after being crammed with these algae.

Schizopera consimilis Sars

This species, while exceedingly common among the Aufwuchs of the rocks, s tot 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. consimilia* 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 occurin 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 specimers 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 me carnivorous, and eats ostracods and chironomid larvae but takes some algo-

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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 addividual 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 stable swimmer it always seems to keep near the bottom. Numerous gut tadyses indicate that it eats detritus, but the gut contents themselves are not by revealing for they always contain a very finely pulverised mass of particles those origin is difficult to determine.

Cyclopoid copepods

All three species of *Microcyclops* occurring on the sandy shore are herbitous, eating diatoms and other small algae, *Eucylops dubius* is also a herbi-No truly carnivorous cyclopoids have been encountered, but M. nyasae 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 grees in the faecal pellets. Some of the Aufwuchs necessarily taken in with the *Vallisneria* may be digested but some diatoms are defaecated while stip possessing green contents.

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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 harvae 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 estulatus) and on a small anisopterid larva. A tiny Micronecta-like bug specared 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 Φ , & 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, indocera and Ostracoda present in the creek would require a detailed study itself, but from what is known of these groups it can be stated that the ecolopoid copepods belong mostly to genera which have been shown to be thivorous (Fryer, 1957 b) and include some (e.g. *Eucyclops agilis*) whose ending habits have been studied in detail elsewhere. On the other hand *Macrocyclops albidus oligolasius* is a carnivore. The Cladocera present feed analy on detritus and small algae but, by virtue of the different strata which 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.

Molluses

A species of *Limnaea*, rather scarce in the creek itself, very quickly colonised be overflow lagoon whilst it was in existence and multiplied there abundantly.

Of the two small molluses Segmentorbis angustus and Gyraulus costulatus which are common in the creek the former is the most abundant. Both occur rank vegetation and both were found to contain detrital matter and by 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 mat	ter present on submerged rocks
Amount of organic	Approximate depth
matter/100 sq. cm. in mg.	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 is 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, show at a glance one of the fundamental differences in the trophic organisation of the two habitats. Here the availability of several primary food sources stand

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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 molluses, prawns and cyclopoid copepods which are unrepresented in the latter zone.

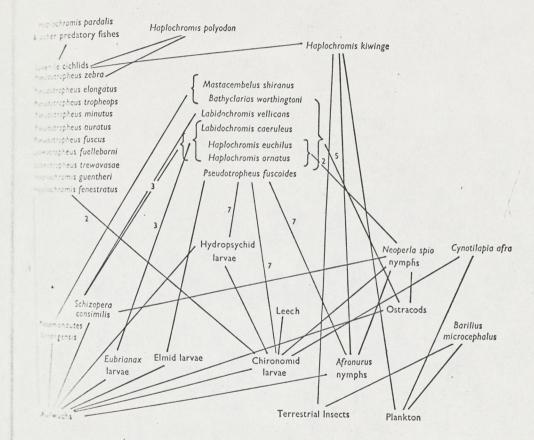


Fig. 89.—Food web on the rocky shore.

(c) The intermediate zone

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

(d) Crocodile Creek

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

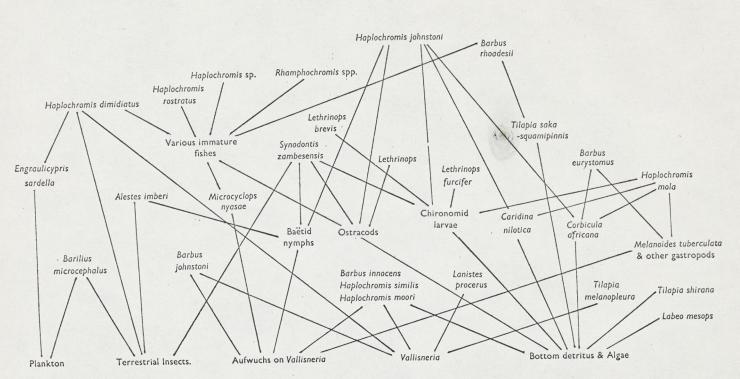


Fig. 90.—Food web on the sandy shore.

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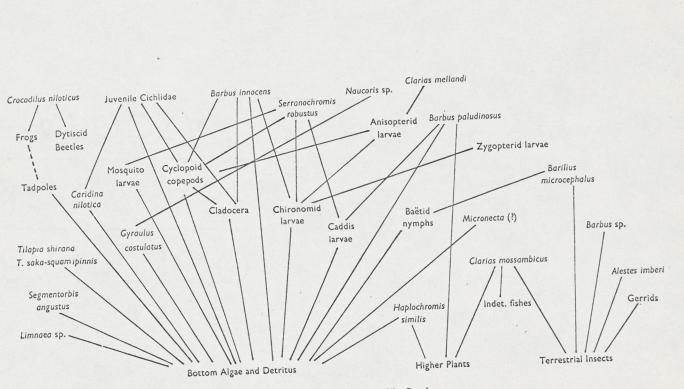


Fig. 91.—Food web in Crocodile Creek.

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a loosely organised assemblage in which the members are distinguished by to more than the varying proportions on which they draw upon the constiments of a common stock ". While this statement is broadly applicable to the pecies considered here the range of foods is much less than that taken by the mnivorous 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 cuts 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 * 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 signifisince is obscure for the Calothrix eaten seems always to pass through the gut argely 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. trewaand Pseudotropheus tropheops, which include Calothrix in their diet the arst 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 ethods 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. impheops, are seldom frequented by it. These differences in "feeding are not great and there is no doubt that both species often take their from the same situations and overlap in food preferences to a great extent.

brackets in Figures of importance. order in arranged are Foods e rocky shore. number of gut TABLE 6 the from indicate fishes cichlid -eating invertebrate six of preferences p

examined.

guts

the

Mayfiy nymphs Chironomid larvae

Chironomid larvao Ostracods Mayfly nymphs Hydropsychid larvao *Schizopera*

Mayfiy nymphs Chironomid larvae Ostracods Hydropsychid larvae

Zooplankton Mayfly nymphs Terrestrial insects Chironomid larvae

Hydropsychid larvae Mayfiy nymphs Chironomid larvae Eubrianaz larvae

er dipterous larvae

ironomid larvae /dropsychid larvae tracods

Pseudotropheus fuscoides (6)

Haplochromis orn

euchilus

Haplochromis

ochromis kiwinge (Juv) (26)

Haplo

Labidochromis caerule (7)

vellicans

abidochromis v (26)

(9)

(9)

Also recorded Hydropsychid larvae, *Diaptomus*, Terres-trial insects (?) Snail, Algae.

Also recorded Neoperla nymphs, Eu-brianax larvao, Elmid larvae, Mites, Algae.

Also recorded Fish, Neoperla nymphs, Eubrianax larvae, Terres-trial insects, Schizopera, Prawn, Snail

Also recorded Algae, Hydropsychid larvae

Also recorded Ostracods, Mites, Case-bearing caddis larvao, *Coreliva* larvae

recorded
 s. Schizopera,
 fly nymphs, Diapto is. Eubrianax larvae,

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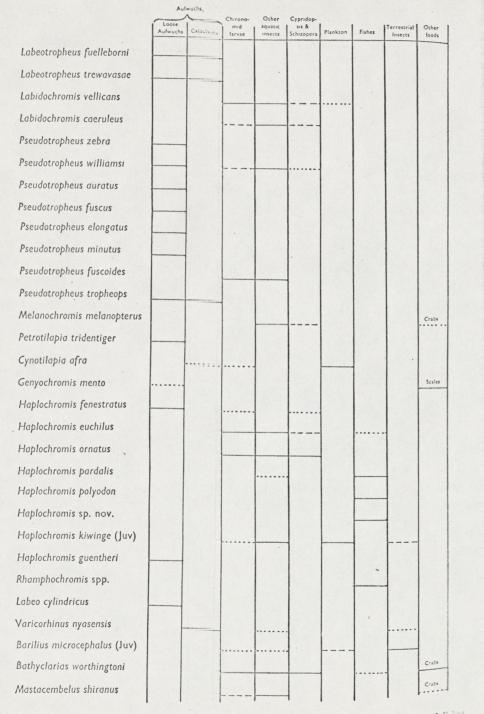
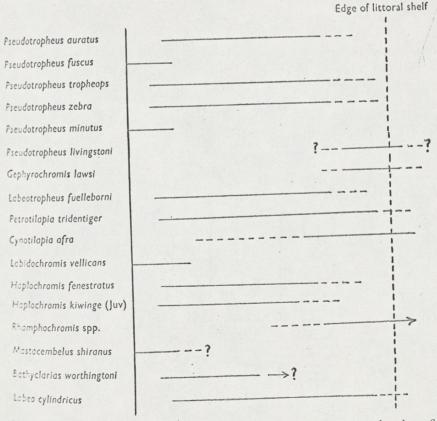


Fig. 92.—Diagrammatic representation of the main foods of the rocky shore fishes. A full have indicates a major food source; a broken line a frequent source and a dotted line set occasional source.

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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.



3.-Diagram showing approximate horizontal distribution of some rocky shore fishes.

Of the remaining five species *Haplochromis fenestratus*, while feeding largely loose Aufwuchs, occasionally supplements its diet with a few chironomid

that of the other species. Because of its narrow mouth it may be able t_0 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 coexistence 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

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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 tishes, namely competition for breeding grounds, will be discussed in Part II.

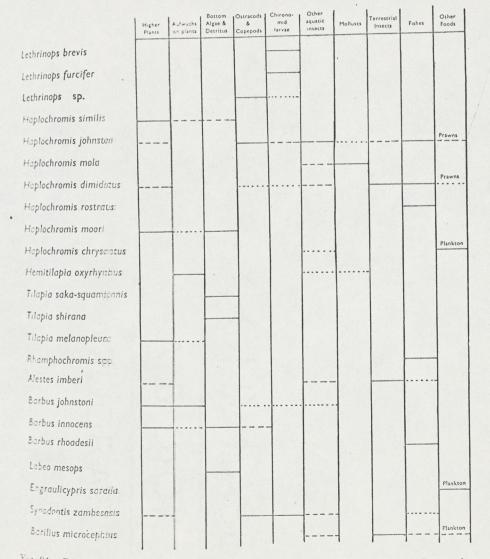


Fig. 94.—Diagrammatic representation of the main foods of the sandy shore fishes. Conventions as in Fig. 92.

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(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 johnstons 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 a abundant, can probably be attributed to the competitive influence of the numerous other species of the genus and their allies which occur there are 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 references, and feeding mechanism to Pseudotropheus zebra has already been winted 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 fod is present alone. Its great numerical abundance in the intermediate zone hows 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 tehaviour may well be a contributary factor to this success. Onto the rocky dore, 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 towsers on the vallisnerial Aufwuchs where rocks are also available as an portant source of food, but it is unable to do so when this food alone is avail-. alle. Moreover C. obliquidens is probably derived from rock-dwelling ancestors and long standing instincts and breeding behaviour connected with rocks would muire 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 ogh the number of species involved is less. Here occur several species be food preferences overlap to a considerable extent but which are fairly eral feeders capable of utilising a variety of foods and presumably able to pensate for the scarcity of one kind of food by turning to another. There also some species which occupy a distinct niche, viz. the bottom scraping tarians of the genus *Tilapia* and young weed-dwelling *Serranochromis* which actively seek out animal prey both among the weeds and on bottom.

INTER-HABITAT MOVEMENTS AND RESTRICTIVE ECOLOGICAL FACTORS

An outstanding feature of the littoral zone of L. Nyasa is the way in which of the species represented are restricted to one major habitat. This is most strikingly if one observes the fishes with a mask and passes from a to a sandy shore. On the former one sees myriads of fishes which hear with startling suddeness as one passes onto the sand which, at first presents a deserted appearance, but which is later seen to house a sy 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 Crocodila 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 Crocodil 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 copepoi 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 imposssible 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 rockon 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 ther 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 habitaenabling 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 prein 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 Eubrianboth 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 (1931) 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 rockdwelling ancestors, has evolved a pattern of behaviour an integral part of which 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 intermediate zone. Such an ancestral tehaviour pattern can scarcely be discounted as a major factor restricting the Estribution of Cynotilapia afra to waters off the rocky shore, for it is now imost 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 inderstand as the species represented in L. Nyasa require a penetrable bottom in which to embed themselves, the similar restriction of gastropods is puzzling. *Limistes procerus* is restricted by its food preferences but there seems to be no taken why the rocks should not provide suitable food for some of the other second why the rocks should not provide suitable food for some of the other there exposed nature of the environment probably hinders the basisation of the rocks. That this is so is indicated by the presence of *Phycopsis* 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 molluses if the opportunity arose is the perhaps partly responsible for their exclusion. The finding of a molluse the guts of specimens of *Genyochromis mento* and *Pseudotropheus fuscoides* the at 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 ticting species to a single major habitat, though it may well have done so the course of evolution of the parent forms of the fishes. There are excepto this generalisation (notably the restriction of *Cyathochromis obliquidens Pseudotropheus lucerna* to the intermediate zone as discussed on pp. 228 (229), but at the present time the majority of species are so specialised in their preferences and, more particularly, in their methods of food collection, that aspects of their biology alone usually restrict them to one major habitat, 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 ecologist as is "the fauna of Great Britain", and one must henceforth the animals of this great lake as comprising a number of very discrete which are as distinct from one another as are the faunas of an English Wood and an expanse of moorland.

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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.

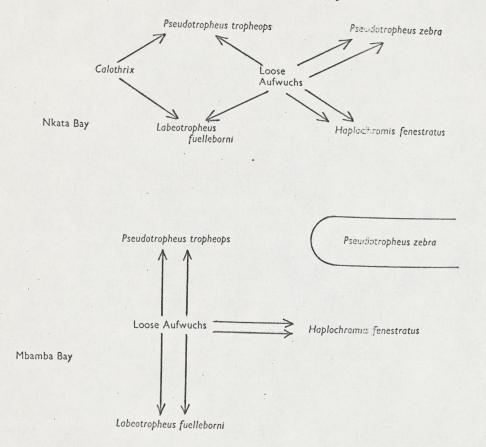


Fig. 95.—Suggested competitive relationships between some rocky shore fishes at Nkata Far (where *Calothrix* and loose Aufwuchs are available as food), and att Mbamba Bay (where only loose Aufwuchs is available).

At Likoma Island (about five miles off the eastern, Mogambique, shore where a total of five days, intensive field work was carried out, and at Ruarac (about forty miles north of Nkata Bay), conditions were very similar in generarespects to those prevailing at Nkata Bay. Some rather stariking differences were noted, however, at Mbamba Bay (on the Tanganyikaan shore) during a two-day visit. Here the rocks are granitic in nature as they are at LikeraIsland 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 fading it than the ecologist. Haplochromis fenestratus, another loose Aufwuchs enter, 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 abbling and chiselling of P. tropheops and L. fuelleborni respectively. There 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 tear Domira Bay) made by Messrs P. B. N. Jackson and K. Howard, the reneral facies was similar to that of similar habitats in the north but produced everal specimens of what appears to be an undescribed species of *Pseudo*tropheus.

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

A NOTE ON PRODUCTIVITY IN LAKE NYASA

The central problem in limnology is that of productivity so it is useful to sider what light the present study has shed on the productivity of Lake vasa. In a series of papers Rawson (summarised in Rawson, 1955) has monstrated that in large deep lakes in North America an inverse relationship the between increase in mean depth and productivity (based on yield of fish, anding crop of net plankton, and weight of bottom fauna). While detailed initiative data are still lacking, the impression gained as a result of everyday evations on these characteristics is that the generalisation applies to the Nyasa, with the exception of the shallow South East arm south of adzulu Island which must be treated as a separate entity. The rest of the however, cannot be treated simply, for the biological economy of each habitat has been shown to depend ultimately on a different kind of

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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 An index of the productivity of the sandy shores. periphyton productivity.

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. 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 favour-

able 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

which belong to the family Cichlidae, are numerous, both specifically and numerically, and many of them show striking adaptations to their mode of lif_{e} , 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. TROPHIC INTERRELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 237

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 cenera. 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), *Labido-chromis* (2), *Genyochromis* (1) and *Gephyrochromis* (2).

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

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

Systematically the Mbuna can be characterised as follows : Cichlidae of all size, seldom more than 20 cm. in total length and frequently smaller. by moderately elongate, with two incomplete lateral lines. Scales dentiete. Nape covered with large numbers of small scales. Scales on check all. Snout short. Dentition various, but always with a short series of to nine conical postero-lateral teeth on each side of the upper jaw, usually ared ; and always with several rows of teeth anteriorly which may be ind or, more usually, bi- or tri-cuspid. Lower pharyngeal bone triangular, to vimately equilateral, with tendency to be indented on posterior margin. The basic for upper pharyngeal bones formed by the parasphenoid in the idle and the basiccipital at the sides. Dorsal fin with fifteen to nineteen ally seventeen to nineteen) spines and seven to eleven soft rays. Anal 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 trophcops Regan Pseudotropheus novemfasciatus Regan Pseudotropheus novemfasciatus Regan Pseudotropheus novembasca Pseudotropheus fuscoides Fryor Pseudotropheus fuscoides Fryor Pseudotropheus anionatus Fryor Pseudotropheus ser nov. Pseudotropheus zebea (Boulenger) Pseudotropheus utiliamsi (Günther) Pseudotropheus utiliamsi (Günther) Pseudotropheus birimpstonii (Boulengor) Pseudotropheus elepans Trowavas Pseudotropheus lucerna Trowavas Pseudotropheus lucerna Trowavas

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 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 slive 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 copheops* Regan, *P. t. gracilior* Trewavas, *P. microstoma* Trewavas, and *P. exceptibilitalmus* Ahl. Reasons for regarding these forms as constituting one tariable 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 inficulty experienced in defining several of the genera, notably those which roup themselves most closely around *Pseudotropheus*. The distinctions tween some members of this genus and the genera *Melanochromis* and *phyrochromis* are so fine that, were one considering the border-line cases at ne, one would not hesitate to merge the genera concerned into one taxonomic the other hand the extreme forms of *Melanochromis* and *Gephyrodromis* are sufficiently distinct from *Pseudotropheus* to merit independent . On the other hand the extreme forms of *Melanochromis* and *Gephyrodromis* are sufficiently distinct from *Pseudotropheus* to merit independent . Cheric status. Thus *G. lawsi* is obviously closely related to *P. lucerna* and *P. d. gans* and there could be few complaints if it were regarded as being a tember of the genus *Pseudotropheus* as it at present stands defined, yet it is diviously congeneric with *G. moorii* which exhibits sufficient non-*Pseudotrodreus* features to merit generic separation. Similarly *P. fuscoides* rests uneasily tween *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 reparate genera. Three striking cases of this phenomenon are found among the Muma. 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 coubtedly adaptive features by bestowing generic distinctness upon them, in thereby to some extent obscuring the phylogeny of the group as a whole ; sumping all the species concerned into one genus whose members would then show an unusually wide range of dental patterns. Neither system is startely 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 poradic 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 * similarly functionless in such species as Pseudotropheus tropheops and Petrotilapia tridentiger in which it may be well developed, feebly developed, completely absent : but the fact that it is always well developed and very Cearly apparent in some species (Pseudotropheus auratus, Labidochromis (meruleus) suggests that here it has been adopted as a specific recognition signal plays some part in the courtship display and is therefore preserved by astural 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

* 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 Hovanitz and partly because it seems TROPHIC INTERBELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 243

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 snal 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.

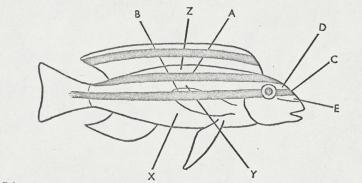


Fig. 96.—Colour pattern of Pseudotropheus auratus. (Diagrammatic). For significance of lettering see text.

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 fattern 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

* Trewavas' (1935) statement that these bands in the male are gold was based on preserved

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 toat 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 because 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 mates. One field observation is relevant to this question. A specimen seen guarding a territory, and therefore presund to be a male, was in a "half way strage" 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 phase of the polymorphic *Pseudotropheus zeibra* and the monomorphic *Labidochronae caeruleus* both males and females of which are similarly and most strikingly coloured. (See Fig. 8 in Fryer, 1986 a).

Colour prolymorphism

Colour polymorphism is shown by at least four species of the Mburs Labeotropheus fuelleborni, L. trewavassne, Pseudotropheus zebra, and P. tropheore 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. fueld chorni is a rather dull blue grey though the male assumes a brighter "buceding dress" from time to time. On female, however, captured at Benji Tsland in the southern part of the lake

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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 to per cent of the females were "normal" in coloration and 50 per cent whibited 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 hast 40 per cent of the body, in others no more than about 20 per cent. The agree of development of the black pigmentation may differ on the two sides f a single fish. Always, however, the pigment was aggregated into distinct blotches, being in this respect quite different from the peppered pattern seen L. fuelleborni. Apart from its reappearance again in Pseudotropheus zebra we 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, letween these stations, also almost certainly refers to this form.

A more complex state of affairs exists in the case of P. zebra. Here both traces 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 erange 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 toply as an indication of their fundamentally similar genetic makeup and * considered as additional evidence that the two genera concerned, which markedly in mouth structure, are closely related. So far as the Nyasan addlids are concerned this opinion is still held. However, similar polymorm, in one form of which the distribution of the black pigmentation is totally 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 Tailed to Haplochromis (Greenwood, 1954, 1956 a, 1956 b, 1957 and personal munications), and is to be seen again in two species of Haplochromis of L. In Lake Victoria Greenwood considers that no reliability can be placed this characteristic as an indicator of phyletic relationship save that its reflected occurrence probably reflects the oligophyletic origin of the Lake atoria species flock. Nevertheless he thinks it "suggestive" that two of the elecies which exhibit it, Haplochromis sauvagei (Pfeffer) and Macropleuro-Le bicolor (Boulenger), show similarities in fundamental syncranial morpho-Taking a broad view, therefore, the conclusion seems to be that the strence of a similar pattern in certain individuals of fishes in three widely

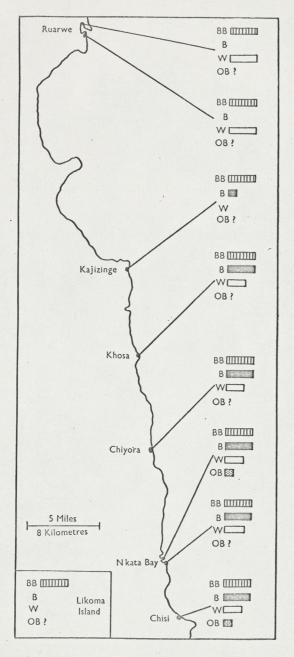


Fig. 97.—Distribution of colour forms of *Pseudotropheus zebra* in a region in the north-area Lake Nyasa and (inset) Likoma Island. Degrees of abundance indicated by the second are, Common : Present : Rare : Absent.

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separated lakes is indicative of the oligophyletic origin of their present-day dehlid 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 stimated by visual observations, in several localities along a forty mile stretch if shore which is predominantly rocky and is interrupted by sandy beaches of by minor extent, together with the state of affairs at Likoma Island which is 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 is miles south of Nkata Bay, no blue or white specimens were seen or collected in my colleagues who specially looked for them there. While it was unfortenately not possible to make observations at as many points as would have then liked in part of the area shown on the map the indications are that the midence of the various colour forms does not necessarily change gradually. If this were so one would have expected the white form, which is very conplement, 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 obur forms and the environment, which is very uniform on rocky shores. It eems possible, however, that some of them, particularly W and B, will be the obvious than their fellows to predators, and particularly to fish-eating test such as cormorants, darters, kingfishers, fish eagles and ospreys, all of which presumably possess colour vision.*

Pseudotropheus tropheops also exhibits colour polymorphism. While very stable 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 atter light in colour and has a number (usually eight) of narrow horizontal orange on the flanks is also common, at least at Nkata Bay. Both males and also of this form are to be found. In males in breeding dress the horizontal states tend to be obscured by the development of darker pigment and bluish the bological differences between it and the "typical" form could be found, by F. Trewavas, to whom a specimen was sent, agreed that it was indistable from her preserved material of *P. tropheops*.

Another form, again originally taken to be a distinct species, is typically pale, almost silvery, in colour and has eight dark vertical bars, of which below the dorsal fin and extend some way into it. The dorsal fin thus ix distinct patches of black pigment at its base. The two horizontal of the basic colour pattern are also quite well developed. This pattern in seen on a juvenile taken from the mouth of a female which had the pattern. Unfortunately all save one of the young of this specimen had that from the mouth during capture so the opportunity of ascertaining or not mixed broods were produced did not arise. This form is rather Nkata Bay but was found to be much more common at Ruarwe. A simens have been seen which are in some ways intermediate in coloratween this form and the typical form, the ground colour being dark, Ad lendum, p. 280

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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 omething 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 thristy 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 prographical 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 severtheless 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 fundiants 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 pelacimode of life yet is still found only on rocky shores, all the other species arbenthic in habits and are usually to be found swimming within about 1 metrof the bottom. They are graceful fishes whose movements are usually un hurried, 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 lease 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 orobserves, as is often possible, a region where a rocky shore suddenly cease 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 abourand in which they are completely absent. Where rocky shores grade morgradually 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 6 or 7 metres increases there is a progressive diminution in number of Mburand, 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 island. For instance, even on the rocky shore studied at Nkata Bay where there is a we marked littoral shelf, a depth of 20 metres is attained within about 70 metros of the shore, and on large tracts of shore the slope is much steeper that this and there are indeed points at which the rocks descend almost vertical to depths in excess of 20 metres.

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

Detailed information on the individual ecological preferences of the spectrum 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 small²⁵ One of these is the algal felt (Aufwuchs) growing on the rocks, which consistentially of diatoms and other loose algae (loose Aufwuchs) and more firm attached filaments, particularly of the blue green alga *Calothrix*, which TROPHIC INTERRELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 251

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 Manochromis melanopterus seems to possess potentialities whose exploitation and permit the inclusion of fish in the diet and, on one occasion, a small fish the found in the gut of this species. The other fishes of the environment have then exploited, however, namely by *Genyochromis mento* which feeds by rasping takes from its larger and less active brethren. (Fryer, Greenwood & Trewavas, 1955). This absence of piscivorous species may not be unconnected with the revalence of small size within the group. (In aquaria all species, whether carnterious or herbivorous feed greedily on the eggs or fry of their fellows if opportaity to do so offers).

The food of the species studied is listed below.

Labeotropheus fuelleborni Labeotropheus trewavasae Pseudotropheus zebra Pseudotropheus livingstonii Pseudotropheus williamsi Pseudotropheus lucerna Pseudotropheus tropheops Pseudotropheus fuscus Pseudotropheus fuscoides Pseudotropheus elongatus Pseudotropheus minutus Pseudotropheus auratus Melanochromis melanopterus Petrotilapia tridentiger Cyathochromis obliquidens Cynotilapia afra

Genyochromis mento Labidochromis vellicans Labidochromis caeruleus Gephyrochromis lawsi

Aufwuchs (including Calothrix) Aufwuchs (including Calothrix) Loose Aufwuchs Loose Aufwuchs Insects + some loose Aufwuchs Loose Aufwuchs Aufwuchs (including Calothrix) Loose Aufwuchs Insects Loose Aufwuchs Loose Aufwuchs Loose Aufwuchs Insects and (in one large specimen) crabs Loose Aufwuchs Loose Aufwuchs Zooplankton + very small amounts of Aufwuchs and insects Fish scales and fins + traces of Aufwuchs Insects Insects Loose Aufwuchs

INDIVIDUAL ECOLOGICAL PREFERENCES

While all species occur among or near rocks it is possible to point to certain cical preferences of a few species, other than those of food, which will to keep them isolated from their near relatives and allow them to inhabit same general habitat without competing to any great extent. Perhaps tost striking example of this is the occurrence in rocky error it.

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.

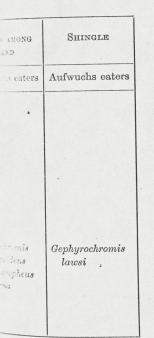
The differences in general ecological preferences and in food preferences are shown in Table 7. Ecological separation is particularly weak among the the Aufwuchs eaters. Here, although the difference between eaters and noneaters of *Calothrix* is an established fact in some areas of the lake, its significance 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 ports at which their behaviors and the latter species construct ports at which their behaviors at the latter species construct ports at which their behaviors at the latter species construct ports at which their behaviors at the latter species construct ports at which their behaviors at the latter species construct ports at which their behaviors at the latter species construct ports at which their behaviors at the latter species construct ports at which the latter species construct ports at



ROCKY	SHORES					
			Aufwuchs eater	rs		
Eaters of leand (Coose Aufwuchs	Aufwuchs Eaters of Loose Aufwuchs onl			s only	
ng mecha- m Type 1	Feeding mecha- nism Type 4	Inshore skulkers		Non-skulkers		Deeper
		Large species	Smaller species	Feeding mecha- nism Type 3	Feeding mecha- nism Type 2	
otropheus lleborni otropheus vavasae	Pseudotropheus tropheops Pseudotropheus novemfasciatus?	Pseudotropheus fuscus	Pseudotropheus minutus	Pseudotropheus auratus Pseudotropheus elongatus	Pseudotropheus zebra Pseudotropheus elegans ? Petrotilapia tridentiger	Pseudot- livings

	Invertebrate e	Mixed feeders	Scale eaters		
Semi-Pelagic plankton feeders	Inshore skulkers	Non- skulkers		· · ·	_
					Fee
Cynotilapia afra	Labidochromis	Labidochromis	Pseudotropheus		
	vellicans	caeruleus Pseudotropheus fuscoides Melanochromis melanopterus	williamsi	Genyochromis mento	Lal fr Lal tr

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TABLE 7

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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

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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 remitted 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 tasure of protection to the eggs which are presumably shed by the female the territory of the male at the end of courtship, and are then taken into

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 rockbut although search was made no eggs were seen.

* 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 bimaculation

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Two exceptional occurrences are worthy of mention. On one occasion three individuals of P. tropheops (sex uncertain) were seen tail chasing. On mother occasion a male of P. auratus guarding its territory was approached a dark-coloured fish, almost certainly a female of P. fuscus, and certainly of its own species, with which it immediately commenced frenzied tail hasing. After a brief pause a second bout took place, and the stranger then oved away. It would appear that this behaviour was elicited by some signal mmon to both and that the cessation of tail chasing represented the point where the courtship behaviour of the two participants diverged and was no ager mutually stimulating. The phenomenon of attempted courtship tween closely related species has been reported for other groups, e.g. butter-(Tinbergen 1953), in which group its occurrence is common knowledge to aturalists, 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, it is not surprising that such behaviour should be occasionally elicited by losely related species of Mbuna. The observation just cited, incidentally, upports 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. Indging from the avidity with which eggs are eaten in aquaria by many rocky dore fishes (including herbivores) it seems probable that they are picked up by the female immediately after fertilisation or they would otherwise be mickly eaten by other fishes. As the courtship behaviour appears to be based in 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 apheops*, *P. fuscus*, *P. zebra*, *P. lucerna*, *P. williamsi*, *P. elongatus*, *Petroapheops*, *Cyathochromis obliquidens*, *Labidochromis vellicans*, *Labeoapheus fuelleborni*, *L. trewavasae* and *Genyochromis mento*.

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

The size of brood is small in comparison with that of many other mouthbrooding 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 *Haplochrowis* 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. Hes). In relation to the size of the parent the eggs are particularly large, being larger than those of some of the mouthbrooding 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.

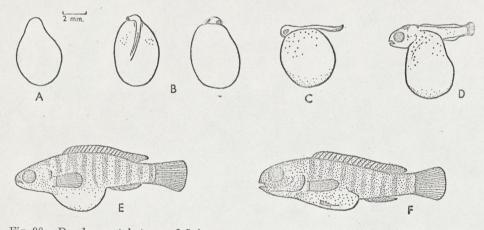


Fig. 98.—Developmental stages of *Labeatropheus* during the period of oral incubation. (Note Both species of *Labeatropheus* are involved in the sequence portrayed here, but in the very early stages of development they appear to be indistinguishable).

There is an efficient correspondence between the number of ripe ovariate 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 egge

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 *Laibeotropheus* passed through during the period of oral incubation are shown in Fig. 98. Study of various developmental stage 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 (*Labeotropher* trewavasae) had a length of about 16 mm. Young Mbuna (species uncerta-19 mm. in length have been collected in the most inshore waters of rock shores, and others, believed to be *Pseudotropheus tropheops*, 20 mm. in length

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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 cosufficient 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 tody of selective mating as envisaged by Kosswig and further observations may throw valuable light on this problem. To date the evidence, while santy 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 inside that there could be competition for breeding grounds. However, this attingency does not seem to arise on account of the fact that breeding takes throughout the year, and that, at any given time, only a fraction of the tail male population is occupying territories. One can always find territorial the but their numbers are few in relation to the total population and their throries are usually well separated. In this they differ markedly from the tail mareas, many males simultaneously occupy contiguous territories if yer, 1956 c).

ADAPTIVE RADIATION

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

Just as the birds of the subfamily Geospizinae of the Galapagos Islands

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. livingston 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. williami* 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 specimenhas its lips produced into pointed lobes and, by analogy with another Nyasa cichlid, *Haplochromis euchilus* Trewavas which has similar lips and where 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, *Cyathochronist* obliquidens has become established under conditions where rocks occur amoust 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. luceria*.

TROPHIC INTERRELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 259

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

ding mechanism, needs under similar conductive to the Pseudotropheus stock Cynotilapia afra is undoubtedly an offshoot from the Pseudotropheus stock is more particularly from the zebra group of the genus. In fact at first ince it is easy to confuse a blue and black barred P. zebra and C. afra which emble each other in form and coloration. The mouth structure too is ry similar in the two species but C. afra differs strikingly in dentition (cf. 5. 16–18 and 28–31 in Part I). This species has ventured, or has been reed away, from the rocks and now leads a semi-pelagic existence in the shore waters where it feeds largely on zooplankton. In spite of this partial mancipation from the rocks C. afra is nevertheless found only in open water st off rocky shores, and occasional individuals are seen or captured among he rocks from which they still occasionally pick up a little food.

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

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

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

E PHYLOGENETIC RELATIONSHIPS OF THE MBUNA AND THEIR EVOLUTIONARY

HISTORY

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

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

The Mbuna are probably among the most long-standing of the cichlids of Nyasa. This is shown clearly by the fact that all the genera, which comprise than one-third of the cichlid genera present, are endemic, and by the that these genera, which appear to be monophyletic in origin, and which all closely related, have nevertheless evolved some highly complex yet by differing specialisations. It seems highly probable, therefore, that the 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 they arose from a *Haplochromis*-like ancestor, and probably from a species. The most generalised present-day species of *Haplochromis* such fluviatile species as *H. wingati* (Boulenger) and *H. bloyeti* (Sauvage).

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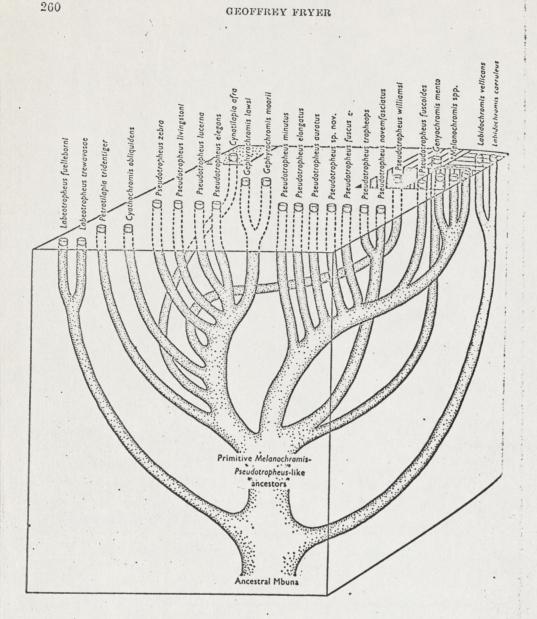


Fig. 99.—Suggested phylogenetic relationships of the Mbuna. Note : Proximity to the base at the "tree" does not necessarily denote primitiveness but indicates rather that diverse is of that line probably took place early in the history of the group. Further, the fact this other genera are shown arising from between the *Pseudotropheus* branches does not between the various preudotropheus the are the various *Pseudotropheus* species to one another. On the other hand, the \mathcal{F}^{rest} *Pseudotropheus* is at present rather ill-defined and merges almost imperceptibly **e**.

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

TROPHIC INTERRELATIONSHIPS OF

A clue as to what the intermedia may have been like is given by the s Fromis living in Lake Victoria. Her that evolution has not gone on in isc Yvasa, one group of species of Haploc the evolution of a Pseudotropheus-like Boulenger) which is scarcely separable this species and the generalised Ha :. nuchisquamulatus (Hilgendorf) ((Like Victoria a Haplochromis with intition, similar to those of Cyathoch Hilgendorf. According to Greenwood iom a form like H. lividus Greenwo idens characteristics, and which i I. nuchisquamulatus whose affinities in not difficult to perceive. In La ir a longer period than in Lake Vic miliate forms should have become en : ore specialised species, but it seems f some of the species of Haplochron masonable indication of the kind of f 19050

Certain fragments of information the ontogeny of the extant species. tages of some of the Mbuna (e.g. Prandal fin such as is to be seen in the

The occurrence of the OB colour p species of *Haplochromis* in Laker Vi brived from *Haplochromis* in Lake successed ancestry of the Mbuna.

An important feature in the evolu comption of an algal diet. Fishes adoption of the habit of feeding straces probably allowed the Mbun view they first colonised the lake. I has been towards perfection of this 1

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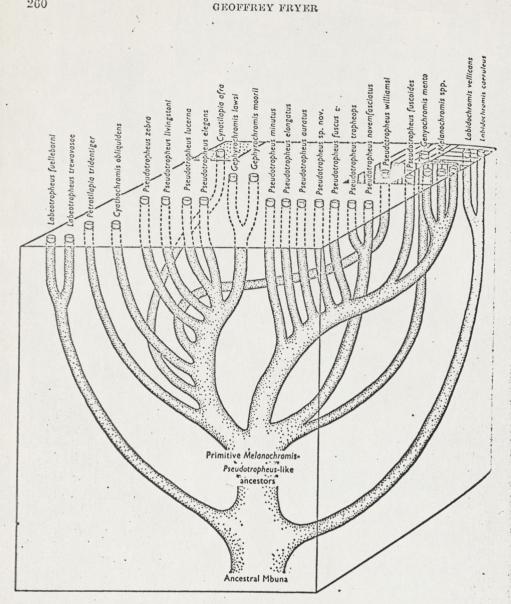


Fig. 99.-Suggested phylogenetic relationships of the Mbuna. Note : Proximity to the bar it the "treo" does not necessarily denote primitiveness but indicates rather that diversion of that line probably took place early in the history of the group. Further, the fact that other genera are shown arising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

The variously marked areas on the upper surface of the cube indicate different for it habits. Stippling : Plankton feeders. Obliquo lines : Scalo eaters. Horizontal Invertebrato pickers. Vertical lines : Invertebrato cators. Solid black : Mixed forest White : Algal browsers.

TROPHIC INTERRELATIONSHIPS OF

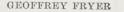
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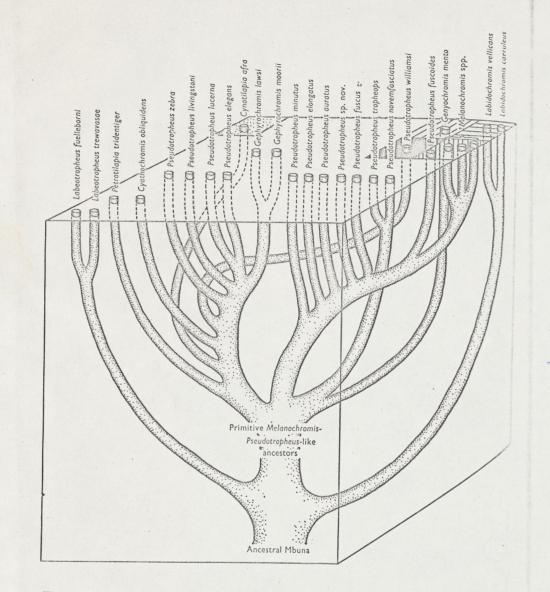


Fig. 99.—Suggested phylogenetic relationships of the Mbuna. Note: Proximity to the base of the "tree" does not necessarily denote primitiveness but indicates rather that divergence of that line probably took place early in the history of the group. Further, the fact the other genera are shown arising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

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

TROPHIC INTERRELATIONSHIPS OF LITTORAL COMMUNITIES OF L. NYASA 261

A due 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 Haplodromis 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 Xyasa, 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 faciliton, similar to those of Cyathochromis obliquidens. This is H. obliquidens Higendorf. According to Greenwood, (1956 b) this species probably arose from a form like H. lividus Greenwood, which exhibits certain incipient oblimidens 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 intermendiate forms should have become extinct in the face of competition from the are specialised species, but it seems fairly safe to assume that the structure H-some of the species of Haplochromis living in Lake Victoria today gives a monable indication of the kind of fishes from which the present-day Mbuna Nr956

Certain fragments of information on this matter can also be gleaned from the ontogeny of the extant species. For instance the early developmental tages of some of the Mbuna (e.g. *Pseudotropheus tropheops*) have a rounded modal 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 pecies of *Haplochromis* in Lakes Victoria and Kivu and in genera clearly between the *Haplochromis* in Lake Victoria is not at variance with the respected ancestry of the Mbuna.

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

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

Study of the morphology and habits of the other genera indicates that the sting of algae from rocks offered better opportunities for radiation, and it is statk this type of trophic specialisation that they tended to evolve, though 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 maxful around the structure).

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*

* Dr Trewavas writes, "Five specimens of *Gephyrochromis moorii* were collected in a finemeshed seine during the Survey of 1939 on the lake shore near the mouth of the River Rukura (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.

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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* rellicans. 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 une telle diversité."

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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 die 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 permiit 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'éxistence 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" manuage 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, howeveer, 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 (1935) 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 our 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 cof fossils, including molluscs and the remains of *Mastodon* and *Hippopolannus*, in lacustrine deposits (the

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chiwondo beds) in northern Nyasaland. On the basis of their fossil content these heds 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 minion 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 stimates 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 not, 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 cone 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 inticularly favourable to speciation in Lake Nyasa, and also that in horses it terms possible that a change of generic magnitude could be effected in about million generations (see Huxley, 1942, p. 61), a zoologist, without taking chisance of any geological evidence, would probably favour an age much fore 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 internet 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 ethern part of its present basin and that it stood at a considerably higher evident that it does today (Dixey, 1926, 1941). Its present form and level the only arrived at after a complex series of downthrusts and faults. There exist therefore have been many ecological changes during the history of the basin. Changes still take place today in the form of annual fluctuations in the 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 wivity.

Making allowance for its considerable irregularities, the total length of the shore-line of Lake Nyasa and its included islands probably exceeds 1000

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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 net 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 hemiphere. 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. Alter natively 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 sand or reed-fringed shores. Even a small sandy gap in a rocky shore is a vereffective 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 preventemixing 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 continue populations. Each species is broken up into innumerable populations various sizes which are isolated to a greater or lesser extent. Over less periods of time changes in the lake level and the silting effects of inflow 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 smong literally thousands which have been seen being two juvenile specimens in which, after capture, the dorsal fin was dull grey. At Likoma Island this in 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 topulations are indistinguishable in structure and habits.

Similarly, at Likoma Island a small percentage of the males of *Pseudotropheus* trepheops 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 were and captured at Ruarwe forty miles to the north and was also seen in one take at Kajizinge only about seventeen miles to the north. Examples of this trid 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 from a 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

An example mentioned elsewhere which involves a structural feature is that of slight detrees in the tips of the teeth of specimens of *Gephyrochromis lawsi* in populations at 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 un doubtedly 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 *Euphydryss* [*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 Timor feeff-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 joras 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. Pobzhansky (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 nost 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, pecularities 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 for (1951), the minimum number of genes that can form a workable isolating techanism is two. It is not claimed that the number is anywhere near this is the Mbuna—and it seems very unlikely that it is—but the undoubtedly tepid 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 to 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 mature, and that they possessed certain characteristics which, potentially at least, could facilitate rapid speciation.

Reference to the means whereby mixing of previously isolated populations and take place has already been made, but two further possibilities merit desideration as both may have been of great importance. Although the and the bund are stenotopic and show a marked avoidance of non-rocky shores it not to be doubted that there must have been occasional migration across there is 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

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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 fool 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 way not obligatory.

Scale-eating may well have arisen under conditions of food searcity 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 deter mine the micro-habitat preferences of certain species such as *Pseudotropheno 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 isak tion, the form evolved under such conditions would tend to seek out such a niche although wider possibilities existed. This tendency would be reinforce

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by the ever increasing competition between species, and a species such as P. *juscus* which had become specially adapted to life in the most inshore strip may have been unable to compete successfully with other species living in *lightly* 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 estabshing 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 partiplarly rare in the area as a whole, and several specimens have been observed rather quiet "pools" on other shores. Restriction of this kind could be the to having acquired special habits in isolation, or to the effects of competition. As genetically distinct populations came together no doubt some species acte forced into those niches to which they were best adapted, and others tobably became extinct. However, among the herbivorous members of the group there can be found today several species whose general habits are · Il very similar, whose horizontal and vertical ranges in no wise differ, and which, although they collect it by different means, eat identical food. The follure 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 carned 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 an 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 ettram, Borley & Trewavas (1942), Trewavas (1947) and Lowe (1952, 1953) where distinct differences in habits can be discerned. In this respect too they "er markedly from Darwin's finches, with which they otherwise show many arkable parallels. In passerine birds closely related species usually occupy afterent 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 studies). In Darwin's finches some species live side by side but differ eize of beak and apparently take different foods, and therefore occupy tent niches. This is not so in certain cases among the Mbuna.

The co-existence of so many closely related species which have similar appears all the more remarkable when the competitive relationships of with similar ecological requirements elsewhere are considered. Thus milarity in ecology between representatives of even different genera is times sufficient to render them mutually exclusive, as is the case of the referred to in common speech as flycatchers in the Tonga Islands. Here,

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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 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 nonpredacious 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 β^{\downarrow} 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 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 pare which I had not seen until my conclusions were reached. It is interesting 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 Cartwride on the effects of predation on game-birds in Canada in the book by Aller

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 Mie-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 abspecies 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 useff to be no nuere 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 semingly 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 theast in part by ethological factors, and it is most striking that, in three eases of pairs of very closely related species, the members of a pair differ tarkedly in cohoration. Thus *Pseudotropheus fuscus* and *P. auratus* which, though they have rather different horizontal ranges, must often meet, differ tarkedly in coloration, *P. fuscus* being, even in breeding dress, rather the subrely coloured while *P. auratus* has the very distinctive coloration (black cold in the fremale; blue on black in the male) described on p. 243. The the remarkable cobalt blue and black *L. caeruleus* (Fryer, 1956 a). The the remarkable cobalt blue and black *L. caeruleus* (Fryer, 1956 a). The third case is that of *Pseudotropheus zebra* and *P. livingstonii*. The three these of *P. livingstonii* captured were all bright golden orange in colour with distinct dark: vertical bars; this coloration differing markedly from that any of the three types of male coloration found in the very closely related *P. auratus* (p. 2465).

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

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

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

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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

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

The adaptive radiation of the group is summarised and an attempt is rade 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 distribation of environments populated by Mbuna is reconstructed. Against this background the probable sequence of events during the evolution of the arious species of Mbuna is reconstructed from the knowledge of the structure, cology and habits of the present-day species. The evidence is wholly comtible with the theory of allopatric speciation, and there is no occasion 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, diviates 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	
	Dira	511010	511010	Lind	
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		
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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		12
»» »»	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
33 33	12.1	22		Ŭ
		(occluding)		
»» »»	12.3		23	12
Labeotropheus trewavasae	9.9	10		
3 7 5 7	10.6		22	15-16
Labidochromis vellicans	6.2		10	8

ADDENDUM

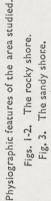
Since the above was written Moreau & Southern (1958) have given a account of polymorphism among birds in what possibly represents a single species of Shrike of the genus *Chlorophoneus*, which bears so many striking similarities to the state of affairs existing in *Pseudotropheus zebra* that the parallelisms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

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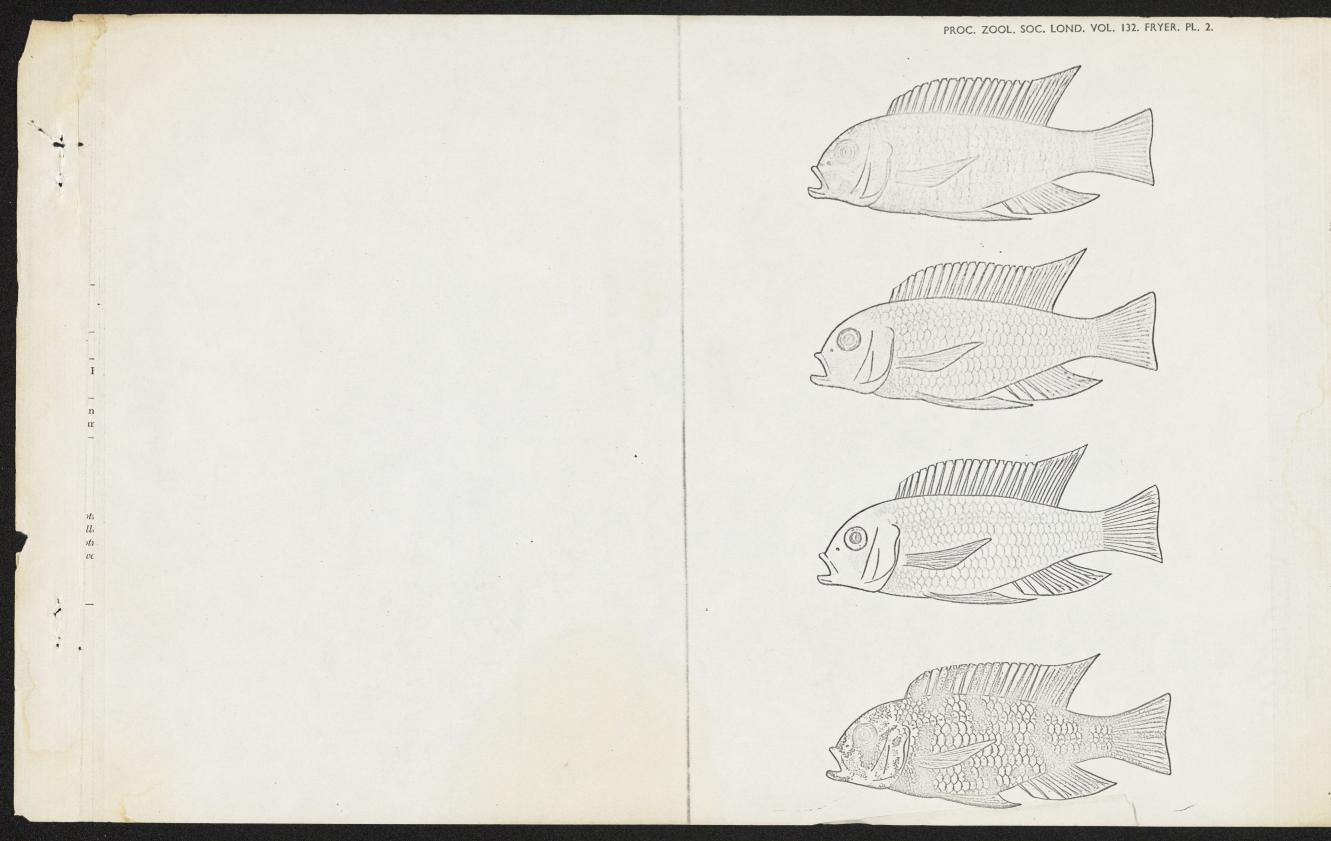






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1965. Proc. Zook. Soc. London, 144: 301-322

HYSTRIX

ut the northern population. North African and Asiatie ly that the cristata-indicanterglacial period of high is seems to be the simplest the little that is known nformation on vegetational more complex history of ene fossil skull of *Hystrix* ibed as a distinct species, show characters of both nination of the specimenters fall within the range e shape of the nasals and with *H. africaeaustralis*.

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PREDATION AND ITS EFFECTS ON MIGRATION AND SPECIATION IN AFRICAN FISHES : A COMMENT

 $\mathbf{B}\mathbf{Y}$

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WITH FURTHER COMMENTS BY P. H. GREENWOOD, A REPLY BY P. B. N. JACKSON AND A FOOTNOTE AND POSTSCRIPT BY G. FRYER

[Accepted 12th November 1963]

Contrary to a recently expressed view very little factual evidence has been brought forward to support the idea that predatory fishes, and especially *Lates* and *Hydrocynus*, have had restrictive effects on speciation among other African freshwater fishes. A considerable body of data supports the view that the effects of these fishes do not differ from those of other predators and that predation has facilitated speciation. Further reasons why *Lates* and *Hydrocynus* cannot be considered as having effects different from those of other predators are given.

The situation in lakes containing these predators is reconsidered. There is no need to attempt to minimize their effects in Lake Tanganyika where their presence and effects are fully compatible with the existence of a rich endemic fauna. The situation in Lakes Albert and Rudolf is more satisfactorily explained by the brief duration of the existence of the present-day lakes and by their recent invasion by a fully differentiated Nilotie fauna, than by imagining that *Lates* and *Hydrocynus* have restricted speciation.

The suggestion that *Lates* and *Hydrocynus* were responsible for the inception of the habit of upstream migration for purposes of spawning is discredited, and what seem to be more probable reasons for the phenomenon are given.

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PREDATION AND SPECIATION

This note is elicited by Jackson's paper (1961 b) on the impact of the tiger fish *Hydrocynus vittatus* (Castelnau) (=*H. lineatus* Bleeker) on other African freshwater fishes. In this paper he seeks to demonstrate the validity of the view put forward by Worthington (1937, 1940, 1954) that predatory fishes, particularly *Lates* and *Hydrocynus*, have retarded speciation. In so doing he incorrectly formulates the contrary view. No one denies that these predators "have influenced speciation "—wherever they are components of the environment they must have played a part—what is in question is the way in which they have done so. He also states that the contrary view "has had little evidence brought forward to support it, but has remained largely speculative". In fact the only other worker who has previously attempted P.Z.S.L.—144

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to provide factual data in support of the idea that predators restrict speciation is Lowe (McConnell) (1959), whose remarks were confined to the genus Tilapiowhich is far from being one of the most important genera concerned, and whose interpretations have already been questioned and in some cases have beet shown to be erroneous (Fryer, 1960).

By contrast the information supplied by Greenwood (1951, 1959 a, 1959 b) Corbet (1961), Iles (1963), Fryer & Iles (1955), and Fryer (1959 a, 1959 b, 1966 supports the contention that Lates and Hydrocynus are by no means the only predators of importance, and that predation facilitates and hastens rathe than impedes and retards speciation. Gordon (1947), on the basis of ecological and genetical studies on Central American poeciliid fishes of the genu-Platypoecilus, has also rejected Worthington's hypothesis and has concluded that "apparently just the opposite effect is seen in the platyfishes-at least as far as multiplicity of genotypes is concerned ". Some of these papers were unfortunately in the press at the same time as Jackson's paper, but he makes no reference to the important work of Greenwood (1959 a), which has produced incontrovertible fossil evidence against the original hypothesis. Nor does he mention that Greenwood (1959 b) and Fryer (1959 a) working on Lakes Victoria and Nyasa respectively, and with different assemblages of species, came indepen dently to the same conclusion about the rôle of the numerous predators in reducing interspecific competition among non-predators, and therefore facilitating their survival.

The re-statement of previous suggestions (p. 616) does nothing to make them convincing, and the use of Lowe's data, which form the mainstay of these, is most unfortunate. To quote her to the effect that " Lates and Hydrocyon do seem to have had a marked effect on fish " tells us nothing What effect ? That Nyasa, without these predators, is the only lake with a species-flock of Tilapia (four species only) is no evidence either for or against the theory. To rearrange Lowe's tabulated data, as does Jackson, tells us nothing. The obvious fallacy here is that, of the lakes which should have been taken into account, only a selection has been considered. A very different result is obtained if data for such important lakes as Mweru Bangweulu, and Kivu, not to mention many smaller lakes, are taken inte account. The entire exercise is in any case rendered meaningless by the fact that several of the lakes implicated in no way exhibit the phenomeno: under discussion! The mere existence of a single endemic species of Tilapi or a pair of species which originated from different stocks, has nothing to d with the presence or absence of Lates, Hydrocynus, or any other fish, in the same lake but is a simple case of geographical differentiation. It has nothinwhatsoever to do with the phenomenon for which, in order to avoid any ambiguity, the term accepted by Worthington, namely Woltereck's cumbrou-"schizotypische Artaufspaltung" can be employed.

Jackson's data on the feeding habits of Hydrocynus lineatus are certainly useful, but it is not logical to conclude that, because it preys heavily on smaller fishes (18-20 cm is recorded as the usual maximum length), and because it has "a very marked effect" on other fishes (p. 616) it has retarded speciation. The facile assumption that suppression or retardation of speciation is the

EFFECTS OF PREDATION ON AFRICAN FISHES

ators restrict speciation ed to the genus *Tilapia*. a concerned, and whose some cases have been

(1951, 1959 a, 1959 b) er (1959 a, 1959 b, 1960) e by no means the only tes and hastens rather n the basis of ecological d fishes of the genus esis and has concluded he platyfishes-at least ne of these papers were i's paper, but he makes a), which has produced pothesis. Nor does he rking on Lakes Victoria f species, came indepennumerous predators in lators, and therefore

does nothing to make form the mainstay of fect that " Lates and fish " tells us nothing. s the only lake with a ce either for or against does Jackson, tells us es which should have considered. A very ant lakes as Mweru. iakes, are taken into d meaningless by the hibit the phenomenon mic species of Tilapia eks, has nothing to do any other fish, in the iation. It has nothing n order to avoid any Woltereck's cumbrous

lineatus are certainly eys heavily on smaller ngth), and because it as retarded speciation. 1 of speciation is the inevitable consequence of predation is indeed a major weakness of the original hypothesis. On the contrary it is an indisputable fact that it is essentially small fishes, among which heavy predation is proven, which comprise the major species-flocks of the great lakes. Larger cichlids, of which *Tilapia* is the outstanding example, and which are less subject to predation when adult, exhibit less spectacular intra-lacustrine speciation. This idea is developed more fully elsewhere (Fryer, 1960). Massive supporting data on the food of non-cichlid predatory fishes of Lake Victoria are given by Corbet (1961) and for *Bagrus* in Lake Nyasa by Iles (1963). Jackson's data for *Hydrocynus*, both here and in a previous paper (Jackson, 1961 a), Hamblyn's (1960) preliminary observations on *Lates niloticus** in Lake Albert, and Anderson's (1961) data on the same species, show clearly that, wherever these predators have played a part, small fishes have comprised the major part of their diet. Their rôle has in fact been the same as that of other predators.

Jackson's criticism of the work of others is of a curious kind. Thus, in referring to the note by Fryer & Iles (1955) he has apparently misread its contents as well as its title. If this note had said what Jackson claims it says his criticism would be justified : in fact it says no such thing. The point it made was that Worthington's view that Lake Nyasa lacked active predators is erroneous; and this is certainly so. Jackson also implies that what Fryer & Iles state they have observed, is untrue, namely that many Nyasan fishes will take eggs or fry of other species whenever the opportunity to do so arises. This is neither "a remarkable statement" nor "improbable in the extreme " but a statement of observed fact. In spite of their often specialised dentition many Nyasan fishes are quite capable of sucking in and swallowing these soft morsels, just as some of them will take an angler's worm. Nor need they be half-starved before they will do so. Well-fed fishes will often gorge themselves on such food if it is offered. The reason for the rarity of such occurrences in nature is probably not unconnected with the apparently universal habit of mouth brooding among the endemic cichlids (Fryer, 1959 b), and with the fact that the egg-eating and larval fish-eating habit evolved in Lake Victoria (Greenwood, 1959 c) is less developed in Lake Nyasa, although jettisoning of eggs may occur under certain conditions (T. D. Iles, in litt.).

Similarly, in his discussion of the rôle of predators in controlling the numerical abundance of prey species (p. 617) Jackson attributes to me the idea that "newer and therefore less numerous forms" (my italics) will be allowed to multiply. The concept of "newness" did not enter into my argument (Fryer, 1959 a), and I am not sure what is meant by the term unless mutants are implied, and their survival would obviously depend on the degree of their overall adaptation. More important is the fact that Jackson fails to see how several predatory species with different habits will in fact be needed to influence the full spectrum of non-predatory species. No matter how catholic the tastes of open water predators they could not greatly influence potential prey species with skulking inshore habits. It is hard to see why Jackson criticizes the concept that predators in Lake Nyasa

* Until the systematic status of the forms of *Lates* in Lake Albert has been clarified it is convenient to use this name.

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will eat whatever prey species happens to be most abundantly available when this is exactly what his own data for Hydrocynus show and is in fact a point which he emphasizes. While, as was acknowledged at the time the idea was put forward as an explanation of the state of affairs in Lake Nyasi (Fryer, 1959 a, p. 272) the argument has its weaknesses, work on other predators—Anderson (1961) for Lates niloticus and Jackson himself for Hydrocynus—shows that this is exactly what happens elsewhere. Similarly Hulot (1956) says "Il est superflu de rappeler la plasticité du régime alimentaire de ces voraces au lac Édouard" and, speaking of Lake Albert, says " une grand plasticité du régime alimentaire se remarque chez certains carnivores". Hamblyn (1960) has also found that L. niloticus fails to exhibit what he calls " palatability preferences".

The meaning of Jackson's remarks about the small size of Nyasan rocky shore fishes (p. 618) is obscure. His conclusion that, because many of the species occurring in this habitat are small, "this seems to argue that the Nyasan rocky shore predators are too mild to have much effect upon the numerous endemic species continually living there, as it has been shown that the impact of predation by *Hydrocynus* is on small fishes " is completely illogical and takes no account of facts. Why should small fishes not be eaten ? Surely one would expect, as is indeed the case, that small fishes can be eaten by small predators. The existence of communities of small fishes does not mean that they are not eaten. Further, Jackson's implication that the littoral fishes of Lake Nyasa are small and numerous because predation effects are small is, to say the least, unreasonable. The effects quoted by him from Rounsefell & Everhart (1953, pp. 47, 366) are purely phenotypic and are in no way comparable with the genotypically determined size limits of the highly specialised Nyasan rocky shore fishes.

Perhaps Jackson's greatest error, however, is in assuming that such fishes as Lates and Hydrocynus exert greater effects on the process of speciation than what he calls "the infinitely milder predators" of Lake Nyasa. For this there is not a shred of evidence, and it has already been pointed out (Fryer. 1960), and is here emphasized, that the method employed for capture of the food is no reflection of the amount consumed. Within limits which are probably small it must take approximately the same weight of prey species to produce unit weight of predator flesh whether that flesh be Hydrocynus. Bagrus, Clarias or any other genus. Differences there will be which will reflect activity patterns as well as digestive efficiency (probably always high in predators). My observations on Lates and Hydrocynus ("swift") and on Bagrus and Clarias ("lurkers"), however, lead me to conclude that differencein behaviour between the two types of predator, while likely to influence the choice of prey, are no reflection of voracity. Jackson's quotation of fishermen's tales concerning the voracity of Hydrocynus (p. 604) is no substitute for critical scientific data. In fact the belief that Lates and Hydrocynus are constantly roving and devouring is erroneous. Like predators in general they indulge in long periods of rest when replete (see also Worthington & Ricardo (1936 a and Hamblyn (1960) for Lates). Their ability to move quickly when require does not mean that they habitually do so. As Manton (1958) has observed.

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Interoceanic Sea-Level Canal: Effects on the Fish Faunas

Past and present zoogeography helps us predict the effects of a forthcoming interoceanic connection.

Robert W. Topp

Although construction of an interoceanic sea-level canal through the Central American isthmus has been earnestly contemplated for nearly a century, the biological consequences of a man-made "Strait of Panama" have received serious consideration only during the past decade. I wish to add another opinion to the growing body of speculation on possible biological outcomes of this venture: that while the respective characters of the western Atlantic and eastern Pacific ichthyofaunas will not be drastically altered by ingress of species from the opposite coasts, there exist opportunities for faunal enrichment, especially in the Caribbean, by transpacific species of Indo-West-Pacific origin. My conclusions are based on a consideration of the paleogeography of Central America and other areas, and of present ichthyofaunal complexes and their respective environments.

In the past, the gargantuan task of digging a suitable channel by conventional means discouraged all but the most ambitious planners, but now, with nuclear energy available as a tool of excavation, interest in the scheme is at high pitch. Although there is little doubt about the physical possibility of excavating a channel with atomic charges (1), the dominant problems at present are problems of politics rather than of engineering (2). In any case, surveys by the agents of the Atlantic-Pacific Interoceanic Canal Study Commission are being completed for two alternate sites, the Sasardi-Morti route in Panama and the Atrato-Truando route in Colombia (3).

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The existing Panama Canal, with its intervening 40 miles (64 kilometers) of fresh water, Gatun Lake, has thus far served as an effective barrier to all but a few euryhaline fish species. Only one, Lophogobius cyprinoides, is known to have established breeding populations on the opposite coast (4). A sea-level canal, however, would constitute an unobstructed two-way transport system for dispersal of free-swimming, shallowwater stenohaline marine fishes, and at least a one-way system for planktonic stages. In effect, a deterrent to marine exchange will no longer exist unless positive steps are taken to preserve the barrier.

Possible biological consequences of allopatric populations coming into contact have been listed by Rubinoff (5, 6); these are, briefly, (i) formation of viable hybrid swarms; (ii) production of inferior hybrid swarms, leading to possible extinction of both species; (iii) limited hybridization, with maintenance of discrete populations; and (iv) replacement or extinction of one species by another. Rubinoff concluded, partly on the basis of experimental evidence, that any of these consequences may occur among the Central American shore fishes, depending upon the species involved. Briggs (7) has expressed the more general view that most of the western Atlantic species would be competitively superior to their eastern Pacific relatives, basing his supposition on the disproportionate richness and stability of the respective ecosystems. A dissimilar view, expressed by several workers who have compared the two faunas and their environments, is that Pacific fishes, living under more rigorous environmental conditions, would have the adaptive flexibility to compete successfully with, and ultimately displace, most of their Atlantic relatives. Finally, a recent statement by Cole (8), based on an incorrect estimate of differences in mean sea level, has suggested an array of frightening eventualities.

Mediterranean-Red Sea Relationships

It has been suggested that faunal changes in the Mediterranean and Red Sea since the completion of the Suez Canal may be instructive in predicting the amphi-American events (events on either side of the isthmus) that would follow excavation of the canal. Many geographical similarities exist, to be sure, there being in both cases two great north-south landmasses narrowing to a width of less than 100 miles at a point some 4800 miles north of the southern end of the landmasses, and both separating two large compartments of water (9). The differences stemming from historical events, however, greatly overbalance these superficial similarities when zoogeographical comparisons are made.

As early as the Cambrian, a considerable part of the Middle East was covered by a shallow tropical sea, the Tethys. In the early Tertiary this same sea was broadly continuous from the West Indies through the Mediterranean, with corridors extending to the East Indies. The rich fossil beds of Lebanon and Monte Bolca (Italy) indicate that the Tethys of this period was truly tropical and distinctly Indo-West-Pacific in character, with rich assemblages of coral and other tropical invertebrates, as well as tropical littoral fishes. In the Mediterranean region itself there were some 65 genera of reef corals, and the fossil record indicates that as far north as Belgium the Paleocene fish fauna was tropical or perhaps subtropical, and the Eocene fauna was mainly tropical (10).

In the late Tertiary two important alterations of the Tethys Sea occurred: (i) in the late Miocene, communication of the Mediterranean with the Red Sea was interrupted by emergence of the Isthmus of Suez (11), which divided the uniform zoogeographical province into two compartments, and (ii) during the Pliocene, climatic deterioration that had begun as early as the late Eocene became accelerated (12). As the Mediterranean cooled, its tropical fauna was gradually destroyed. This destruction may have been hastened by desalinizations resulting from the temporary blockage of the Strait of Gibraltar toward the end of the Miocene (13). Following these events the impoverished Mediterranean began to accept colonizers through the Strait of Gibraltar, so that the ichthyofauna of the Mediterranean is now more closely related to that of the Atlantic than to any other (14).

Since the opening of the Suez Canal in 1869, the Mediterranean has received at least 24 immigrant fish species from the Red Sea (15), some of which may be replacing native species (16). In view of the geologic history of the area, it is not difficult to understand why the descendants of the preadapted Tethys fauna, with their long-thwarted potentials, are redeploying so rapidly.

As would likewise be expected, there are no reliable records of Mediterranean fish species having penetrated the Red Sea. Although this is partly due to the canal's hydrography, it may also be due to the inability of the Atlanto-Mediterranean fishes to compete with the well-adapted Red Sea ichthyofauna.

Amphi-American Relationships

While the tropical American ichthyofauna has experienced a regime of paleogeographical events similar to that of the Middle East, it has approached a condition of amphi-American parallelism rather than dissimilarity. The reason for this seeming paradox becomes apparent when the history of the area is considered.

The Tethys Sea that influenced Middle East faunal distributions simultaneously maintained continuity with large portions of Middle America. In the middle Cretaceous the broad Central American region was generally submergent and apparently presented no serious obstacles to the dispersal of shallow marine organisms (17). Tertiary Central America, according to Whitmore and Stewart (18), was characterized by a shifting pattern of island groups and of peninsulas attached to one continent or the other. During this time the equatorial surface currents delivered a steady influx of colonizers westward into what is now the Caribbean province and, in turn, through the Central American seaways into the eastern Pacific (19).

From the fossil record we may infer that the Tertiary fauna was distinctly West Tethyan in character, and that the eastern Pacific fauna was quite similar to the fauna of the remainder of the Caribbean province. This continuity of ecological conditions has been recently demonstrated by Woodring (20), who found practically identical fossil molluscan faunas along the Caribbean coast of central Panama, in northern Colombia, in the Atrato Trough, and near the Pacific coast of Colombia, Darien, and Chiriquí.

During the Pliocene the Central American isthmus was completed; thus the Americas were connected for the first time in geologic history (21). At the same time climatic changes similar to those affecting the Mediterranean were occurring in Central America, destroying a portion of the fauna while displacing the remainder southward and replacing it with cold-water forms. By the time of the continental ice sheets the ocean waters were sufficiently cooled to allow crossing of the equator by organisms that are now "antitropical" in distribution. Such forms now barely reach the existing tropical fauna (22).

Up to this point the histories of the Middle East and Central America coincide, both areas having experienced (i) submergence of vast, continuous areas beneath tropical seas; (ii) widespread distribution of tropical shallow-water faunas; (iii) orogenic disturbances interrupting the continuity of the sea by land bridges; (iv) climatic deterioration causing a cooling of the waters; (v) replacement of the tropical faunas by northerly forms; and (vi) rewarming of the seas following the periods of continental glaciation.

At this point, however, the analogies cease. During periods of climatic amelioration the original Mediterranean fishes were denied readmission to their former domain by a barrier which obstructed their northward movement, whereas in Central America this was not the case. When the American fishes were displaced southward during periods of cooling, many took refuge along the coasts of South America. During warmer periods they attained their earlier latitudinal ranges without obstruction from the newly formed isthmus. Northeastern South America, for example, is thought to have been a refuge for much of the western Atlantic fauna during the Pliocene and early Quaternary (10). The similarities of the present fauna on the two sides of the isthmus furnish convincing evidence that the former distributions were in large part restored.

These similarities were first noted by

Günther (23), who postulated the existence of former marine continuities even before this had been demonstrated by geologists. The similarities are most striking at the generic level, where coincidence for amphi-American fishes (45 percent) far exceeds that (19 percent) for fishes on the two sides of the Atlantic (24).

At the species level, only about 1 percent of the fishes are judged to be identical amphi-American species-pairs (25); this indicates not only the effectiveness of the geographical barrier but the amount of speciation that has occurred during the past 3 or 4 million years of geographical discontinuity.

Much of the ichthyofaunal dissimilarity at the species level undoubtedly reflects the dissimilar environmental conditions which developed on opposite sides of the isthmus as the seaways became disrupted. These differences, summarized by Rubinoff (6), include differences in temperature, salinity, transparency, tidal amplitude, and associated biota. On the whole, the Pacific coast now presents a much more rigorous and fluctuating environment than the Atlantic coast does.

Meek and Hildebrand (26), in attempting to explain the differences in fish faunas, speculated as follows:

. . . before the last passage between the Atlantic and Pacific Oceans was closed to marine fishes, the representatives of certain families had already found that one side of the "divide" was better suited to their particular needs than the other. The result, with respect to such families, was that when at last the passageway was completely closed that most of the species of some of them were on one side of the isthmus, while those of another were on the opposite coast.

Although this may account for certain initial differences, it is unlikely that the faunas had segregated to so great a degree while the sea was still continuous. It is more likely that they diverged after being separated into environments with differing selective pressures.

At this point we can profitably compare the present amphi-American situation with the situation that existed on either side of the Isthmus of Suez before the canal was built. We have seen that in the latter case there was a tremendous imbalance between the two biomes, while in Central America there exist historically well-adapted faunas on both sides of the isthmus that are closely related in many respects but differ as a reflection of the differing

environments. It should, then, be clear that it is unsound-or at least unfairto make predictions about amphi-American faunal interchanges on the basis of events on both sides of the Isthmus of Suez after excavation of the canal. And, at the same time, we should avoid making emotionally charged analogies to the introduction of various pests (for example, goats or rabbits) into previously pristine habitats. The Suez events involved the reintroduction into an otherwise unsaturated area of a fauna well qualified to live in the new environment. The pest situation involves the introduction and expansion of prolific nuisances without the hindrance of predators or effective competitors.

Conclusions and Prognosis

Finally, we may return to the original question of the effects of unleashing the two Central American ichthyofaunas, one upon the other. Having no valid precedents that approach the magnitude of this forthcoming experiment, we must rely heavily on our general knowledge of zoogeography and evolution, and must temper our predictions by an understanding of the history of the area and its faunal complexes.

The higher taxa are already characterized by a high rate of amphi-American coincidence, and thus can undergo few changes; rearrangements will be primarily at the species level. In Rubinoff's (6) list of possible biological effects, three of the four involve some degree of hybridization. The lifelong observations by Carl Hubbs on hybridization and speciation in fishes supply a multiplicity of examples and comment, all of which dissuades me from believing that hybridizations of any significant extent will occur. Even among species that can be readily crossfertilized in aquaria there is, according to Hubbs (27), an extreme infrequency of recognized fish hybrids in nature. Hubbs (28) has, moreover, noted that interspecific crossings are least likely to occur in tropical marine waters (as compared to temperate or fresh waters), for "much greater opportunities have existed [in tropical marine waters] for the development and operation of the multitudinous fine adjustments involved in the location, with precise timing, of the proper breeding grounds and the proper mates." Among subspecies-the taxon to which some of the amphi-American "species-pairs" may eventually

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be relegated—there may be ecological, behavioral, or other blocks to successful interbreeding, so that, even in the absence of genetic isolating mechanisms, fusion is countered by "the effective adaptation of each subspecies to its own habitat, so that a high breeding potential is realized and the appropriate habitats are saturated with their own respective pure stocks" (27).

Some gene flow will occur, to be sure, especially when an individual crosses the isthmus and is forced to breed with genetically dissimilar individuals, but here again there is serious question as to whether such introgression will result in an enrichment of the gene pool or in elimination of the genes of the invaders.

As for the more serious possibility of replacement or extinction of fish species by better-fitted groups from the opposite coast, widespread occurrence of such phenomena appears improbable when considered in the light of paleogeography and present faunal adjustments. It is difficult to believe that any great number of fish species will be preadapted to colonize an environment which not only is less hospitable in terms of their own background but is, moreover, occupied by well-adapted related forms.

Of course, it would be folly to assume that no changes at all will occur. Species with generalized ecological requirements, such as the piscivorouscarnivorous grunts (Pomadasyidae) or porgies (Sparidae), may find the canal easy to transit in either direction and may become established on the opposite coast. Another source of potential colonizers, the Indo-West-Pacific fauna, may have a far greater impact on the ultimate composition of the Atlanto-East-Pacific fauna, and particularly on the fauna of the Caribbean.

As Ekman (10) has demonstrated, the Mesozoic and Eocene fauna of the Atlanto-East-Pacific was not inferior either in quality or in quantity to the fauna of the present-day Malay region. But the Atlanto-East-Pacific is far from having recovered from the impoverishments suffered during the Cenozoic climatic changes. Briggs (29), for example, has found that western Pacific fishes are indeed transgressing the East Pacific Barrier to become established in the eastern Pacific. Of the 62 species of shore fishes documented on both sides of the Pacific, most of the eastern Pacific representatives are confined to offshore islands,

but they are nevertheless potential colonizers of both the eastern Pacific coast proper and the environmentally more hospitable Caribbean. In this regard, some concern has arisen over the possible spread of the transpacific sea snake, *Pelamis platurus*, into the Caribbean (30).

A complicating factor is the change that may occur at lower trophic levels, providing new niches and causing shifts in feeding patterns, with corresponding declines in adaptive levels among the resident fishes and increased competitive advantages for the invaders. Since many of the Central American invertebrate and floral groups are imperfectly known (31), it is dangerous to make predictions about other levels of the food chain. But, if my reasoning may be extended in a general way to groups other than fishes, it should follow that widespread extinctions will not occur. There is good evidence that much biotic transfer may, in fact, be already occurring. Fouling animals, for example, may be making regular transits through the present canal on the hulls of ships (32, 33), and planktonic larvae and other microscopic organisms may be transiting in the saltwater ballast which is taken aboard ships to increase their maneuverability through the canal (33, 34). These same agencies in world commerce are recognized as steady and powerful influences in the worldwide spread of marine organisms (35).

Another imponderable is the question of parasites, for we may find preadapted species unleashed upon particularly vulnerable hosts which have not had the opportunity to make genetic defensive adjustments. The native sturgeon of Lake Aral, for example, was seriously damaged by a parasitic worm, *Nitzschia sturionis*, carried by an introduced sturgeon (35). Studies aimed at assessing such possibilities are clearly in order.

As for hydrographic changes resulting from a sea-level canal, these will certainly be minor, with only local effects. The array of calamitous effects suggested by Cole (8), based on an idea that "the Pacific Ocean stands higher than the Atlantic by a disputed amount which I believe to average 6 feet," are unfounded. The Pacific Ocean is higher, but the mean difference is not disputed and stands at 0.77 foot at the present Panama Canal (36). The combined effects of tidal oscillation and the mean difference in sea level would cause the water in the channel to move

alternately toward the Atlantic and then toward the Pacific, with a net advance toward the Atlantic of about 5 miles per day (36). This rate of advance, applied linearly to channel dimensions of a cut excavated by nuclear charges (1), gives an average flow of a little more than 500 cubic meters per second, a value corresponding to the flow of a small river, or less than 1/400 the average discharge of the Amazon River.

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Although the transported Pacific water would at times be cooler by a few degrees than the water of the Atlantic, it would be of nearly the same salinity, and changes in the physical environment would be minimal. The greatest contribution of this Pacific water to ichthyofaunal change would be its role in providing a transitional area on the Atlantic side in which Pacific fishes could be harbored, possibly with competitive advantage, and from which propagules could be dispatched.

Under hydrographic conditions similar to those proposed by Meyers and Schultz (36), a sea-level canal may remain an effective barrier to weak swimmers or plankton from the Atlantic. Freshwater drainage into the canal would provide a deterrent to strictly stenohaline marine organisms only if it were deliberately and constantly controlled.

The rather general predictions I have made represent only one of several opinions recently advanced, and should in no way detract from the critical and immediate need for preliminary surveys and analytical studies of the sort outlined by Rubinoff (6). If my views are incorrect, and if widespread or disastrous biological effects are felt, no amount of hindsight will be of avail. Our only consolation will be that the establishment of a man-made sea-level

interoceanic connection may merely have hastened what may well occur by natural means in, say, a few million years.

Summary

Although an interoceanic sea-level canal through Central America will allow easy exchange of stenohaline marine fishes, the characters of the existing ichthyofaunas will not be drastically altered by ingress of species from the opposite coasts. The Suez Canal cannot be taken as a valid precedent in spite of superficial analogies, for, in the case of the Suez Canal, well-qualified Red Sea faunas were reintroduced into the otherwise unsaturated Mediterranean. In Central America, historically similar faunas exist on either side of the isthmus, their differences being only a reflection of their differing environments. It is therefore unlikely that any great number of fish species will be preadapted to colonize an environment which not only is less hospitable in terms of their own background but is occupied by well-adapted related forms.

Opportunities for enrichment exist in the Atlanto-East-Pacific province, and the greatest potential source of Caribbean colonizers may be the western rather than the eastern Pacific. Factors which complicate predictive efforts are changes in lower trophic levels, and parasites. Hydrographic changes will be minor, having only local effects.

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