

Figure 71 Transect C at Ruarwe, giving the depth distribution and numerical abundance of the Mbuna species. Territorial males of each species were counted except for those species marked (*) where both sexes were counted. Numerical abundance = fishes 50 m^{-2} .

by *P. minutus* and *P. cf. Melanochromis perspicax*.

At all sites most Mbuna species occupy the shallows (Table 33). In almost all other areas studied the greatest number of individuals occur at 3–10 m, but on the north-western shores the number of individual cichlids is greatest at 8–15 m. The greater number of Mbuna individuals in deeper water is due to the large number of non-territorial individuals of the genus *Cynotilapia* and of the *Pseudotropheus zebra* species-complex which inhabit these depths.

Figures 73–75 show that there are 14 Mbuna which live mainly in the intermediate habitats of this study area. Only *Cynotilapia axelrodii* ventures any distance away from rocks; the other species hold territories over sand, near to rocks. *Labidochromis caeruleus* is a non-territorial species which has not demonstrated any clear preference for rocky or intermediate habitats.

Time available for the survey of the north-western shores was so limited that only the Mbuna were studied. Fryer (1959a) gives a comprehensive account of the non-Mbuna in

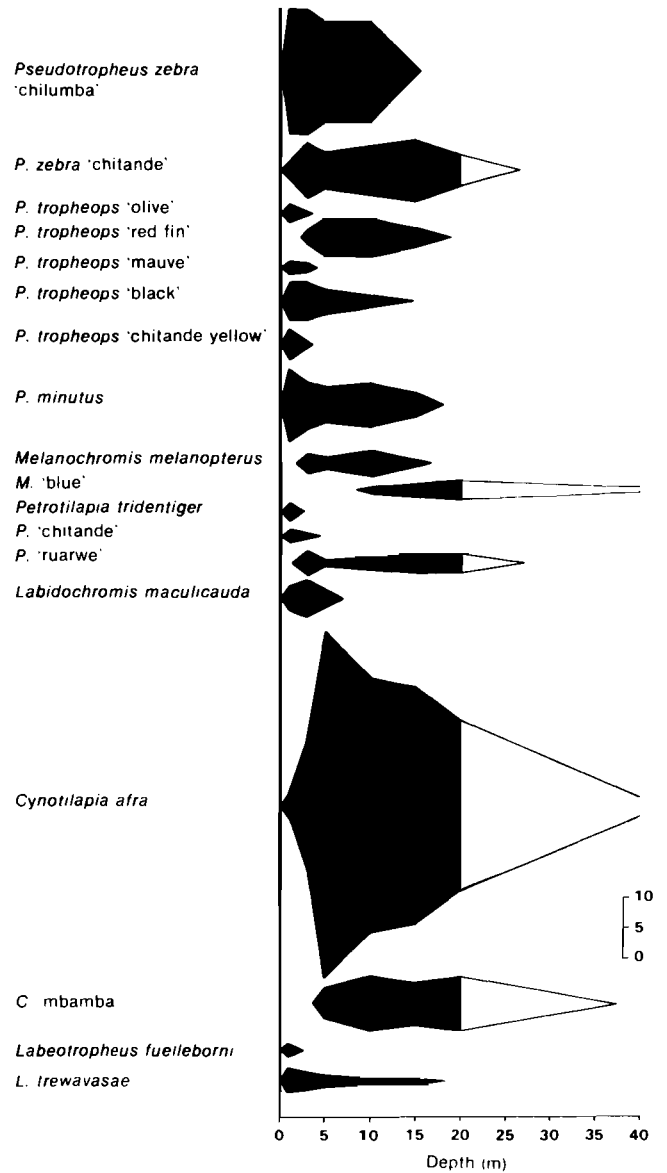


Figure 72 Transect D at Chitande, giving the depth distribution and numerical abundance of the Mbuna species and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (*) where both sexes were counted. Numerical abundance = fishes 50 m^{-2} .

Nkhata Bay and all we can usefully add is that *Cyrtocara linni*, which was not recorded by Fryer, is present on all shores.

DISCUSSION Aquarium fish resource

The principal objectives of this survey were to determine the variety and depth of the ornamental fish resources, particularly the Mbuna, to develop a numerical baseline against which the effects of exploitation might be measured in the future, to provide an aid to the identification of Mbuna and to identify those heavily exploited species which were in need of protective legislation.

The results indicate that the variety of ornamental fishes is far greater than originally realized; 196 Mbuna species/taxa were found and we have been informed that exporters of these fishes are continuing to discover additional species during their exploration of submerged reefs and previously unexploited coastlines (N.J. Edwards pers. comm.). It is

Table 33 The number of Mbuna species and the number of individual cichlids of all species recorded at different depths in transects along the north-western shores of Lake Malawi. The number of individual fishes was not counted below 20 m depth, as indicated by the dashes

	Depth (m)									
	1	3	5	10	15	20	25	30	35	40
Nkhata Bay (A)										
No. Mbuna species	17	24	21	16	14	14	12	5	4	4
No. individuals										
all cichlids in 50 m ²	168	167	188	253	305	295	-	-	-	-
No. individuals m ⁻²	3,4	3,3	3,8	5,1	6,1	3,9	-	-	-	-
Nkhata Bay (B)										
No. Mbuna species	20	20	15	14	12	12	8			
No. individuals										
all cichlids in 50 m ²	243	235	344	296	210	143	-			
No. individuals m ⁻²	4,9	4,7	6,9	5,9	4,2	2,9	-			
Ruarwe (C)										
No. Mbuna species	15	15	19	16	15	11	10	7	6	3
No. individuals										
all cichlids in 50 m ²	251	283	280	305	240	192	-	-	-	-
No. individuals m ⁻²	5,0	5,7	5,6	6,1	4,8	3,8	-	-	-	-
Chitande (D)										
No. Mbuna species	18	16	15	13	12	9	6	4	4	4
No. individuals										
all cichlids in 50 m ²	185	294	280	295	211	144	-	-	-	-
No. individuals m ⁻²	3,7	5,9	5,6	5,9	4,2	2,9	-	-	-	-

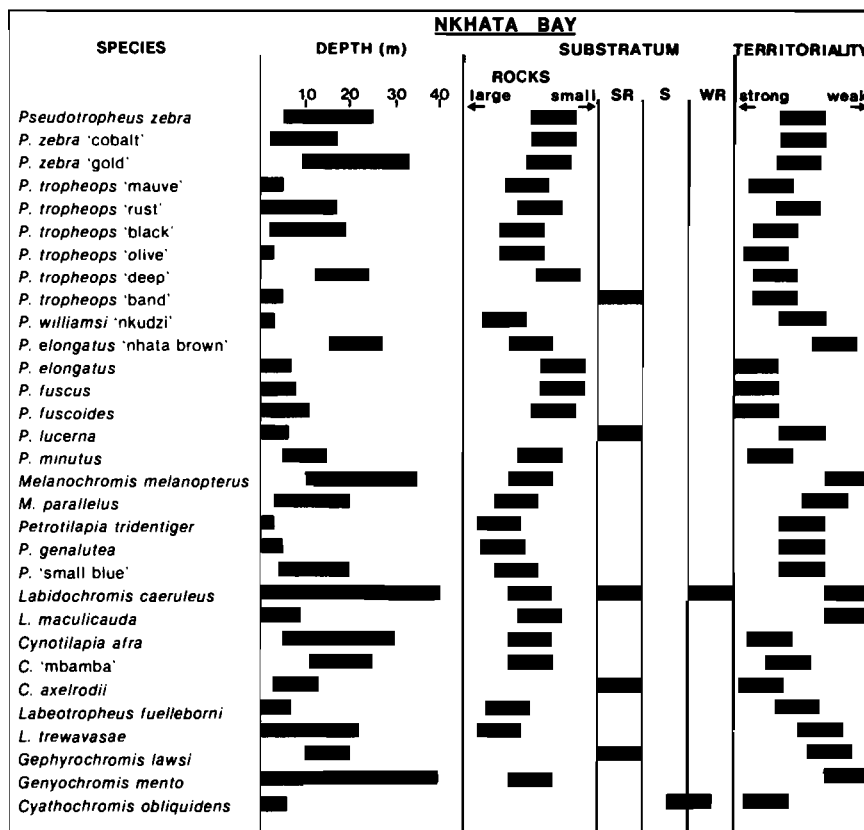


Figure 73 A summary of resource utilization of the Mbuna community at Nkhata Bay. For rest of legend see Figure 28 (p.254).

conceivable that the number of Mbuna species might exceed 300 when all rocky shores in the territorial waters of Malawi, Mozambique and Tanzania are thoroughly studied.

The value of the ornamental fish resource resides mainly in its species richness, for although many species are widely distributed and numerous, most species are restricted to

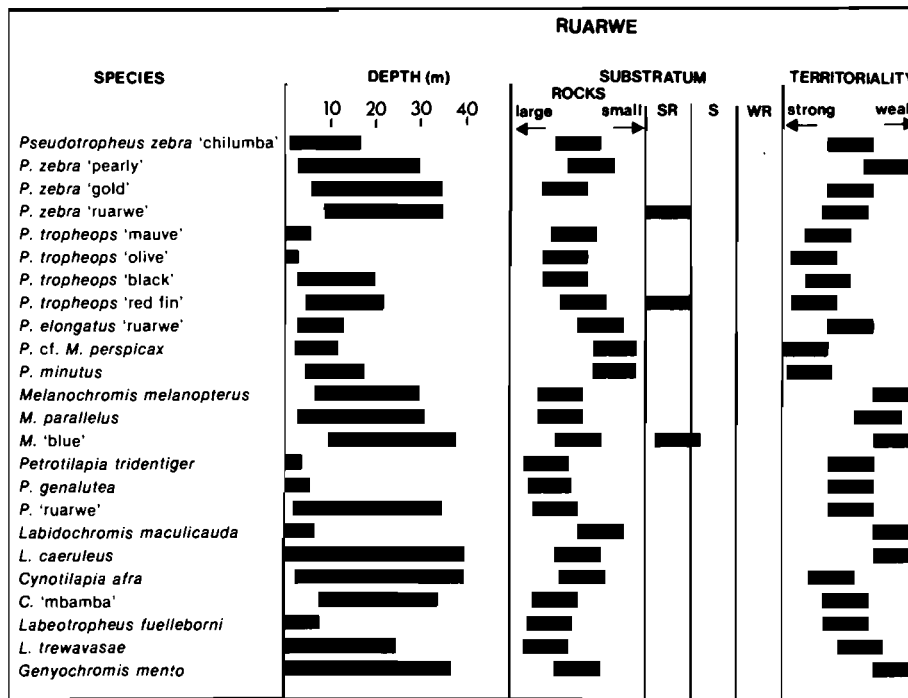


Figure 74 A summary of resource utilization of the Mbuna community at Ruarwe. For rest of legend see Figure 28 (p.254).

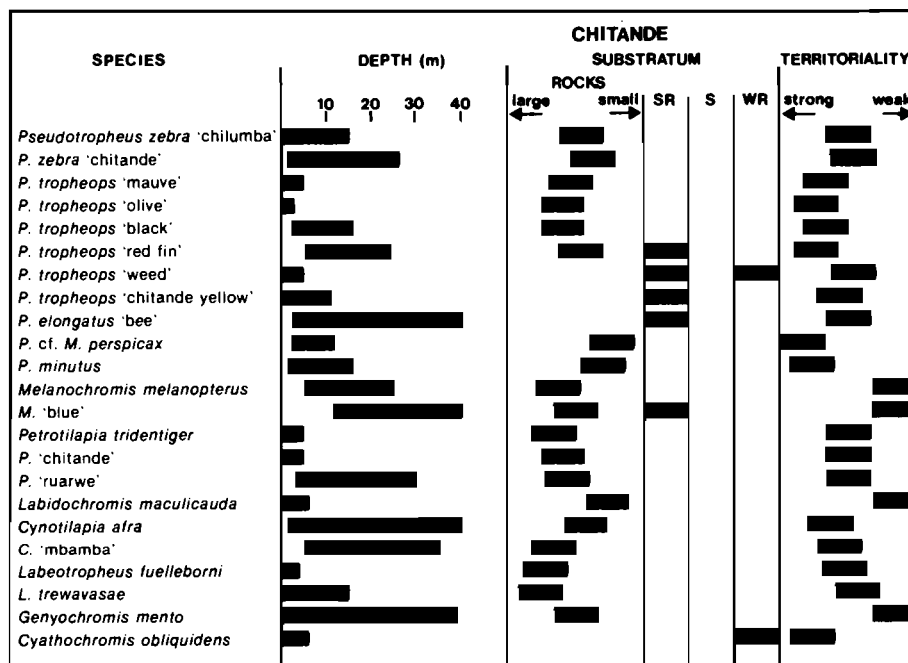


Figure 75 A summary of resource utilization of the Mbuna community at Chitande. For rest of legend see Figure 28 (p.254).

small areas and may have total populations of only a few thousand individuals. Such populations are likely to be particularly sensitive to fishing pressure. A number of these populations were subject to heavy exploitation (e.g. *Pseudotropheus elongatus* 'ornatus', *Melanochromis* 'red', *M. joanjohnsonae* and others) and recommendations regarding their protection were made to the Malawi Government (Ribbink 1980).

An indication of numerical abundance of most lithophilous Mbuna is given by the transect data. However, Mbuna had been exploited for about 17 years prior to the survey and so our transect data do not necessarily reflect the true natural baseline. For most species only territorial

males were recorded and we believe that their numbers approximate fairly accurately the numbers which would occur in an unexploited population, except where fishing pressure has been exceptionally heavy. This assumption is based on experiments in which we found that the removal of territorial males resulted in their replacement by conspecifics from the non-territorial supernumerary reserve of individuals (Sharp 1981; unpubl. data). The tendency, therefore, would be to have the same number of territorial individuals, but a diminished supernumerary reserve. Heavy exploitation eventually reduces the number of territorial males of a particular species within a defined area and the size of males holding territories also decreases (Sharp 1981).

Translocations

An unfortunate consequence of the ornamental fish trade is that a number of Mbuna have been taken from their native localities and released at sites where they do not occur naturally. Those areas with the most introduced species are Thumbi West Island and Otter Point. Several species have also been introduced to the islands of Maleri, Namalenje and Likoma.

There is no record of how many species were introduced to the various localities; nor do we know how many individuals of each were released. Our claims that these species were introduced are based on (i) information received from exporters of ornamental fishes, (ii) the fact that most introduced species are concentrated around the sites of release or around the holding facilities from which they are believed to have escaped, and (iii) on deductions regarding the natural distribution of the fishes and a knowledge of those species which were popular on the aquarium fish market at the time introductions were made.

Very small populations of some introduced species were recorded. For example, at Thumbi West Island very few *Pseudotropheus zebra* 'fusco' (only one individual), *Melanochromis* 'black-white johanni', *Labidochromis strigatus* and *L. freibergi* were found. There is little direct evidence that these populations are growing. Studies of otoliths suggest, however, that the life expectancy of at least some Mbuna species is about three years under natural conditions (B. Taubert, pers. comm.) and as the introductions to Thumbi West all took place before June 1976, those fishes found in 1980 are probably the offspring of introduced adults. In contrast, all other introduced species, particularly *Pseudotropheus zebra* 'cobalt', are actively breeding; all have been seen mouth-brooding, and fry and juveniles have been found. These populations are undoubtedly growing and it is estimated that 7 000 *P. zebra* 'cobalt' occur at Thumbi West. It is not known whether any of the introduced species constitute a direct threat to endemic fishes, but it may be assumed that they occupy space and utilize food resources which would otherwise be used by one or more native species. It is possible that species such as *P. zebra* 'cobalt', which have become well established at Thumbi West and Likoma Islands might eventually displace certain indigenous species.

Zoogeography

Our study shows that only two lithophilous species, *Genyochromis mento* and *Labeotropheus fuelleborni*, occur in every study region (Table 13), but even these species are absent from some stations within these regions. Of the fishes of the intermediate habitats, only *Cyathochromis obliquidens* is widely distributed and it is possible that a more thorough investigation of intermediate zones will show that this species occurs all around the lake in suitable habitats. All other Mbuna have narrower natural distributions (Tables 2–12) and many species are restricted to tiny rocky outcrops or to small parts of larger rocky shores or intermediate zones. As a consequence of these narrow distributions, the species assemblage in each area is unique. Invariably, at stations of similar habitat the number of shared species decreases as the distance between stations increases. Frequently, too, where species are common to several adjacent stations they differ in relative abundance: being rare at one, but numerous at another. This variability in the

numerical abundance of a species and in the species composition of cichlid communities throughout the lake means that widespread species are subject to the interactions of a different group of fishes at each locality.

The larger areas of rocky shores usually have the greatest species richness because they possess a greater diversity of habitats and can accommodate a wider variety of species than can small, stenotypic areas. For example, in area 1 (Figure 22), the island of Thumbi East has a variety of habitats and supports 21 Mbuna species (Table 15) whereas the smaller island of Zimbabwe comprises a stenotypic environment of mainly large rocks which supports only nine species. Those species which live among small rocks, or in intermediate zones, or which favour sediment-rich zones would not find suitable habitats at Zimbabwe.

The greatest species-richness is found at Likoma Island which is the largest island in the lake. This high species-richness is due partly to the large size of the island which can accommodate geographical barriers to dispersal, partly to its variety of littoral habitats and also to the variety of physical conditions occurring at the island (e.g. areas exposed to strong currents and to wave action and also those of calm sheltered inlets). It is also possible that contributions to the Mbuna fauna of Likoma Island were made on a number of occasions from populations along the nearby Mozambique coast. However, until the Mbuna of Mozambique are studied this will remain a conjecture.

The stenotopy shown by most Mbuna species appears to be a consequence of their sedentary nature. Fryer (1959a) has already shown that a behavioural trait of the majority of Mbuna is that they tend to remain in their preferred habitat and are unlikely to cross hostile habitats which separate areas suitable for habitation. The introduced species provide further evidence of the poor rate of dispersal of some Mbuna. Despite the four and a half years since they were introduced most of these species are still restricted to areas close to where they were released (Table 24). Furthermore, observations of the movements of tagged Mbuna demonstrate that many species are highly philopatric (Sharp 1981).

Habitat preference

Although depth *per se* may limit the vertical distribution of at least some species of Mbuna (Hill & Ribbink 1978; Marsh & Ribbink 1981; Ribbink *et al.* in press) there are several clear indications that the distribution of a species is more strongly influenced by a tendency to remain within its preferred habitat. For example, species such as *Pseudotropheus heteropictus*, *P. zebra* 'bevous', *P. elongatus* 'bee' and *Cynotilapia* 'lion', which live at the sand-rock interface do so at a variety of depths. Furthermore, in areas where the topography permits, these fishes remain in this fringe habitat from the shallows to depths of at least 40 m. Those fishes which are associated with sediment-rich habitats, such as *Pseudotropheus cf. gracilior*, are normally distributed according to the depth at which sediment occurs. Consequently they enter the shallows of sheltered regions, but are restricted to deeper waters in wave-washed areas.

Frequently, fishes which are normally associated with a particular depth will be absent from, or rare at, that depth if the rock type is unsuitable. For example, the bimodal distribution of the two *Petrotilapia* species at Boadzulu Island (Figure 30) is attributed to the presence of small rocks at 3–10 m depth, which are unsuitable for habitation by

these larger fishes. By contrast, this area supports numerous *Pseudotropheus zebra* (Figure 30). In the transect at the western part of Thumbi West the waist of the bimodal distribution of *P. zebra* at 10 m depth (Figure 41) corresponds with the presence of large rocks which are not normally frequented by this species. At Nakantenga Island the bimodal distribution of *P. zebra* 'red dorsal' (Figure 48) reflects the presence of a small area of intermediate habitat dividing two optimal habitats. Similarly, the species composition on a rocky shore may change abruptly when the nature of the rocks changes suddenly. For example, those species which live among large rocks, such as the *Petrotilapia* spp. and *Labeotropheus* spp. will be absent or rare among small rocks in an adjacent area.

Fryer (1959a) estimated that six to seven individual fish lived on every square metre of the rocky bottom at Nkhata Bay. On the basis of these observations and those at other sites in the lake, Fryer & Iles (1972: 285) suggested that the fish assemblages inhabiting the rocky shores of Lake Malawi are among the densest for a freshwater body in the world. Fryer (1959a) also noted that most Mbuna live in the shallows. At Nkhata Bay he found that with an increase in depth beyond 6–7 m there is a progressive diminution in numbers and that very few of these fishes occur below 20 m. The occurrence of the greatest number of fishes in the shallows is attributed to the higher productivity of this region where light intensity is greatest, where temperatures are highest and where Aufwuchs is believed to grow in superabundance (Fryer & Iles 1972).

Our survey confirms that the number of rock-frequenting fishes is greatest in the shallows, sometimes exceeding 10 individuals m^{-2} and that the number does decrease with depth. There are, however, at least 26 Mbuna species which occur to 40 m depth and many of these undoubtedly penetrate deeper than this. Although the shallows support the greatest biomass and species richness we found that the extreme shallows are normally frequented by fewer species than the 3–10 m zone. A likely explanation for this is that some fishes such as *Pseudotropheus zebra* are less able to cope with the surge of wave-washed areas than other species, such as *Labeotropheus fuelleborni*, and are therefore infrequent visitors to surge zones.

Trophic groups

The morphological and behavioural adaptations to specialized modes of feeding in Mbuna have received considerable attention because of their ecological and evolutionary implications (Fryer 1959a; Fryer & Iles 1972). Furthermore, these morphological features provide the basis for the taxonomic distinction between most genera and between many species (Trewavas 1935; Fryer 1959a; Fryer & Iles 1972; Lewis 1982). The manner in which the Mbuna partition their food resources was first studied by Fryer (1959a) who laid considerable emphasis on the specialized modes of food collection. He also examined gut contents from virtually all species which occur at Nkhata Bay. He recognized six principal trophic groups: (i) plankton feeders; (ii) invertebrate feeders (not plankton); (iii) mixed feeders; (iv) lepidophages; (v) loose Aufwuchs feeders and (vi) those fishes which take filamentous algae. Since the stomachs of all the Mbuna we studied, except *Melanochromis* 'lepidophage', contained a variety of food substances we have discarded the omnivorous category and have added two categories: egg-and-parasite eaters and piscivores.

Planktivores

The only planktivore known to Fryer (1959a) was *Cynotilapia afra*, but now 10 species of *Cynotilapia* are recognized and all appear to take plankton. However, virtually all Mbuna will feed upon plankton when it is abundant regardless of their trophic specializations. Indeed, the stomachs of many fishes which are not primarily planktivorous may be crammed to capacity with plankton. This factor created a complication during the survey on occasions when our visits to a particular area coincided with an abundance of plankton, as happened twice at the islands of Chinyankwazi and Chinyamwezi. On such occasions we were unable to establish what other components of the food resource were used by at least some members of the community. The readiness with which certain species leave the rocks to feed upon plankton varies. Although this has not been quantified it can be said with confidence that members of the *Pseudotropheus zebra* species-complex, the *P. tropheops* species-complex and the genus *Petrotilapia* enter the water column more readily than most members of other genera and species-groups. The members of the *Pseudotropheus williamsi* species-complex remain close to the rocks when feeding on plankton as do those of the *P.* 'aggressive' species-group. Some members of the *P. elongatus* species-group, such as *P. elongatus* 'dinghani', *P. elongatus* 'chinyamwezi', *P. elongatus* 'ornatus' and *P. elongatus* 'chisumulu', venture several metres into the water column to feed on plankton, but the remaining members of the group appear reluctant to move away from the substratum. Similarly, most members of the *P.* 'miscellaneous' species-group appear closely tied to the substratum, though *P.* 'yellow-tail' is an exception and was frequently seen 3–8 m away from rocks schooling among the *Cynotilapia* species and feeding upon plankton. Among the *Melanochromis*, *M. melanopterus*, *M. vermivorus*, *M. auratus*, *M. cf. chipokae*, *M. parallelus* and *M. crabro* have been seen 2–3 m above the rocks taking plankton. All of the *Labidochromis* species remain close to the substratum when feeding. Both members of the genus *Labeotropheus* feed upon plankton and *L. fuelleborni* occasionally joins schools of other Mbuna to feed in the water column. It is not known whether members of the genus *Gephyrochromis* feed upon plankton, but *Cyathochromis obliquidens*, *Iodotropheus sprengerae* and *Genyochromis mento* all eat plankton and will rise 1–3 m into the water column to collect it.

Invertebrate feeders

Those species which are apparently specialized to feed upon benthic invertebrates are included in this category. It is inevitable, however, that species which feed from the algal mat will collect some of the invertebrates which it harbours. Fryer (1959a) records that *Labidochromis maculicauda* (his *L. vellicans*) and *L. caeruleus* feed principally upon invertebrates, and argues that their long forceps-like teeth, large eyes and slender bodies are adaptations for picking out small invertebrates from the algal film (Fryer & Iles 1972: 494). The only other species of *Labidochromis* which had their stomach contents dominated by Invertebrata were *L. ianthinus*, *L. chisumulae* and *L. mylodon*, the last having enlarged pharyngeal teeth to crush molluscs (Lewis 1982). The remaining species of *Labidochromis* feed mainly upon filamentous algae and loose Aufwuchs so it seems that while the long forceps-like teeth may be highly effective at col-

lecting invertebrates from the algal mat, they are also used to collect the Aufwuchs itself.

Melanochromis melanopterus is categorized by Fryer (1959a) as an invertebrate feeder though he notes that it might be a piscivore. Although this species does eat many invertebrates we believe that it and the other large members of the genus *Melanochromis* are primarily piscivorous (see below). However, *M. joanjohnsonae* and *M. labrosus* are apparently invertebrate feeders, while *M. vermivorus* and *M. 'maingano'* contained high proportions of both Invertebrata and Aufwuchs. Fryer (1959a) also found that *Pseudotropheus fuscoides* consumed a high proportion of Invertebrata and so he considers this species to be primarily an invertebrate feeder.

Although the members of the *Pseudotropheus williamsi* species-complex feed upon a variety of food substances, insects predominate and so these fishes are also categorized as invertebrate feeders.

Lepidophages

Until *Melanochromis* 'lepidophage' was discovered at Makanjila the only other Mbuna species known to eat scales and fins was *Genyochromis mento*, whose habits were originally described by Fryer *et al.* (1955). Scales also occur occasionally in the gut contents of a wide variety of Mbuna, but we believe that these scales were lying on the Aufwuchs mat and were ingested by chance. Scales might occasionally be shallowed by rivals which bite each other during intraspecific combats.

Liem (1980) records that *Petrotilapia* species readily bite fins and scales off other fishes, but as he was referring to the physiological and anatomical capacity of these fishes to perform such acts, it does not necessarily follow that scales and fins are the normal fare of members of this genus under natural conditions. Indeed, scales and fins occurred rarely in the stomachs of members of this genus.

Egg and ectoparasite feeders

Many Mbuna readily feed upon the eggs and yolk sac larvae shed by mouth-brooding individuals trapped in nets. We have also noted that a wide variety of species will attempt to steal eggs from spawning pairs. These fishes are opportunists which meet with limited and occasional rewards. In contrast, *Melanochromis crabro* successfully steals eggs from the catfish, *Bagrus meridionalis* (Ribbink & Lewis 1982). In addition to stealing eggs from *B. meridionalis*, *M. crabro* acts as a cleaner removing branchiuran ectoparasites from the catfish. Ectoparasites and catfish eggs are not always available and so *M. crabro* also feeds on various components of the Aufwuchs mat and on plankton (Ribbink & Lewis 1982).

Piscivores

Behavioural observations have shown that many Mbuna species, including specialized herbivores within the genera *Pseudotropheus*, *Petrotilapia*, *Cynotilapia*, *Labeotropheus* and *Cyathochromis* eat the fry of other fishes opportunistically. It appears, however, that only the larger members of the *Melanochromis melanopterus* species-complex are morphologically and behaviourally adapted to piscivory. Stomach content analyses of *M. melanopterus*, *M. cf. chipokae*, *M. 'slab'*, *M. parallelus* and *M. 'blue'* suggest that adults feed regularly upon fry which almost certainly constitute their principal food.

Aufwuchs feeders

The vast majority of Mbuna feed upon Aufwuchs. Some take mainly filamentous algae while others feed almost exclusively upon loose Aufwuchs, but as it is virtually impossible to feed on one component of the Aufwuchs and not take some of the other, it is common for fishes to have a mixture of both.

Filamentous algae. Of the Aufwuchs feeders those species which consume predominantly filamentous algae are a minority. Furthermore, as filamentous algae appear to pass through the gut undigested (Fryer 1959a) the true nutritional value of feeding upon filamentous algae is obscure. It was suggested that some of the ensheathing mucus on the filamentous algae is digested (Fryer & Iles 1972: 277). Another possibility is that the fishes ingest filamentous algae in order to digest the numerous epiphytes on the algal strands. Instead of brushing these from the filamentous algae, as do the *Petrotilapia* spp., *Pseudotropheus zebra* and others, they collect the filamentous algae and digest the loose Aufwuchs living on it. Feeding behaviour (nipping, plucking, jerking) and analyses of stomach contents indicates that many members of the *P. tropheops* species-complex, the *P. elongatus* species-group and the genus *Labidochromis* ingest mainly filamentous algae. Of these only *Pseudotropheus cf. microstoma* takes a high proportion of C3, all the remainder take predominantly C1 and C2 in differing proportions. Eight species of *Labidochromis* feed principally on filamentous algae, four on invertebrates, two on loose Aufwuchs, two have very mixed diets and one was not studied (Lewis 1982 and the results above).

Loose Aufwuchs. Most lithophilous members of the *Pseudotropheus zebra* species-complex, all members of the *P. 'aggressive'* species-group, most of the *P. 'miscellaneous'* species-group, two members of the *P. tropheops* species-complex, several species of *Melanochromis*, all *Petrotilapia* spp., two species of *Labidochromis*, both members of the genus *Labeotropheus*, *Gephyrochromis lawsi* and *Cyathochromis obliquidens* feed mainly upon loose Aufwuchs. In addition, variable quantities of loose Aufwuchs occur in the stomachs of virtually all other Mbuna.

* * *

It is apparent that all Mbuna species (except perhaps adult *Melanochromis* 'lepidophage') take a variety of foods and many species have identical diets. It follows, therefore, that analyses of stomach contents alone are unlikely to adequately demonstrate how food resources are partitioned, except perhaps for the few lepidophages, egg-and-parasite feeders, invertebrate feeders and piscivores. A feature of Mbuna ecology is that very little food partitioning is apparent from analyses of stomach contents. The food resource taken most commonly is loose Aufwuchs and at least four markedly different trophic specializations have evolved to collect it. The dentition of members of the *Pseudotropheus zebra* species-complex, of the genus *Petrotilapia* and that of *Cyathochromis obliquidens* is different, but all three groups utilize essentially similar feeding behaviour for the collection of loose Aufwuchs. Those members of the *Pseudotropheus* 'aggressive' species-group which consume loose Aufwuchs have stouter teeth and a different mode of food collection than the other three groups. They are also highly territorial and usually have algal gardens. Thus, *C. obliquidens* which inhabits intermediate zones and the members

of the *P.* 'aggressive' species-group may be readily distinguished ecologically from the members of the genus *Petrotilapia* and from the lithophilous members of the *P. zebra* species-complex. However, Fryer (1959a) found the *Petrotilapia* species and the members of the *P. zebra* species-complex to have a complete overlap in diet and habitat. He attributed their co-existence to the presence of a superabundance of Aufwuchs. Furthermore, Fryer & Iles (1972: 270 & 298) suggested that these species, and also other groups of Mbuna, lived in an apparent contradiction of the competitive exclusion hypothesis.

It is our view that the Mbuna do not contradict the competitive exclusion hypothesis. The zonation of species according to depth and microhabitat, particularly species-specific selection of sites for territories, was partly demonstrated by Fryer (1959a) and is more fully demonstrated here. Such partitioning of space enables species to feed upon the same food components, but to collect it from different areas. For example, although Fryer (1959a) considered *Pseudotropheus zebra* and *Petrotilapia tridentiger* (both are now known to comprise more than one species: Holzberg 1978; Marsh *et al.* 1981) to be identical in their food and habitat requirements, our survey has shown that in general the *Petrotilapia* spp. favour larger rocks and shallower water than the members of the *Pseudotropheus zebra* species-complex. Furthermore, Holzberg (1978) demonstrated that the various members of the *P. zebra* species-complex at Nkhata Bay differ in their preferred feeding areas and in feeding behaviour. Similarly Marsh (1981) found that sibling species of *Petrotilapia* favoured species-specific feeding areas, though it is possible also that the largest species (*P. tridentiger*) might have competitively excluded the smaller species from optimal areas. These studies demonstrate that not only are these two groups of fish ecologically separated, but that there is also partitioning among the member species of each genus. Another example comes from the genus *Labeotropheus*. Fryer (1959a) found it impossible to point to any difference in habitat preferences between the two sibling species at Nkhata Bay. He also found the gut contents to be indistinguishable and the mouth structure, dentition and mode of feeding to be identical. A closer study of these species at the island of Thumbi West revealed that they do occupy different habitats despite considerable overlap in the shallows and that, at the time of study, *L. fuelleborni* fed mainly from the upper surfaces of rocks while *L. trawavasae* favoured the under-surfaces (Ribbink *et al.* in press).

A food resource may also be partitioned by co-existing species which are of a different size. For example, Fryer (1959a) argues that as *Pseudotropheus minutus* is a small species with a small mouth it may exploit crannies which are inaccessible to all but the juveniles of the species with which it lives. Similarly, the narrow-mouthed *Labidochromis* spp. may collect filamentous algae or benthic Invertebrata from crevices which cannot be used by the broader mouthed species, such as members of the *Pseudotropheus tropheops* species-complex and the genus *Labeotropheus*. It has also been suggested (p.193) that the ability to feed with the side of its elongate snout enables *Pseudotropheus tursiops* and *P. tursiops* 'mbenji' to utilize food in narrow cracks and gaps between rocks which would be inaccessible to fishes of similar size which have terminal or subterminal mouths (e.g. members of the *P. zebra* species-complex and of the *P. tropheops* species-complex).

As there are strong indications that members of Mbuna communities do partition their resources (Fryer 1959a; Holzberg 1978; Marsh 1981; Sharp 1981; Ribbink *et al.* in press, and this survey), it seems that the postulated negation of the competitive exclusion principle might be more apparent than real (Greenwood 1981). Furthermore, the comment by Smith & Tyler (1973), that how and where a fish feeds might be more important to resource partitioning than on what it feeds, is particularly appropriate when considering the ecology of herbivorous Mbuna.

It is somewhat enigmatic that fishes which are highly specialized trophically should consume such a wide variety of food items that many species cannot be assigned confidently to specific trophic categories. This may be a consequence of insufficiently detailed research, but part of the answer probably lies in the fact that the various components of the Aufwuchs mat co-exist in such an intricate mesh that a fish cannot pluck, nip, nibble, brush or comb the mat without collecting a range of food items in addition to those for which it is specialized. Furthermore, it has become increasingly apparent that, in addition to having morphological and behavioural adaptations for specific diets, cichlid fishes of the Great Lakes of Africa are opportunistic feeders. Indeed Greenwood (1981) now emphasizes that the term 'specialization', in the context of feeding, does not mean that a species feeds exclusively upon one food, but is used to indicate its usual diet. This comment receives further qualification in the same paper when reference is made to a 'trophically specialized species'; Greenwood states that 'it retains the ability to utilise the food source tapped by its ancestors, and also has the capabilities to exploit sources not open to the ancestors because they lacked the dental and other necessary specialisations'. This ability of 'trophic specialists' to feed upon a wide spectrum of dietary components was evident in the present study of the Mbuna. It appears that most Mbuna species, no matter what their 'usual diet' might be, will take advantage of other sources of nutrition should the opportunity arise: they rise from the bottom to feed upon zoo- and phytoplankton; they feed upon eggs or fry of other fishes; they eat fish flesh and worms.

The probability that at least some Mbuna would have a broad range of feeding capabilities was predicted by Liem (1980). He found that despite the expected narrow range of operation of a *Petrotilapia* sp. and of a *Pseudotropheus zebra*, each species had eight distinct kinematic and electromyographic profiles. A species of *Cynotilapia* which he studied had five profiles, while a member of the genus *Melanochromis* was categorized as an ambush predator, with *Cyrtocara polystigma*, *C. livingstonii* and *C. compressiceps* each having three profiles. The pursuit predators had fewest profiles, each having only two (e.g. *Rhamphochromis* spp.), but no Mbuna was categorized as a pursuit predator. Although Liem's prediction that specialized Mbuna species may feed in a number of different ways and upon a variety of food resources is supported by our field observations, analyses of stomach contents suggest that the *Melanochromis* spp. and the *Cynotilapia* spp. take a wider spectrum of food items than indicated by the number of profiles which were found by Liem (1980). McKaye & Marsh (1983) put Liem's predictions to the test and found that under natural conditions *Petrotilapia tridentiger* and *Pseudotropheus zebra* do behave as facultative feeders, despite their trophic specializations.

Analyses of stomach contents (Marsh 1981; Sharp 1981; Lewis 1982; Ribbink *et al.* in press; and above) show that there is considerable individual variation among conspecifics caught at a particular site, and that conspecifics of different localities usually differ from one another in the proportion of particular food items in their stomachs, as do individuals caught at different depths and at different times of the year. Furthermore, conspecifics of different size usually take different food and territorial individuals seldom have exactly the same proportion of the various dietary components in their stomachs as non-territorial conspecifics. It is apparent, therefore, that a true understanding of the feeding ecology of Mbuna will only emerge as a result of a long-term study which pays attention to all these variables.

Since Mbuna are able to feed upon a broad spectrum of dietary components there is some difficulty in appreciating how trophic specialization evolved. D.H. Eccles (pers. comm.) and also McKaye & Marsh (1983) suggest that trophic specialization may be important only when food resources are limited for it is then that competition will be intense. At these times reliance on trophic specializations will be emphasized and survival might be dependent upon those advantages which accrue from such specializations.

Perhaps the evolutionary success of the cichlids of the African Great Lakes can be attributed partly to an adaptability which provides them with the resilience necessary to cope with environmental changes in food availability; they are specialists which have the ability to feed opportunistically upon alternative resources. By retaining a dietary flexibility these cichlids may have avoided the 'evolutionary trap' (Lowe-McConnell 1969) which has resulted in the extinction of many specialized island faunas (Mayr 1963).

Speciation

A great deal has been written about speciation in African cichlid fishes and the nature of the subject is such that much is speculative, some aspects are controversial while others remain enigmatic. Comprehensive reviews by Fryer & Iles (1972) and Greenwood (1974) should be referred to for detailed consideration of cichlid evolution and speciation. It is against the background set by these and other authors that we discuss our findings.

It is now widely accepted that allopatric speciation gave rise to the contemporary cichlid species-flocks (Fryer 1959a, 1969, 1977; Marlier 1959; Fryer & Iles 1972; Greenwood 1974). However, earlier workers, impressed by the great number of species endemic to each lake, and noting that fishes in general are vagile animals, had difficulty in identifying intralacustrine barriers which might have kept populations apart for sufficient time to permit speciation in allopatry. With regard to Lake Victoria it is believed that the spatial isolation required to separate the developing taxa is a correlate of both the way in which the lake originated and of later, tectonically induced, changes in the lake basin and its outflows (Greenwood 1965, 1974; Fryer 1969, 1977; Fryer & Iles 1972). It seems that the present Lake Victoria was a drainage basin across which a number of major rivers flowed from east to west. The lake was formed when the flow of these rivers was impeded by a gradual but large scale upward warping of the area to the west of the present lake. This uplift led to a reversal of river flow and a backponding of the western reaches of these rivers to form dentritic protolakes which grew, became linked and eventually formed a single expansive water body. During the lake's history,

climatic changes are believed to have produced marked fluctuations of lake levels which probably led, on a number of occasions, to the formation of peripheral water bodies and perhaps even to the re-establishment of the original protolakes. On the basis of the geological data Fryer & Iles (1972) constructed a model of the manner in which topographical and climatic events could have provided a variety of smaller and larger lakes, at times partially or wholly interconnected, at other times partially or wholly isolated from one another. It is postulated (Greenwood 1965, 1974; Fryer & Iles 1972) that the initial differentiation of the main phyletic lines and the development of trophic radiations within these lines must have taken place among the haplochromine species inhabiting the protolakes. From these origins numerous populations have at different times been isolated within the peripheral water bodies of the lake basin, and if each were given sufficient time in isolation new species could arise to ultimately produce the present-day cichlid species-flock.

That the time period spent in isolation need not be very long is demonstrated by the evolution of species in about 3 500 years in a peripheral water body, Lake Nabugabo, which lies alongside Lake Victoria (Greenwood 1965, 1974). The species found in Lake Nabugabo were isolated from parent stocks in Lake Victoria and then diverged. This example adds considerable credence to the postulate that the formation of many such peripheral water bodies during the history of Lake Victoria is largely responsible for the evolution of the present day species-flock. Fryer (1969) argues that although Lake Victoria is usually considered along with the rift valley lakes as one of the great examples of intralacustrine speciation it does not in fact exhibit this phenomenon at all. His contention is that if the history of the species-flock (now believed to number more than 250 species: Van Oijen *et al.* 1981) has been interpreted correctly, all the speciation that has occurred took place as a result of the complete physical isolation of populations in separate bodies of water. Fryer & Iles (1972) argue further that there is no proven case of truly intralacustrine speciation among Lake Victoria haplochromines. However, one should not dismiss completely the possibility of intralacustrine speciation and Greenwood (1979b) suggests that some of the deep-water species may have arisen within the lake, as deep-water habitats were unlikely to have become available until the basin settled into more or less its present form. Furthermore, F. Witte (pers. comm.) has found that fishes of non-rocky habitats in Lake Victoria vary geographically, and even over distances of several kilometres major changes in haplochromine species composition occur. This localization of species suggests that intralacustrine allopatric speciation is a possibility. In our opinion the recently discovered rock-frequenting species are the group most likely to have arisen *via* intralacustrine speciation as 'there are indications that the populations of the different rock islands are rather isolated and that little migration occurs between islands isolated by relatively deep troughs' (Van Oijen *et al.* 1981). A similar situation exists among the rock-dwelling fishes of the rift valley lakes which are almost certainly the products of intralacustrine speciation.

The genesis, history and physiography of the rift valley lakes Tanganyika and Malawi, differ markedly from those of Lake Victoria (Fryer & Iles 1972; Greenwood 1974), and it is likely that intralacustrine speciation is largely responsible for the species richness of these lakes (Fryer 1969). Although the rift valley lakes were subject to considerable

changes in water level during climatic vicissitudes in their history it is unlikely that they ever dried up, or passed through a period of shallow, isolated lakes like those of early Lake Victoria (Fryer 1977). The possibility of some speciation based on complete isolation in separate basins cannot be completely ruled out for Lake Malawi (Greenwood 1974), although there are no explicit data to support the idea (Fryer 1977). If such speciation did occur its contribution to the evolution of the species-flocks is likely to have been small. Similarly it is unlikely that effective long-term fragmentation of Lake Tanganyika occurred, and although it is possible that the two separate troughs which form the lake could have been isolated during dry periods, it is not known whether this ever happened (Fryer & Iles 1972).

Mayr (1963) suggested that multiple colonizations of the lakes by a variety of riverine species might account for the species richness, but most authorities believe that few fluviatile cichlids invaded the lakes (Regan 1921; Trewavas 1935; Fryer 1959a; Lowe-McConnell 1969; Greenwood 1974). Fryer (1977) suggests, however, that multiple colonizations by a single species may have occurred. He argues that a riverine species might have entered protolake Malawi on several different occasions, and, as the developing lake spread, at a number of disparate points. At each invasion the original ancestral species was confronted by altered conditions each requiring different adaptations and each giving rise to new species.

The fossil record of fishes of these rift valley lakes is so poor that it gives little clue to their history (Fryer & Iles 1972). So to understand how intralacustrine speciation may have occurred it is necessary to examine the evidence presented by contemporary species. The most striking evidence comes from zoogeographical data which demonstrate that most populations of rock-dwelling cichlids are localized, sometimes having a total distribution range which is restricted to a small rocky outcrop or to part of a more extensive shore (Marlier 1959; Fryer 1959b, Matthes 1962; Fryer 1969; Fryer & Iles 1972 and the data herein). In addition, within these areas of limited distribution many species have preferred habitats which further restrict their range on rocky shores. In the following discussion we focus initially on the way in which local populations may have originated, then we examine extrinsic and intrinsic factors which maintain geographic isolation of contemporary populations, and finally consideration is given to those factors which facilitate conspecific recognition, particularly mate recognition, and prevent interbreeding of differentiated populations.

Fryer & Iles (1972) and Fryer (1977) suggested that a relatively generalized ancestral Mbuna lived over both sand and rock, but having acquired a preference for feeding on epilithic algae while in its riverine provenance it continued to favour the rocky environment to which it was preadapted. In addition, another group of colonists, comprising different species from those which favoured rocky habitats, lived in both habitats, but favoured sandy areas. Both groups tended to specialize, become adapted to their preferred habitat and in so doing they tended to exclude the other group from this habitat. Fryer (1959a) and Fryer & Iles (1972) believe that from these origins the lithophilous Mbuna diverged progressively from the sand-dwelling haplochromines. Once they were specialized for life in rocky zones the early Mbuna populations became restricted to rocky shores and could then be fragmented into a number of geographically isolated populations by topographical events which set the scene for

intralacustrine allopatric speciation.

Greenwood (1974) questioned Fryer's hypothesis on two counts. Firstly, he claimed that the theory failed to explain how the early relatively unspecialized invaders were confined to and isolated in particular habitats. It seems that he was concerned that gene flow between rock and sand populations would be unimpeded, not realizing that Fryer (1959a) was referring to two populations which were differentiated when they colonized the lake. The point was clarified by Fryer (1977). Secondly, Greenwood (1974) asks how the newly derived stenotopic taxa achieve lake-wide distribution, the implication being that their strong attachments to habitat islands would prevent them from becoming widely distributed. It seems that while most Mbuna species are closely tied to their preferred habitat and while populations are restricted to particular, often small, geographic areas, all Mbuna are not inflexibly stenotopic. For example, we found that certain lithophilous species (e.g. *Labeotropheus fuelleborni*, *Petrotilapia* spp., *Pseudotropheus zebra* and members of the *P. tropheops* species-complex migrate over sand to artificial reefs separated from rocky shores by 100 m (Khuyu Bay, Likoma Island) and by about 150 m (Zambo, Monkey Bay; unpubl. data). There is no reason to believe, therefore, that ancestral Mbuna were more closely tied to rocky zones than extant forms. On the contrary, Fryer's hypothesis suggests that they were eurytopic, but had a developing preference for rocky habitats.

Further, Fryer (1977) pointed out that considerable changes in lake level during the history of Lake Malawi might have forced populations to vacate areas which were becoming unsuitable, to take up residence elsewhere. There is geological evidence (Dixey 1926, 1941; Crowley *et al.* 1964; Fryer 1959a, 1969, 1977; Fryer & Iles 1972; Beadle 1974, 1981; Crossley 1982) that the water level of Lake Malawi fluctuated considerably during its history with indications of changes of more than 100 m. Such changes in lake level would have caused the lake to spread during pluvial periods, incorporating areas previously uninhabited by fishes, thus permitting colonization of new regions. During interpluvial periods the lake would have shrunk, driving populations, which might include species unique to those previously flooded areas, into other parts of the lake. Similarly, fluctuations in water level would increase or decrease the size of rocky zones, expose or drown areas, and fragment or unite similar habitats. Some of the ways in which these changes might have occurred are depicted diagrammatically by Fryer (1977: Figure 3).

The impact that changes in lake level may have had on Mbuna communities is appreciated from the fact that few of the rocky shores studied in 1979/1980 extend beyond 40 m depth; usually they give way to sandy bottoms in shallower water. Thus, most of the present rocky zones would become uninhabitable to lithophilous fishes if the lake level were to drop by 40 m. Furthermore, as a rocky shore diminishes in area with falling lake level, so the rock-dwelling species on it are concentrated in the remaining habitable areas and may be subject to intense competition. On the other hand, submerged rocky reefs which are at present too deep for most Mbuna species might become suitable habitats for colonists when the lake level dropped.

A further perspective on the effects of altering lake level is given by the recorded changes in the recent past. Between 1915 and 1980 Lake Malawi rose 7.2 m (Crossley 1982)

making new rocky zones available to Mbuna and rendering other shores less suitable to certain species. Assuming that the elevation of the sandy bottom has remained unchanged then many of the littoral rocky shores studied in 1979/1980 would have been dry in 1915 (e.g. Nkopola, Mpandi, Kanchedza, Chigubi, Senga Point, Rifu, Sani, Bandakushu, Makanjila). Many rocky shores in shallow water would have had a substantially smaller area submerged than at present (e.g. Nkudzi, Domwe, Nankoma, Otter Point), while rocky outcrops in deep water (e.g. Chinyamwezi, Chinyankwazi, Zimbabwe) would have had an increased area available to those Mbuna which are restricted to the shallows. Some rocky reefs that were submerged in 1980 would have been prominently exposed 65 years ago (e.g. Crocodile Rocks — perhaps dry in 1915, Mazinzi Reef, Eccles Reef, West Reef, Ndumi Rocks and Mara Rocks).

As several Mbuna species are now resident on rocky shores that were exposed in the recent past it is apparent that they crossed the sandy beaches to reach these shores. None of these shores, however, is inhabited by many Mbuna species; Rifu, Sani and Senga Point each have only three or four species (Table 26). It is clear that at least some Mbuna are able to leave their preferred habitats, cross sandy regions and colonize newly available shores (see also artificial reefs, p.299).

Fryer (1959a) recorded microhabitat preferences among Mbuna and suggested that once these preferences are established, perhaps during a period of isolation, appropriate habitats will be sought out when the fishes colonize new shores. Our survey confirms that most Mbuna species are largely restricted to specific habitats. Furthermore, translocations of Mbuna species from one part of the lake to another by exporters of aquarium fishes have shown that Mbuna introduced at new sites occupy the same depth zone and habitat as conspecifics in their provenance. The origins of these habitat preferences are of interest since changes in lake level may have played a guiding role. For example, it is suggested that species adapted to live in purely rocky zones might have been forced down the rocky shore by a falling lake level and then been obliged to live for the duration of a relatively stable period at the interface between rocky and sandy zones. If these species become adapted to such intermediate zones, which now represent their preferred habitat, then when other habitats become available with a subsequent rise in lake level these fishes would remain in the mixed zone. In extreme instances a change of lake level may have forced Mbuna to live over sand, giving rise to species which habitually occupy this zone (e.g. *Pseudotropheus livingstonii*, *P. elegans*). Similarly, a change in lake level might have rendered a habitat type (e.g. large rocks) inaccessible, forcing fishes to take up residence in another (e.g. small rock) habitat to which they would become behaviourally and physically suited and which they would seek out when it became possible to expand their distribution.

Sympatric sibling species were encountered at virtually every site studied and are particularly numerous at Nkhata Bay (seven species of the *P. tropheops* species-complex; three species of *Petrotilapia*; three species of *Pseudotropheus zebra* species-complex and two species of *Labeotropheus*), and at Maleri Island (six members of the *Pseudotropheus zebra* species-complex; four of the *P. tropheops* species-complex; three *Petrotilapia* species and two *Labeotropheus* species). The occurrence of so many sympatric sibling species provides a potentially fertile field

of speculation and research for proponents of sympatric speciation. However, allopatric speciation could adequately account for the phenomenon in the following manner. Changes in water depth could divide a single gene pool into two or more gene pools which might diverge during periods of isolation, each becoming adapted to the particular set of environmental circumstances to which it is subject. When secondary contact is achieved by, for example, a re-establishment of the original lake level (see Fryer 1977 for possible mechanisms of division and bringing together of populations) each might seek out its preferred habitat and remain, by virtue of this and other differences, reproductively isolated from sympatric populations. It is not necessary to postulate that six sibling species would have arisen simultaneously after a single change in lake level, although multiple splitting of gene pools could result from a single change in lake level and may account for at least some of the speciation in the Great African Lakes (Greenwood 1974; Fryer 1977). It is more likely that a number of changes in water depth occurred, some of which resulted in new species.

The hypotheses presented above suggest how changes in lake level could have led to speciation, extinction, enforced migrations and the development of preferred habitats; they also provide an explanation for the occurrence of diverse species assemblages — often including sympatric sibling species — on the rocky shores. Undoubtedly, changes in lake level must be ranked as one of the most powerful factors which contributed to the differentiation of Mbuna populations. Variations in temperature, water chemistry, currents, isolation, productivity, the physiography of rocky habitats and other factors in Lake Malawi will affect geographically segregated populations in different ways and promote divergence of gene pools. The selection pressures imposed by these factors are relatively mild and the ensuing adaptations will result in species better suited to their own unique situation. In contrast, changes in water level can produce immediate harsh selection to which the fishes adapt, migrate or die.

An outstanding feature of Mbuna is that no population has a lake-wide distribution and the vast majority of populations are restricted to particular localities. A number of factors inhibit Mbuna dispersal. The principal extrinsic barriers are sandy beaches, deep troughs and open water. Theoretically it is possible for these fishes to swim across unsuitable habitats and it is unlikely that these barriers are absolute. Nevertheless, the zoogeographical evidence strongly suggests that, with the exception of rocky shores that are close to one another and linked by sandy beaches in shallow water, gene flow between geographically separated populations is effectively non-existent.

The failure to cross physical barriers may be accounted for by a number of intrinsic characteristics of Mbuna. Important among these is the stenotopy of most Mbuna, as they remain in a preferred depth range and all species studied in pressure tanks are limited in their physiological ability to penetrate depth (*Melanochromis joanjohnsonae* is limited to 25 m: Hill & Ribbink 1978; *Petrotilapia tridentiger*, *P. genalutea* and *P. nigra* are all limited to less than 50 m: Marsh & Ribbink 1981; *Labeotropheus fuelleborni* and *L. trewavasae* are limited to 25 m and 40 m respectively: Ribbink *et al.* in press). This inability to compensate for depth means that these species, and perhaps most other Mbuna, would be unlikely to cross deep troughs separating rocky shores.

Dobzhansky (1951, quoted by Fryer 1977: 161) notes that speciation rate is greater in animals in which parental care is well developed, for these animals have a tendency to increased philopatry and, consequently, sharply reduced dispersal. Mayr (1969: 339) cites mouth-brooding cichlids as an example, stating that 'by the time the young cichlids become independent, they have become thoroughly habituated to the very localized station of their parents'. The principal reason for habituation of fry to a mother's territory is that it keeps the fry localized, facilitating their protection and collection (Albrecht 1963; Lowe-McConnell 1969; Ribbink *et al.* 1980) and increased philopatry is an incidental consequence of this behaviour. The cichlid fishes of the rocky shores which show the guarding behaviour referred to by Mayr (1969) are not the highly philopatric Mbuna, but the larger more vagile haplochromines (Ribbink *et al.* 1980). Mbuna produce a few large eggs, incubate these for a protracted period in the mouth and eventually release large, independent fry which immediately hide in small cracks or holes among the rocks. In 3 600 h of diving we never found an Mbuna parent guarding its free-swimming progeny; in contrast, other rock-dwelling haplochromines were found guarding fry on hundreds of occasions. Since all adult fishes, including herbivorous Mbuna, eat fry opportunistically, young Mbuna fry are forced to remain in their refuges until they are large enough to avoid predators. This predatory pressure increases philopatry and it is possible that individuals of at least some Mbuna species spend their whole lives within an area of a few square metres. It is suggested, for example, that the groups of OB male *P. zebra* at Mvunguti, Likoma Island and elsewhere are the undispersed adults from one or a few broods. A further indication of philopatry in Mbuna may be inferred from the apparent clinal gradation over short distances of *C. afra* at Likoma Island (p. 236).

A comparison which clearly illustrates how parental care can increase philopatry can be made between Mbuna and coral reef fishes in tropical oceans. Both groups comprise small, colourful fishes which show many ecological and behavioural similarities. However, they differ fundamentally in one important respect: many species of coral reef fishes are widely dispersed in suitable habitats (Sale 1977) and show very little variation over enormous geographical areas, whereas Mbuna show marked insularity and considerable geographic variation. The difference is due to the fact that coral reef fish larvae are planktonic and become widely dispersed by ocean currents, while Mbuna are mouth-brooders.

Before leaving the discussion of parental care we shall digress from philopatry to develop a point raised by Fryer (1977). Mouth-brooding cichlids carry fry or zygotes (11 – 80 progeny are carried by Mbuna, pers. obs.) and so it is possible that a founder population could be established by a single female successfully transporting her progeny across a discontinuity. Such an event seems unlikely under normal circumstances, for our field observations indicate that mouth-brooding Mbuna are relatively inactive and tend to remain hidden. So the chances of these fishes vacating their refuge in their preferred habitat are even lower than those of non-brooding individuals. However, under adverse conditions, such as those produced by a change in lake level, mouth-brooding individuals may be forced to migrate and if one is successful in crossing inimical barriers, a founder population may be established. Founders carry such a small

reservoir of genetic diversity that the population founded by them is highly vulnerable to inbreeding (Mayr 1963). This is partially ameliorated in many cichlids, including Mbuna, which practise polyandry i.e. each of a number of different males spawns with the female fertilizing one or more eggs. Thus, within a single brood genes are contributed from a wider spectrum of the parent population and therefore contain a larger fraction of the total variation of the parent species than is possible from a monogamous mating. All other factors being equal, such founder populations stand an enhanced chance of success.

The speciation rate of the cichlids of the African Great Lakes is so dramatic that metaphors such as 'explosive speciation', 'explosive evolution' and 'evolutionary avalanche' have come into use (Fryer & Iles 1972; Liem 1973; Greenwood 1974, 1981). No precise speciation rate can be determined for any species, though inferential evidence (Greenwood 1965) suggests that 3 500 years were sufficient for the differentiation of the Nabugabo species from Lake Victoria sister species. It is argued further (Greenwood 1974) that reproductive isolation between these sister species may have been achieved in an even shorter period. Confirmation of the rapid rate of speciation of Mbuna comes from the genetic studies of Kornfield (1978) though he was also unable to establish a precise time scale.

Mbuna evolution is likely to have been episodic: rapid during periods of changing environment (e.g. fluctuations in lake level) and slow during periods of equilibrium (e.g. periods of relative stability in lake level), thus conforming to the model of punctuational evolution proposed by Eldredge & Gould (1972). Other factors which are more consistent with the model of punctuated equilibria than with that of phyletic gradualism (see Vrba 1980 for a comparison of the two models) are the strong indications that small populations of Mbuna were geographically isolated in new environments and that many splitting events are likely to have occurred during periods when populations were fragmented by environmental changes. Greenwood (1979a, 1981) believes that the haplochromines of Lake Victoria also provide good examples of punctuational evolution. Further support for this model comes from Beadle (1981: 140) who, while writing generally about speciation of fishes in African lakes, argues that the rate at which new species appeared in the past was certainly not uniform and suggests that great changes in environment 'were followed by an outburst of speciation in adaptation to the new conditions'. For example, it is generally believed that a surge of cichlid diversification followed the initial colonization of the lacustrine environments by the ancestral riverine cichlids.

The evolutionary success of the Cichlidae relative to other fish families in the African lakes has been attributed to a number of factors. Lowe-McConnell (1969, 1975), noting the remarkable adaptive radiation of cichlids, particularly the haplochromines, considers that the genetic machinery of these fishes is geared to take advantage of new evolutionary opportunities. In her opinion the cichlids possess a 'genetic plasticity'.

Fryer (1969) and Lowe-McConnell (1969, 1975) argue that as cichlids aerate their own eggs and yolk-sac larvae they were pre-adapted to a lacustrine existence by being independent of running water for breeding, thus having an advantage over anadromous fishes. Other aspects of breeding behaviour, such as continuous breeding and the possibility that several broods are produced annually, have also been

invoked as factors which might have accelerated speciation of lacustrine Cichlidae (Fryer & Iles 1972; Lowe-McConnell 1969, 1975; Greenwood 1974). Lewis (1981), however, believes that breeding seasonality holds greater evolutionary advantages. Fryer (1959a, 1977 citing Dobzhansky 1951) notes that animals in which parental care is most highly developed are the groups in which evolution is proceeding most rapidly and as the cichlids have elaborate parental behaviour they are cited as an example.

The possible accelerating effects of competition on speciation have received attention (Fryer 1959a; Lowe-McConnell 1969, 1975; Fryer & Iles 1972; Greenwood 1974), but no unequivocal examples are given in support. The controversial role of predators has been accorded more speculative attention than it warrants in view of the limited knowledge of predation in the African lakes (Worthington 1954; Jackson 1961b; Fryer 1965; Fryer & Iles 1955, 1972; Lowe-McConnell 1969, 1975; Greenwood 1974; Beadle 1981). Fryer (1960) suggested that the smaller size of the haplochromines conferred on them an ability to speciate more rapidly than the larger tilapiines. Whether size *per se* influences speciation rates is a moot point (Vrba 1980) and the common observation that animal species of large size (e.g. tilapiines) are rarer than smaller species (e.g. haplochromines) is not necessarily proof. Nevertheless, with regard to the Mbuna it is the smaller species that are most philopatric, demonstrate the greatest insularity and which are the most likely to speciate rapidly as a consequence. The principal thrust of the comparison of tilapiine and haplochromine speciation focussed not on their respective sizes but upon the observation that tilapiines appear generalized (eurytopic), r-selected and have not speciated greatly, whereas the haplochromines are specialized (stenotopic), K-selected and speciose (Fryer 1960, 1977; Fryer & Iles 1969, 1972). Vrba (1980) cited several authors who have suggested that narrow adaptation (as exemplified by the haplochromines) may be correlated with rapid diversification rates. She argues further that 'narrow SMRSs are in most cases likely to be found in species with other narrow environmental adaptations' and that 'fast speciation rates will be associated with stenotopic SMRSs and also with other stenotopic adaptations'. Vrba then developed her 'effect hypothesis' in which she takes as a macro-evolutionary analogue to an r-strategist, a clade that consistently produces many species called 'increasers'; the analogue to a K-strategist might be a clade which produces species resistant to extinction, called 'survivors'. She argues that the intrinsic rate of speciation is likely to be higher in the increaser, or stenotopic, subset than in the survivor, or eurytopic, subset of a clade, noting that while the direction of speciation is random the evolutionary trend is towards specialization. The Mbuna are a speciose, narrowly adapted group whose members show considerable specialization and they undoubtedly qualify as 'increasers' on the survivor-increaser scale of the 'effect hypothesis'.

Although there was a tendency among the earliest workers to consider the cichlid species-flocks as unique evolutionary phenomena, perhaps showing unusual modes of speciation (see Greenwood 1974, 1981 for references), it is now appreciated that the evolutionary processes which gave rise to these fishes were rapid, but not unusual. The high rate of speciation of Mbuna is attributed mainly to (i) the geographical isolation of small populations to patches of rocky habitat, (ii) the effects of changing lake levels, (iii) the

philopatric tendencies of these fishes, (iv) their stenotopic nature, (v) the retention of their ability to feed upon alternative resources, thus avoiding the evolutionary trap discussed by Lowe-McConnell (1969) and (vi) their apparent ability to adapt rapidly to new environments.

In his discussion of cichlid speciation in the African Great Lakes, Mayr (1969: 334) commented appropriately that '... each lake consists of an archipelago of suitable areas, with each habitat island (such as a rocky shore) separated by a barrier (such as a sandy or muddy shore) from other suitable areas'.

His reference to archipelagos leads to a comparison of cichlids with the Galapagos finches, the Hawaiian honeycreepers and the Hawaiian fruit flies which are all well known for their speciation and adaptive radiation within geographically restricted archipelagos. Such a comparison has been made before (Fryer 1972; Fryer & Iles 1972; Greenwood 1973, 1974, 1981); in all groups differentiation has been primarily towards trophic specializations and in all groups the adaptational successes have been effected through simple anatomical changes. Speciation appears to be the consequence of geographical isolation and adaptation to new environments by members of all groups.

Evidence for allopatric speciation of Mbuna is excellent and the indications that other groups of fishes are geographically restricted within Lake Malawi (Eccles & Lewis 1977, 1978, 1979; Iles 1960; Trewavas 1935) suggests that these non-Mbuna also arose as a result of allopatric speciation. In contrast, there is no evidence of non-allopatric modes of speciation. Consequently, there is a tendency to give scant regard to the possibility that sympatric or other non-allopatric modes of speciation may occur. Beadle (1981: 140) is critical of writers who 'seem to have assumed the impossibility of any but allopatric speciation' of African Great Lake cichlids. The possibility of sympatric speciation has been considered by McKaye (1980) who suggests that it may result from the development of stable polymorphism in Mbuna and perhaps other cichlids. He believes also that allochronic speciation may have occurred among the tilapiines of Lake Malawi. In the absence of evidence, such models are speculative. It is difficult, however, to understand how the different endemic species of Lake Barombi Mbo in Western Cameroon arose (Trewavas, Green & Corbet 1972). It is a small crater lake, 2.5 km in diameter and 111 m maximum depth with only the upper 20 m being oxygenated. The lake appears to be free of physical barriers to the movement of fishes and there is no reason to believe that such barriers were present during the history of this lake. Seventeen species of fishes occur in the lake of which 12 are endemic and these include all 11 species of cichlid. In the absence of indications of how allopatric speciation could have occurred there may be a need to invoke sympatric models of speciation, but until further research has been concluded, one should maintain an open mind.

Species recognition

The ability of cichlids of the rocky shores to recognize conspecifics is excellent. Recognition is often achieved when a potential mate or rival is several metres away. Territorial males, for example, may swim 2–7 m to embark upon courtship or to chase away conspecific males (pers. obs.). It is likely that anatomical features, coloration, behaviour, aspects of preferred habitat and perhaps even co-adaptation of breeding seasonality are important components of the

specific mate recognition system (SMRS) of cichlids. Our categorization of genera and species-groups is dependent upon the anatomical and behavioural features which are characteristic of each group. Furthermore, we distinguish between closely related sympatric Mbuna populations in the field according to differences in coloration and preferred habitat. The value of these characteristics to us for identification and to the fishes in mate recognition are discussed here.

Coloration

An impressive feature of many Mbuna populations is that the coloration varies geographically so that every local population is characterized by a unique set of colours and markings. These colours and markings are species-specific (or population-specific) and show little variation within a population of sexually active males at any particular site. This implies that they are subject to stabilizing selection and form part of the SMRS. There is compelling evidence that colour is widely used by cichlids for communication and the frequently repeated observation that colours intensify during courtship (Noble & Curtis 1939; Baerends & Baerends-van Roon 1950; Wickler 1963; Fryer & Iles 1972; Marsh *et al.* 1981) suggests that species-specific colours are used in mate recognition. It has not been established how important colour and markings are for mate recognition in cichlids, though it is generally assumed that since colours are valuable to humans for identification of closely related species (Lowe 1952; Barel *et al.* 1977; Eccles & Lewis 1979; Van Oijen *et al.* 1981; Marsh *et al.* 1981; Lewis 1982) their role must be considerable. Greenwood (1965, 1974), for example, records that Lake Nabugabo *Haplochromis* species are only slightly different anatomically from their Lake Victoria sister species, 'but the differences in male coloration are very trenchant' (Greenwood 1974: 112). These colour differences developed in only 3 500 years and Greenwood (1974: 112) argues that 'if male coloration is of prime importance as a recognition signal (and there is little evidence to negate these suppositions) then we have a clear-cut example of the rapidity with which a *Haplochromis* species can originate'. Undoubtedly, Greenwood believes that differences in colour between the Lake Victoria parental species and the Lake Nabugabo daughter species are of sufficient consequence to prevent interbreeding. Fryer (1977) introduces a cautious note when he suggests that colour *per se* may be less important at times of mating than might be assumed from its striking nature and specific distinctness. He does not deny, however, that species-specific colours play a role in mate recognition, he merely questions whether they play a primary role.

Both Greenwood (1974) and Fryer (1977) note that the Lake Nabugabo species developed different colours from their parent populations as a consequence of 'fortuitous' genetic reorganization in isolation, not as a means of isolating the members of the species pairs, which never encounter one another. This is consistent with a basic tenet of the recognition concept (Paterson 1978) which holds that natural selection acts to increase the organism's 'fitness' in its new environment. There is no evidence, however, which suggests that the evolution of a new set of colours in isolated populations of Mbuna is an adaptive response to the environment. It seems probable that differences in Mbuna coloration originated as a consequence of genetic drift and were then fixed by stabilizing selection. There is no doubt that

colour plays a crucial role in the lives of cichlids and it is probable that species recognition is effected by differences in colour as well as other components of the SMRS.

Mbuna are colourful fishes and despite the apparent high mutability of colour it is parenthetically of interest that very few colours are utilized. As a generalization, and listed in order of greatest occurrence: blue, yellow and black dominate male coloration, while greys, brown and blacks dominate female coloration. Greens are virtually absent, reds are scarce and white is uncommon. Furthermore, body patterns are limited to vertical bars and longitudinal bands and the same fin patterns are found with little variation in a wide spectrum of Mbuna. The colourful nature of the Mbuna then is dependent on subtle variations on a basic theme, rather than the introduction of diversity of patterns and colours. No Mbuna species, for example, has the oblique bars prevalent among sand-dwellers e.g. *Cyrtocara sphaerodon*.

Behaviour

Courtship and spawning behaviour of cichlids follows closely co-adapted sequences in which signals are exchanged between partners. These sequences are known for a number of fishes (Baerends & Baerends-van Roon 1950; Fryer & Iles 1972). The breeding behaviour of cichlids is, in general, more complex than that of other fishes. Greenwood (1974) believes that this complexity offers opportunities for the evolution of a variety of new ways in which mate recognition may be assured. Fryer (1977) considers that differences in courtship behaviour (movements) are most important in the maintenance of specific separation of at least some species. He substantiates his stand by citing Noble & Curtis (1939) who showed that the dominant element in mate recognition of the west African cichlid, *Hemichromis bimaculatus*, is movement and that colour serves mainly to accentuate this. These opinions lead one to expect that differences in courtship and spawning behaviour could be useful aids to species identification. Some differences have been found among African cichlids, e.g. Trewavas (1973) drew a taxonomic distinction between mouth-brooding and substratum-spawning tilapiines; Wickler (1962) noted differences in the timing of egg-laying, fertilization and egg-collection in three-different haplochromine species. However, a remarkable aspect of riverine and lacustrine cichlids in Africa is that the basic components of aggressive and courtship behaviour (i.e. lateral-display, tail-beating, frontal-display, mouth-fighting, side-shake, follow-shake, lead-swim and spawning patterns: Baerends & Baerends-van Roon 1950; Ribbink 1971) are essentially similar and have apparently resisted change. It follows that in a species-flock, such as the Mbuna, differences in the behavioural components and in the sequences in which they are performed might be difficult to detect. This proved to be the case, as not a single overt example of a species-specific behavioural difference was found. It is possible that superimposed on these basic behavioural patterns are species-specific differences which are too subtle for detection in the field. Nevertheless, the fundamental co-adapted behavioural characters involved in cichlid aggression, courtship and spawning have resisted change despite the spectacular speciation and adaptive radiation of African cichlids. Paterson (1980) stresses the resistance of co-adapted SMRS to selection pressures in large populations. In cichlids the uniformity of basic aggressive and courtship patterns and

therefore the apparent resistance to change, transcends many taxonomic categories and appears to have survived in small populations. If this observation is accurate then the value of these behaviours within a specific mate recognition system is questionable. In addition to seeking species-specific behavioural subtleties which might be superimposed on the basic courtship patterns, a useful line of research would be a comparison of the respective rates of execution of these behavioural components by different species. An unconfirmed impression is that Mbuna species of small size go through the motions more rapidly than larger species.

Differences in aggressive behaviour between species are clearer. Although the behavioural components appear to be the same in all species, the vigour of execution of the behaviour patterns concerned with the maintenance of territories varies among Mbuna so that the following distinctions can be made:

- (i) *Iodotropheus sprengerae* and *Genyochromis mento* appear to be non-territorial.
- (ii) *Labidochromis* spp. with the exception of those from Likoma Island: *L. gigas*, *L. flavigulus*, *L. strigatus*, *L. freibergeri*, *L. lividus* and *L. zebroides*, are not territorial.
- (iii) Members of the *Melanochromis melanopterus* species-complex hold large territories which they vacate when feeding. Territories are used for spawning and are defended against conspecifics only. In general this group is weakly territorial.
- (iv) *Labeotropheus trewavasae* is weakly territorial, whereas *L. fuelleborni* males hold territories which they defend against conspecifics.
- (v) Most species of *Pseudotropheus*, all species of *Petrotilapia*, *Cynotilapia* and also *Gephyrochromis lawsi* hold territories which they defend fiercely against conspecifics though they may tolerate encroachment by other species. Algal gardens are rare in the territories of these fishes.
- (vi) Several members of the *Pseudotropheus tropheops* species-complex, of the *P. elongatus* species-group and all of the *P. 'aggressive'* species-group are strongly territorial; both sexes may defend territories from which all intruders are excluded and in which algal gardens develop.

Preferred habitat

'Mating partners are also co-adapted with respect to preferred habitat and preferred breeding season' (Paterson 1978: 371) and it is with regard to these two factors that the most pronounced divergence in breeding behaviour is found. Lowe (1952) and Lowe-McConnell (1959) record that differences in both timing and location of breeding sibling species of tilapiines effectively separates them in Lake Malawi. Similarly, spatial and temporal differences in the breeding requirements of many sand-dwelling haplochromines segregate these in Lake Malawi (Reinthal pers. comm.). Among sand-dwelling cichlids, nest size, nest-shape and the siting of nests varies between species, but is relatively constant within a species suggesting that nests are species-specific characters. Indeed, nest size and shape are useful aids to species identification (pers. obs.) and are probably important components of the SMRS, especially since nests are spawning sites. No temporal segregation of breeding activity was found among Mbuna. Most species appear to breed throughout the year but have a marked peak in August-September and a smaller peak in February-March

(unpubl. data).

Spatial segregation of Mbuna species on a rocky shore is apparent and the choice of spawning sites also appears more-or-less species-specific. Those species which occupy areas in which sand occurs dig saucer-shaped nests. Some favour areas alongside rocks (e.g. those members of the *Pseudotropheus tropheops* species-complex which occupy intermediate habitats: *P. zebra* 'patricki', *P. zebra* 'fusco'), while others excavate hideaways beneath rocks (e.g. *Labidochromis flavigulus*, *Pseudotropheus* 'lime', *P. 'polit'*, *P. 'burrower'*, *P. 'aggressive grey head'*). Most lithophilous species hide among the rocks to spawn and so differences in spawning sites are not readily discerned except in the broad sense that they are in the preferred habitat of the species. A number of Mbuna which do not normally live near sand (e.g. *Pseudotropheus zebra*, *Labeotropheus fuelleborni*, *L. trewavasae*, *Petrotilapia* spp., *Melanochromis vermivorus*) and would not usually have the opportunity to excavate nests under natural conditions, do dig nests in aquaria when placed over sand. Clearly, the ability to dig nests is retained even if never used in the natural environment.

We recognize species under-water by differences in body shape and size, head and jaw structure, coloration and markings, angle and manner of feeding, by species-characteristic modes of swimming and by differences in vigour of territoriality, and it is assumed that Mbuna use much the same criteria. Further, as co-adapted partners are likely to be finely tuned to one another it is likely that they respond to nuances of behaviour and morphology too subtle for us to detect. Of all the behaviour patterns it is those concerned with the various feeding specializations which enable us to distinguish most readily between different genera and species-complexes. In contrast, those behavioural elements associated most closely with courtship and spawning are of least value in species identification.

If mate recognition is accomplished before the initiation of courtship, as field observations suggest, then the role of movement in mating behaviour may not be central to species recognition as implied by Fryer (1977).

In view of our limited knowledge at present it is a spurious exercise to speculate further on the respective roles of colour, behaviour, morphology, preferred habitat and other factors which bring co-adapted partners together. All contribute their part to the totality of an SMRS.

Rock-frequenting cichlids of other African Great Lakes

Rock-dwelling cichlids occur in each of the African Great Lakes and preliminary comparisons of these communities demonstrate a number of close parallels.

Although most of the bottom substrata of Lake Victoria are muddy or sandy, small isolated rocky areas do occur. These rocky habitats are inhabited by Mbuna-like fishes (Van Oijen *et al.* 1981). The 16 species discovered include epilithic algal scrapers, insectivores, molluscivores, a zooplanktivore, a paedophage and a crab eater. In a comparison of the Lake Victoria rock-dwelling community with the Mbuna, Van Oijen *et al.* (1981) found that:

- (i) Both communities are darkly coloured in contrast with sand-dwellers and open-water species.
- (ii) Rock-frequenting species of both lakes have small deeply embedded scales on chest and nuchal area.
- (iii) Similar trophic adaptations of jaws and teeth occur in

the rocky communities of both lakes, particularly among the algal scrapers, insect pickers and zooplanktivores. Furthermore, the Lake Victoria species take hooks baited with worms or meat suggesting that, like the Mbuna, they are facultative opportunists as well as specialist feeders.

- (iv) Populations of the different rocky islands of Lake Victoria are isolated and it appears that little migration occurs between them as the fishes show a reluctance to cross the inimical deep habitats that separate islands. Limited migration does occur, however, as Van Oijen *et al.* (1981) found that a rocky jetty which was situated more than 100 m from the nearest rocky shore was inhabited by *Haplochromis nigricans* within months of its construction.

Another example of parallel evolution is demonstrated by *Paralabidochromis victoriae* Greenwood, 1956. This Lake Victoria species is so similar to *Labidochromis vellicans* of Lake Malawi with regard to its dentition, its jaw structure and general morphology that it could have been placed in the same genus. However, as the two species are endemic to different lakes and have separate phylogenies, Greenwood (1956) chose to erect the genus *Paralabidochromis* for the Lake Victoria species. Only one specimen of *P. victoriae* has been found and it is not known whether the species frequents rocky zones, but as it differs from the other rock dwellers in that it lacks the minute scalation of chest, nape and cheek (Lewis 1982) it is conceivable that it is not a member of the rocky community.

Lake Malawi and Lake Tanganyika are both deep, narrow, long rift valley lakes with clear water and fairly extensive rocky shores. These lakes do not share a single cichlid species, but the unique cichlid fauna of each exhibits several striking examples of convergent evolution. Both lakes support speciose, colourful communities of small rock-dwelling fishes whose members appear to fill very similar ecological roles in each lake and many have strong morphological parallels. Indeed the close similarities of the fishes of these two lakes have occasioned comment before (Regan 1921, 1922; Fryer & Iles 1972; Lowe-McConnell 1975; Stiassny 1980; Lewis 1981; Yamaoka 1982). This remarkable degree of parallelism is well illustrated by the *Petrochromis* species of Lake Tanganyika which are very similar morphologically (particularly with regard to dentition), behaviourally and ecologically to the *Petrotilapia* species of Lake Malawi (Fryer & Iles 1972; Liem 1980; Yamaoka 1982). Similarly, the genus *Tropheus* closely resembles members of the *Pseudotropheus tropheops* species-complex, as indicated by Regan (1921) when he erected the genus *Pseudotropheus*. In addition, the *Labidochromis* species of Lake Malawi have much in common with *Tanganicodus irsacae* of Lake Tanganyika.

A further parallel is that populations of rock-frequenting cichlids of Lake Tanganyika are usually restricted to particular geographic localities, being isolated from one another by unsuitable habitats. A particularly good example is provided by *Tropheus moori* which exists as a number of different geographic races, or perhaps subspecies, each differing from the others with respect to coloration (Marlier 1959; Matthes 1962; Fryer & Iles 1972). In addition, a number of sibling species occur sympatrically (Marlier 1959; Fryer & Iles 1972). Thus, in many respects the rock-frequenting fishes of the three Great Lakes of Africa exhibit a remarkable degree of parallelism at the community level, at

the species level and with regard to species proliferation and adaptive radiation.

Furthermore, the restriction of cichlid populations to habitat islands strongly suggests that intralacustrine allopatric speciation is the main cause of the considerable species richness in the rift valley lakes, and was a contributory factor to speciation in Lake Victoria.

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