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# A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi

A.J. Ribbink, B.A. Marsh, A.C. Marsh, A.C. Ribbink and B.J. Sharp

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# A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi

A.J. Ribbink, B.A. Marsh, A.C. Marsh, A.C. Ribbink and B.J. Sharp

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Most aquarium fishes exported from Lake Malawi are cichlids of 10 rock-frequenting genera collectively referred to by their Chitonga name, Mbuna. These fishes provide a classical example of intralacustrine allopatric speciation. The distribution of 196 species is given with notes on habitat preferences, depth distribution and behaviour. Considerable emphasis is placed on coloration and markings for identification and it is argued that they are important for mate recognition. Brief notes are given on some of the other rocky shore fishes particularly in the genus *Cyrtocara*. The value of the aquarium fish resource resides principally in its species richness. Most Mbuna species are geographically restricted and stenotopic. The majority occur in the upper 20 m. Mbuna are trophic specialists, but have the ability to feed opportunistically on a variety of food resources. Resource partitioning is effected by different trophic groups. Evidence suggests that species within a particular trophic group which feed upon apparently identical food material, collect it from different microhabitats.

S. Afr. J. Zool. 1983, 18: 149–310

Die meeste van die akwariumisvisse wat vanaf die Malawimeer uitgevoer word, is sikklede van 10 rotsbewonende genera, waarna gesamentlik verwys word as Mbuna, hul Chitonga-naam. Hierdie visse toon 'n klassieke voorbeeld van binnemeerse allopatriese spesiasie. Die verspreiding van 196 spesies en notas oor hulle habitatvoorkeure, diepteverspreiding en gedrag word gegee. Daar word aansienlike klem gelê op kleure en merktekens vir identifikasie en daar word aangevoer dat dit belangrik is vir broeipaarherkenning. Kort aantekeninge word gegee betreffende ander vissoorte wat die rotsagtige kusstreke bewoon en in besonder die genus *Cyrtocara*. Die waarde van die akwariumisvisbrone berus hoofsaaklik op sy spesierikdom. Die meeste Mbuna-spesies is geografies beperk en is stenotopies. Die meerderheid kom in die boonste 20 m voor. Mbunas is trofiese spesialiste, maar het die vermoë om opportunisties te voed op 'n verskeidenheid voedselbronne. Voedselvoorraadverdeling word deur verskillende trofiese groepe bewerkstellig. Gegewens dui daarop dat spesies binne 'n bepaalde trofiese groep, wat op klaarblyklik identiese voedselitems voed, dit vanuit verskillende mikrohabitate versamel.

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## INTRODUCTION

In 1962 the first live fishes were exported from Lake Malawi to aquarists. Since then a lucrative trade in ornamental fishes has expanded so that by the mid-seventies more than 400 000 were exported annually. A group of rock-frequenting cichlid fishes belonging to 10 genera, collectively referred to by their Chitonga name Mbuna (see p.157 for details of Mbuna), form the basis of the trade. However, with the exception of the pioneering work of Fryer (1959a) on Mbuna ecology, virtually nothing is known of their biology, numerical abundance and distribution. Indeed, more than 70% of Mbuna are undescribed and the taxonomic affinities of many are uncertain. It is convenient, therefore, to categorize members of the genera *Pseudotropheus* and *Melanochromis* as species-complexes (monophyletic) and species-groups (polyphyletic). To facilitate dissemination of information, undescribed species are given descriptive names herein which have no taxonomic validity. A more comprehensive systematic treatment is forthcoming.

Although Fryer (1959a) restricted his detailed study to a 250-m stretch of rocky shore at Nkhata Bay, his brief excursions to other parts of the lake indicated that the species assemblages at different localities varied and that at least some species have very limited distributions. Exporters of ornamental fish confirmed this observation, finding that many Mbuna species are endemic to particular areas. As some of these species are restricted to tiny regions and exist in small numbers the possibility of over-exploitation was real. Therefore, to determine the effect of commercial exploitation on this natural resource and to develop an identification guide to these and other ornamental fishes, a conservation-orientated research programme was initiated by the Malawi Fisheries Department in November 1977. Part of the programme involved a survey of ornamental fishes to plot their distribution, to establish baseline data of numerical abundance and to develop a basis for identification. Our survey was restricted to Malawian waters, leaving the Tanzanian and Mozambique coasts unexplored. The results are reported here. This report also includes ecological and behavioural information which, when considered in conjunction with the zoogeographical data and historical evidence, throws light on the possible modes of speciation which may have contributed to the evolution of an estimated 400–500 species of Cichlidae which are endemic to Lake Malawi.

Lake Malawi (9°30'–14°30'S/33°52'–35°20'E), the

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third largest of the African lakes after Lake Victoria and Lake Tanganyika, lies near the southern end of the western Rift Valley in a direction slightly east of south. Lake Malawi is estimated to be between one and two million years old (Dixey 1926; 1941; Banister & Clarke 1980); it is younger than Lake Tanganyika (two to ten million years old: Lowe-McConnell 1969; Fryer & Iles 1972; Banister & Clarke 1980), but older than Lake Victoria (750 000 years old: Greenwood 1974). The lake is approximately 600 km long, has a maximum width of about 80 km and a surface area of nearly 31 000 km<sup>2</sup> (Figure 1). Its altitude above mean sea level is given as 457 m by Fryer & Iles (1972) and 471 m by Banister & Clarke (1980). The maximum depth is uncertain and is given as 704 m (Fryer & Iles 1972; Malawi Government maps 1974 edition), 758 m (Welcomme 1972) and 770 m (Beadle 1981). Although the lake is essentially a single basin it does have two deep troughs in the northern region (Banister & Clarke 1980). By virtue of its tropical setting, Lake Malawi is permanently stratified having a warm epilimnion overlying a cooler hypolimnion (Beauchamp 1953). Similarly, the surface waters are well oxygenated but become poorly oxygenated with increasing depth so that there is very little oxygen between 200–250 m and the waters beyond these depths are totally anoxic (Beauchamp 1940; 1953; Ricardo-Bertram, Borley & Trewavas 1942; Eccles 1974). The lake experiences marked seasonal variations in wind, temperature and precipitation. During the warm season (September to March) winds are light — except in squalls and thunderstorms — and usually blow from the north-east. In the cool season (April to August) strong south-easterly winds prevail often attaining 40 km h<sup>-1</sup> (Eccles 1974) and sometimes blowing at 60–70 km h<sup>-1</sup> (Ricardo-Bertram *et al.* 1942). These winds generate surface waves 3–4 m high (Eccles 1974) and currents which can be so strong around islands and rocky outcrops that divers have to return to boats by pulling themselves along ropes.

Surface temperatures vary seasonally from 23 °C in June – July to 28 °C in December – January (Eccles 1974) and we have recorded surface temperatures of 30 °C in sheltered bays on hot, windless days in December.

Seasonal fluctuations in lake level vary between 0,4 and 2,2 m; normally the lowest level is in December and the peak in May. In addition to these seasonal fluctuations longer term progressive changes have occurred. The level is believed to have fallen by about 5 m in the period 1865 to 1915 (Pike & Rimmington 1965) and records show that it rose by 7,2 m between 1915 and 1980 (Crossley 1982). During its geological history the level of Lake Malawi altered considerably (sometimes by more than 100 m) in response to climatic and tectonic events (Dixey 1926, 1941; Fryer 1959a; Crowley, Pain & Woodward 1964; Banister & Clarke 1980).

Relative to the sculptured coastline of Lake Victoria, Lake Malawi has a smooth coast with few major indentations or notable bays. About 70% of the coastline consists of gently sloping sandy beaches, vegetated areas and swamp and the remaining 30% comprises steep rocky shores. The topography of the bottom is poorly known, but trawling records of the Fisheries Department indicate that in the oxygenated regions most of the bottom is sandy or of organic ooze. Furthermore, our diving records (see below) show that about 70% of the rocky zones visited give way to sandy plains in water less than 40 m deep. From these observations we estimate that less than 5% of the potentially inhabitable

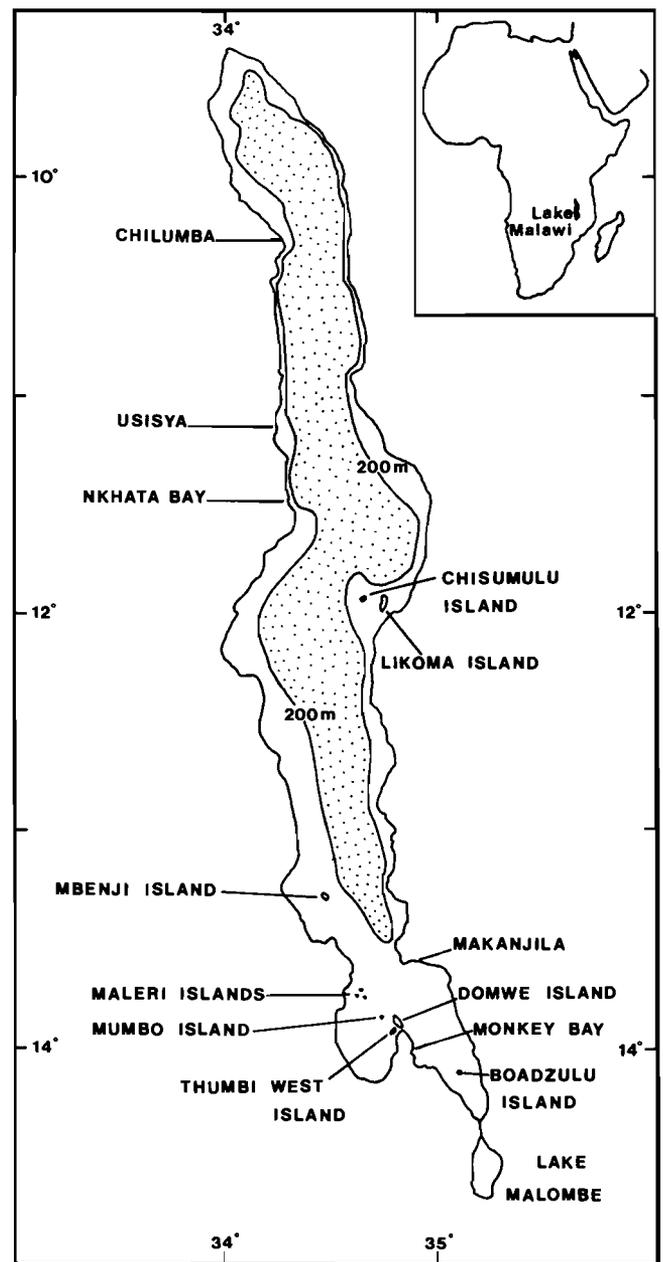


Figure 1 A map of Lake Malawi with an insert of Africa showing the location of the lake. The position of some of the more important study sites and of the 200 m depth contour are indicated.

substrata of Lake Malawi is suitable for rock-dwelling Mbuna. All islands are entirely or mainly rocky but these are separated from one another and from the mainland by sandy plains and deep water. Similarly, rocky mainland shores are broken by sandy beaches and other habitats which are unsuitable for lithophilous fishes.

Fishes were first collected for scientific purposes during David Livingstone's exploration of the western shores of Lake Malawi (then Lake Nyasa) and were described by Günther (1864). Thereafter a series of collecting trips (the history of which is given by Jackson 1961a) provided material for taxonomic studies (e.g. Günther 1893; Boulenger 1901, 1909–1916; Regan 1921; Trewavas 1931, 1935). At the time these collections were made it was not fully appreciated that many species were limited to particular localities within the lake and so inadequate attention was paid to geographic details in some instances. By contrast, in more recent taxo-

onomic studies (e.g. Eccles 1973; Eccles & Lewis 1976, 1977, 1978, 1979; Lewis 1980, 1982; Marsh 1983) attempts have been made to accurately define type localities. When Lake Malawi cichlids became popular aquarium fishes it became fashionable for aquarists to describe new species. These amateur descriptions have been criticized (Lewis 1980, 1982) as they do not give precise type localities, are of poor quality, inaccurate and create more problems than they solve. Although most work on the fishes of Lake Malawi has been taxonomic, fewer than 300 species are described and it is estimated that a further 200 await description. Most taxonomic reports contain deductions regarding the ecology and feeding behaviour of the fishes from analyses of stomach contents and from examination of the jaws, dentition, cranial musculature and gills.

Pioneering ecological work on cichlid fishes was conducted by Lowe (1952, 1953) on the tilapias, by Fryer (1959a) on the rock-frequenting fishes of Nkhata Bay and by Iles (1960) on the open-water planktivores. The studies of Turner (1977a, 1977b) and those of Eccles & Lewis (1977, 1978, 1979) have added substantially to knowledge of the sand-dwelling cichlid fishes.

It became apparent from the early collections that each of the Great Lakes of Africa contains numerous endemic species of fish. Endemism is now known to exceed 90% among the cichlid species in all the Great Lakes except Lakes Rudolf and Albert (Greenwood 1973). In Lake Malawi cichlid endemism is greater than 98%, although the proportion of endemic species is lower in other families of fishes. The 'explosive speciation' of the fishes within the Great Lakes of Africa has been such that Lakes Victoria, Tanganyika and Malawi each contain more species than any other lake in the world (Fryer & Iles 1972; Greenwood 1974).

There has been considerable speculation and debate about the ways in which intralacustrine speciation may have taken place (see review by Fryer & Iles 1972, and comments by Greenwood 1974 and Fryer 1977). Indeed, as early as 1913, Plate (cited by Greenwood 1974) suggested that the cichlid fishes of Lake Tanganyika might show a mode of speciation which differed from the usual kind. Speciation within the lakes is no longer considered to have taken place in inexplicable ways, but many unresolved problems still remain. Adaptive radiation and speciation within these lakes is so impressive that Fryer (1972) considers that, 'from an evolutionary point of view, they (*the fishes of the Great Lakes*) are vastly more illuminating than the two remarkable groups of birds, Darwin finches of the Galapagos Islands and the Honeycreepers of Hawaii' (italics are ours). This view is shared by Greenwood (1973) who states 'the cichlid fishes are more outstanding than the better-known Galapagos finches'.

Although there are 10 families of fishes in Lake Malawi, the Cichlidae dominate the ichthyofauna in an ecological and taxonomic sense and, as in the other Great African Lakes, they show a wider spectrum of adaptive radiation than all other families combined. Only one non-cichlid (*Synodontis njassae* Keilhack, 1908) is sold regularly as an aquarium fish and so despite the ecological importance of the non-cichlids they have not been included in this survey.

The cichlids are represented by two groups: the tilapiines of which there are seven species and the haplochromines which include all other species, currently estimated at 400–500. Tilapiine fishes are seldom kept in aquaria by hobbyists and are not included in this study though *Tilapia*

*rendalli* Dumeril 1859 and *Oreochromis shiranus* (Boulenger 1896) were occasionally found on rocky shores. Thus, it is from the haplochromines that virtually all the ornamental fish are drawn for export and it is on this group that the survey focussed.

The haplochromines are trophic specialists which have undergone spectacular adaptive radiations (Fryer & Iles 1972; Greenwood 1974) and are represented in Lake Malawi by 23 genera of which the most speciose genus is *Cyrtocara* (Greenwood 1979b), formerly referred to as *Haplochromis*. Jackson (1961a) lists 21 of the haplochromine genera of Lake Malawi; the remaining two are *Astatotilapia* (Greenwood 1979b) and *Iodotropheus* Oliver & Loiselle, 1972.

Lake Malawi haplochromines are considered to have originated from a fluvialite, generalized, ancestral form not unlike the present day *A. calliptera* (Regan 1921; Trewavas 1935; Fryer & Iles 1972). However, Greenwood (1979b) believes that these haplochromines are of polyphyletic origin and that lineages related to *Thoracochromis* as well as to *Astatotilapia* and even to *Chetia* and *Serranochromis* may have contributed to the group. The haplochromines have been referred to collectively as a 'species-flock' but since they probably did not stem from a single, fairly recent ancestor the term should not be applied to the group as a whole (following Greenwood 1980). Nevertheless there are species-flocks within the group: the barracuda-like piscivores of the genus *Rhamphochromis*, the sand-dwelling members of the genus *Lethrinops*, the semi-pelagic plantivores collectively referred to by their local name Utaka (Iles 1960), the 10 genera comprising the Mbuna (Fryer 1959a) and perhaps the *Trematocranus* and *Aulonacara* species.

Fish for the aquarium trade are drawn from a number of these species-flocks, as well as some of the monotypic genera, but as the Mbuna are the most heavily exploited they were studied in the most detail. However, the other cichlids are frequently very numerous; they include all the larger cichlid predators, a number of algal grazers, benthic detritivores, planktivores, lepidophages and fishes which are adapted to feed on invertebrates. These non-Mbuna also occupy territories when breeding and caring for fry and thereby utilize space that would otherwise be available to Mbuna. Clearly, these non-Mbuna are important components of the littoral ecosystem of rocky zones.

Mbuna are small, darkly or brightly coloured, essentially lithophilous fishes (Trewavas 1935; Fryer 1959a). The species-flock comprises the following genera: *Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Iodotropheus*, *Labeotropheus*, *Labidochromis*, *Melanochromis*, *Petrotilapia*, *Pseudotropheus*.

## METHODS

### Scuba

Sampling fishes of rocky areas cannot be done effectively by pulling a net over rocks. Similarly trapping, angling, fish poisoning and electrofishing are of limited use especially in deep waters. Probably the most effective technique for studying fish of rocky habitats is by scuba diving, but this method also has limitations. For safety, and because of the decrease in effective working time at increasing depth, we limited ourselves to a maximum depth of 40 m. Although there are certain species on the rocky shores beyond this depth, most species are restricted to waters that are shallower than 40 m.

The work reported here is the result of over 3 600 man-hours on scuba.

### Catching

Nylon monofilament nets (8-mm mesh, knot to knot) with a leadline foot-rope were laid among the rocks. Nets were 10 m long and 1,5 m deep. Except when in strong currents these nets hung vertically suspended by small floats in the head rope. Fishes were chased into them by divers, removed by hand and either kept alive in keep-nets or injected with 10–20% formalin while under water. Live fishes were used for colour notes, photography or behavioural studies in aquaria. Those injected with formalin were used for analyses of stomach contents and reproductive condition.

Representatives of most species referred to here are lodged in the reference collection of the J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa.

### Transects

Numerical abundance and distribution of species according to depth were determined by means of both line and point transects.

#### Line transects

Line transects (Figure 2) were laid along 1;3;5;10;15 and 20 m depth contours. Two 6 mm diameter nylon cords, 25 m in length, held 2 m apart by a galvanized pipe at each end were used. Thus, an area of 50 m<sup>2</sup> was demarcated. Fishes within the demarcated areas were counted after waiting at least 3 min for them to recover from any diver disturbance. For most species sexually active males, in breeding dress and apparently defending territories, were counted. Typically these fishes remain close to the rocks but display in open water. As one could not always be certain that male fishes in breeding livery were actually defending territories, males in breeding dress close to the substratum which remained within the transect area were recorded as being territorial. Such an approach is probably reliable since the majority of fishes appeared undisturbed by divers, although members of the genus *Melanochromis* (e.g. *M. auratus* and *M. parallelus*) occasionally vacated their territories to follow divers. The complication caused by this behaviour was resolved by including in the enumeration those individuals whose site of origin was uncertain, but excluding those which were seen to swim into the area from elsewhere. The tendency, therefore, would be to over-estimate these species. Conversely, shy species which hid from divers are likely to have been underestimated.

Both sexes of some Mbuna species hold territories and where we were unable to distinguish between the genders both were enumerated and the text figures are annotated accordingly. On the other hand, neither sex of some species, particularly of the genus *Labidochromis* (see below), is territorial. Whenever adults were found in the transects they were counted and if we were unable to differentiate between sexes this is indicated on the text figures.

Initially, fishes were counted by several divers, but once agreement between divers was found to be good, only one diver counted. This reduced disturbance. Accuracy depended upon the diver counting only one or at most two species on each traverse of the transect. As transects were conducted during daylight hours nocturnal species are poorly represented or absent. The presence of nocturnal and cryptic species, plus large numbers of fry and juveniles



Figure 2 Divers retrieving a line transect.

within some of the areas studied was confirmed by rotenone poisoning and night dives (unpublished data).

The 50 m<sup>2</sup> line transects used during the survey could not be laid effectively over rocks larger than 3–4 m diameter, nor were fish counts in such areas accurate. Usually, therefore, line transects were not laid in areas dominated by large rocks. Such areas were sampled by observation, catching, photography and by point transects.

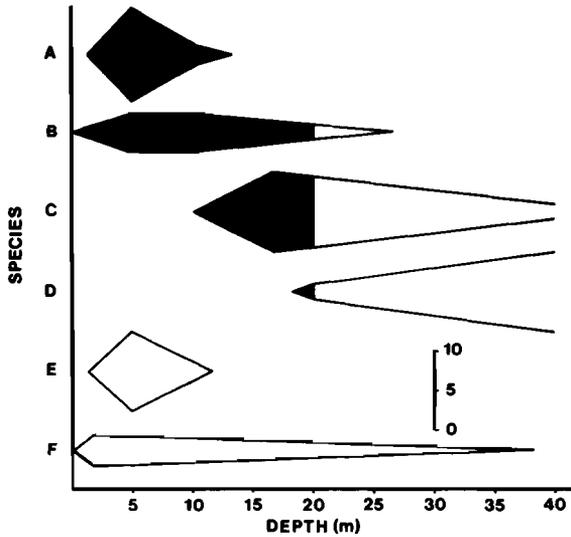
#### Point transects

The term 'point transect' is essentially the same as the 'point census' used by MacArthur (1964) to represent the number and kinds of birds that could be seen by a stationary observer at a point during a short time interval. It is also similar to 'point diversity', a term used by Slobodkin & Fishelson (1974) to describe the diversity of fishes at particular points on a coral reef.

When conducting point transects divers stopped on both descent and ascent at each 5 m depth interval to a maximum depth of 40 m to record those species present. Under conditions of poor visibility it was necessary to make short excursions along depth contours to identify fishes. We seldom spent more than 3 min at each point stop. While swimming between points a record was made of the first and last observation of each species to determine the limits of their depth distribution. At each point the relative abundance of the various species was estimated and the depth at which each species appeared to be most common was noted.

Point transects were used as deep-water continuations of line transects at 25; 30; 35 and 40 m. Line transects were not laid at these depths for to do so requires an inordinate amount of compressed air and so much time at depth that protracted periods of decompression under water become essential. Point transects were also used in place of line transects where large, steeply sloping rocks made it difficult or impossible to lay effective line transects and where time available at a particular site was too limited.

Where point transects are deep-water continuations of line transects they indicate the depth distribution of a species and whether that species becomes less numerous (Figures 3B & 3C) or more abundant (Figure 3D) beyond 20 m. Point transects are unshaded in the figures to indicate that they represent extrapolated estimates rather than accurate counts. Where point transects were used to replace line transects entirely the figures are totally unshaded, indicating that species abundance is estimated. The estimates and extrapolations to 50 m<sup>2</sup> are based on considerable experience of



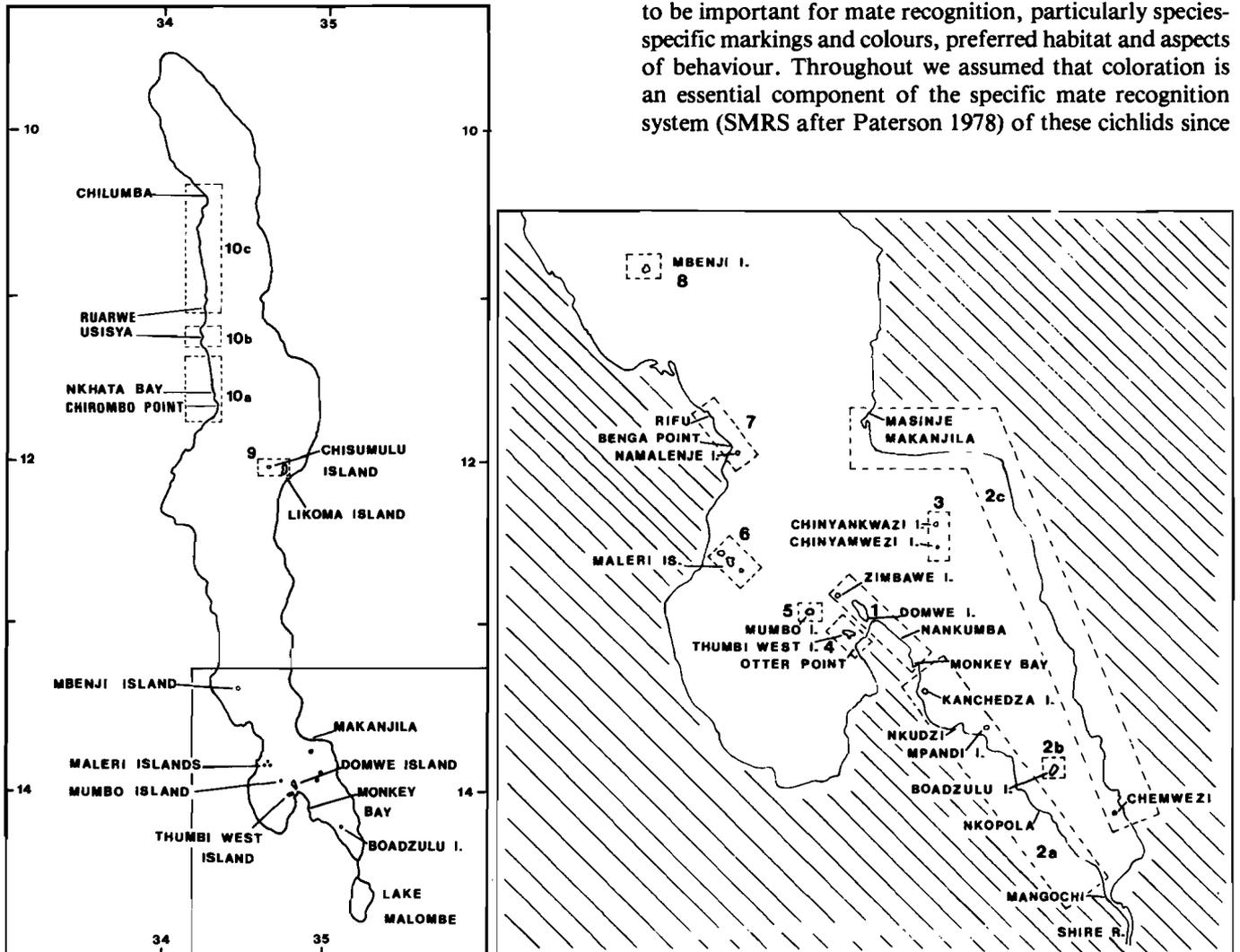
**Figure 3** The convention used to show numerical abundance of different species with depth. Solid black sections are line transects in which the individuals were counted. Open sections are point transects in which fish numbers were estimated, as for species E and F. All individuals of species A occur in the line transect. Species B extends beyond the line transect to 25 m. Species C extends from 10 m to beyond the limits of the point transect, but numbers were decreasing with depth. Species D occurs in the final line transect at 20 m, but increases in numbers beyond the 40 m limit. The vertical scale indicates the number of individuals in each 50-m<sup>2</sup> transect.

Mbuna populations observed under water and while they are unlikely to give absolute accuracy, they probably do give fair indications of relative abundance.

The fishes of the rocky shores were studied at 121 diving stations within the 14 major study areas depicted in Figure 4. Twenty-nine line transects and six point transects were conducted. The position of each diving station is given by the detailed figures in the section on fish communities (p.249 – 290). At diving stations where transects were not conducted, notes were made on the ecology, behaviour and coloration of the fishes present.

**Taxonomy and Identification**

Probably the greatest taxonomic problems among extant vertebrates are those posed by the African Cichlidae. Not only are innumerable species undescribed, but within each species-flock many closely related species are so similar that they are extremely difficult to distinguish from one another (Fryer 1956b; Fryer & Iles 1972; Greenwood 1974; Barel, van Oijen, Witte & Witte-Maas 1977; Eccles & Lewis 1977, 1978, 1979; Lewis 1980, 1982; Marsh 1983). Mayr (1969) recommends that when encountering taxonomic difficulties it is important to focus on the biological meaning of species. In the Cichlidae this is of utmost importance for it is often impossible to distinguish between preserved specimens of closely related species and reliance must be placed upon species-specific characteristics of live fishes. In our work heavy dependence was placed on those factors considered to be important for mate recognition, particularly species-specific markings and colours, preferred habitat and aspects of behaviour. Throughout we assumed that coloration is an essential component of the specific mate recognition system (SMRS after Paterson 1978) of these cichlids since



**Figure 4** The 14 major study areas in Lake Malawi are indicated by the dotted blocks and are numbered 1 – 10c.

colour is used in cichlid communication and is intensified during periods of sexual activity (Baerends & Baerends-van Roon 1950; Fryer & Iles 1972; Greenwood 1974). It has been suggested that differences in colour between populations may prevent interbreeding of those populations (Greenwood 1965, 1974; Fryer & Iles 1972; Fryer 1977). The colours of many species are so characteristic that immediate identification is possible in the field without reference to other morphological features (Marsh, Ribbink & Marsh 1981) and the importance of species-specific coloration as a taxonomic tool has already been stressed (Fryer & Iles 1972; Greenwood 1974; Barel *et al.* 1977; Lewis 1980, 1982; Van Oijen, Witte & Witte-Maas 1981).

The biological species concept (defined by Mayr 1942) encounters fewest difficulties when applied to single communities where the interactions of sympatric species (non-dimensional species: Mayr 1969) can be observed directly and morphological, ecological and behavioural differences noted, particularly whether interbreeding occurs. Holzberg (1978) and Marsh *et al.* (1981) distinguished between sympatric sibling species on the basis of differences in coloration, preferred habitat, territoriality and most important, they confirmed that assortative mating took place. In so doing, they illustrated the value of the biological approach to species recognition in Mbuna.

When dealing with allopatric populations, especially those restricted to islands (rocky zones set in sandy areas or deep water are islands of suitable habitat for Mbuna), direct comparative observations are impossible and experimental work is unlikely to conclusively indicate the taxonomic rank that should be designated to these populations. Thus morphologically similar allopatric populations which differ in coloration and perhaps also in aspects of ecology and behaviour may be demes, subspecies, semispecies, super-species, sibling species or of some other category. Furthermore, since island populations are likely to be evolving rapidly (Mayr 1969) those populations which are not already fully differentiated species are possibly incipient species at various stages of speciation. Mayr (1969) considers it preferable to treat allopatric populations of doubtful rank as subspecies since the use of trinomials conveys two important pieces of information: closest relationship and allopatry. Such an approach cannot be applied successfully to many Mbuna because while allopatry may definitely be established, the information available at present is insufficient to determine closest relationships within groups of sibling species. There are, for example, seven members of the *Pseudotropheus tropheops* species-complex at Nkhata Bay, but at Likoma Island there are four species of this complex. All species at Nkhata Bay differ from those of Likoma Island in coloration and at present none can be matched in a way which establishes closest relationship. Hence all 11 are considered to be different species. By contrast, there are three species of the *Pseudotropheus tropheops* species-complex at Chisumulu Island of which two are so similar to Likoma Island forms (see p.281) that there is little doubt that these are conspecific despite slight geographical variation.

To categorize closely related allopatric populations within the genera *Pseudotropheus*, *Melanochromis*, *Petrotilapia* and *Cynotilapia* we applied the biological species concept. In doing so we assumed that if those attributes of a population such as general anatomy, coloration and markings, preferred habitat and behaviour were the same as, or very

similar to, those of another population then species recognition would occur and the populations would interbreed if they chanced to become sympatric. On the other hand, if components of the specific mate recognition system (SMRS) differed between populations we considered that species recognition would not take place, that interbreeding would not occur naturally and that the populations were therefore distinct species. Many decisions were not clear-cut, however, as populations might share some SMRS components but not others. The problem of categorizing these populations was resolved by applying the specific mate recognition concept strictly, emphasizing differences and regarding populations that differed as being potentially non-interbreeding i.e. different species.

The remaining Mbuna genera are regarded as follows: *Cyathochromis* is a monotypic genus which has allopatric populations that show geographical variation, but since the basic markings, ground coloration and habitat preference remain little changed throughout its distribution all populations are considered to be conspecific. *Iodotropheus* is a monotypic genus which shows virtually no geographic variation and all populations are currently treated as conspecific. *Genyochromis* is a monotypic genus which shows considerable geographical variation and may eventually prove to be polytypic. At present, however, so little is known of this genus that it is convenient to treat all populations as conspecific.

The genus *Labeotropheus* has two species: *L. fuelleborni* Ahl, 1926 and *L. trewavasae* Fryer, 1956b. *L. fuelleborni* is deep-bodied, restricted to the shallows and the males are aggressively territorial. *L. trewavasae* is slender-bodied, occurs from the shallows to depths exceeding 30 m and is weakly territorial. As the differences between the species are consistent throughout their distribution range the two species are readily distinguishable and each population has a known closest relationship. For this genus, therefore, emphasis is placed on what is believed to be an intraspecific consistency in habitat preference and anatomy. It is realized, however, that the colour differences between some geographically isolated populations are so great that specific mate recognition and hence interbreeding might not occur should the populations happen to become sympatric. A number of allopatric populations might also warrant the rank of subspecies, but the detailed data necessary to make such designations are not yet available. As a temporary measure, therefore, only two species of *Labeotropheus* are recognized, each of which comprises a number of differently coloured, geographically isolated populations.

The genus *Labidochromis* was revised by Lewis (1982) and his diagnoses are followed.

No allopatric populations of the genus *Gephyrochromis* were found and so the problem of categorization does not arise.

Undescribed taxa are given descriptive names which are presented in quotation marks to indicate that the names have no taxonomic validity. This form of descriptive annotation is preferred to the use of numerals or letters as it facilitates communication. The same temporary nomenclatural system was developed independently by a research team working on the haplochromines of Lake Victoria to resolve similar problems (Van Oijen *et al.* 1981).

Although details of colour, size, geographic distribution and ecology are given for many undescribed species it should be clear that these do not constitute formal descriptions and

that the names given in quotation marks do not conform to the rules of zoological nomenclature. Similarly, the illustrations given are aids to identification and are not for taxonomic purposes.

To facilitate identification of the fishes, descriptions of their coloration and markings are given. Most species of Mbuna show marked sexual dichromatism and so colour notes on both sexes are given. Fry and juveniles are usually coloured in the same way as adult females, but at the onset of sexual maturity the coloration of males begins to deviate from the female pattern. Thus a gradation of colours, ranging from those of females to those of males in breeding livery, occurs within a population. Colour also differs with changes in the emotional state or hierarchical position of the fish (Baerends & Baerends-van Roon 1950; Fryer & Iles 1972; Barel *et al.* 1977). The colours and markings of males are most intense when they are sexually active and it is within this relatively uniformly motivated group that individual variation is smallest. For these reasons the colours of sexually active males are given in the colour descriptions which follow. The coloration of adult females is given unless otherwise stated.

Females of at least five species (*Pseudotropheus zebra* Boulenger, 1899; *Labeotropheus fuelleborni* Ahl, 1926; *Labeotropheus trewavasae* Fryer, 1956b; *Genyochromis mento* Trewavas, 1935, and one or more members of the *Pseudotropheus tropheops* species-complex) exhibit polychromatism. Though largely restricted to Mbuna, polychromatism does occasionally occur in other fishes of Lake Malawi (Eccles pers. comm.). Furthermore, polychromatism is a feature of cichlids elsewhere in Africa (Fryer & Iles 1972; Greenwood 1974). Though it was believed that polychromatism is confined to females (Fryer & Iles 1972) it does rarely occur in males of the genus *Labeotropheus*, and among members of the *Pseudotropheus zebra* species-complex and the *P. tropheops* species-complex. *Genyochromis mento* also exhibits polychromatism, but so far only female colour morphs have been found.

Female *P. zebra* are normally blue and black barred (BB), but have an uncommon orange and black blotched (OB) form and occasionally a pure orange (O) form occurs. Males are (BB); rarely a blue and black blotched form is found

and is referred to as male OB.

*G. mento*, both species of *Labeotropheus* and several members of the *Pseudotropheus tropheops* species-complex all have an OB and O colour form, but the usual colour form is referred to as normal (N).

A guide to the terms used to describe colours and markings in this paper is given in Figure 5. The terminology conforms closely to that used by Barel *et al.* (1977) for describing colours of Lake Victoria haplochromines, but we use the terms 'bar' (following Fryer 1959a) to depict vertical stripes and 'band' to depict longitudinal stripes. 'Egg-dummies' occur on the anal fin, but similar markings on the dorsal fin are referred to as 'ocelli'. Coloration of pectoral fins is not given, except where they deviate from the transparent whitish colour characteristic of most Mbuna taxa.

Colour notes of live fishes were made under water on plastic slates or were taken from freshly caught specimens and from photographs. It is necessary to photograph cichlids in natural conditions if colours are to be accurately portrayed as these fishes change colour when they die or are handled so that many brightly coloured species become grey, brown or black. Most photographs were taken under water though some were taken in aquaria.

Nikon F2 cameras with SB5 flash units were used. For underwater photography these were housed in Hydro Oceanic Products Camera and Ikelite flash housings respectively. The cameras were powered by MD 2 motor drives and the flash units by Nicad cells. The lenses most suitable for recording these small fishes were 105 mm Nikkor for underwater photographs and a 55 mm Nikkor-macro for aquarium photographs. Photographs of underwater habitats and of divers were taken with a 24 mm Nikkor lens. Ektachrome daylight film was used.

### Food resource and feeding

Exposed rock surfaces down to at least 40 m are covered by a felt-like algal mat (Aufwuchs) which is composed of firmly attached filamentous algae (collectively referred to as *Calothrix* by Fryer 1959a). Associated with the algal strands are enormous numbers of microscopic epiphytes, principally unicellular algae, diatoms and bacteria as well

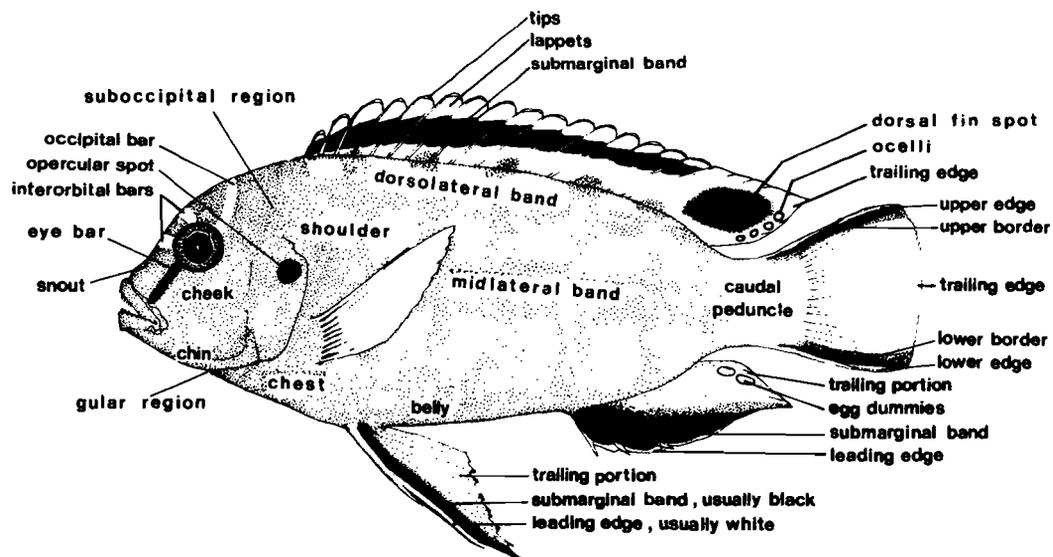


Figure 5 An illustration of the markings and the terminology used to describe them.

as protozoans and a fine organic detritus. These components of the Aufwuchs adhere loosely to or live among the firmly attached filamentous algae and are termed 'loose Aufwuchs' by Fryer (1959a). This term is also used here. The Aufwuchs mat also harbours a rich benthic fauna of insect larvae, small crustaceans and molluscs (see Fryer 1959a) which are referred to as benthic Invertebrata here. Benthic Invertebrata also occupy sandy regions and occur beneath the sediment mantle which covers rocks in many areas. Those areas which are wave-washed or subject to strong currents are free of sediment, but in deeper water and sheltered bays a fine sediment settles on the rocks and is sufficiently thick to cover the Aufwuchs in some areas.

Extremely little is known about the algal components of the Aufwuchs of Lake Malawi and it seems that most filamentous and unicellular algae are undescribed. Three main forms of filamentous algae were recognized in the field and microscopically, but none have been positively identified even though samples have been sent to algologists (see acknowledgements). Consequently these are referred to as C1, C2 and C3.

C1 forms a green mat which covers much of the sediment-free rocky surface in shallow water (0–10 m). It appears to be composed of a *Cladophora* species and a co-dominant, probably *Calothrix parietina*. The algal filaments of both these species are long and branching. C2 is also a shallow-water alga (0–12 m) which predominates on open rock surfaces. Its thin reddish-brown strands are unbranched and usually radiate in tufts from the points of attachment. C3 forms a coarse green algal mat in deeper water (6–40 m) and usually occurs under a thin layer of organic sediment. The dominant filamentous alga of C3 is a species of *Cladophora*.

Fryer (1959a) found that many fishes are dependent upon Aufwuchs as a primary food resource and are anatomically and behaviourally specialized to feed mainly upon particular components of the algal mat. Some species brush loose Aufwuchs from between the filamentous algae, others crop the filamentous algae and a number harvest the benthic Invertebrata from the Aufwuchs. Typical food-collecting behaviour can be associated with the type of food gathered and so a preliminary broad classification of fishes into trophic groups may be made from observation of feeding. Those which brush (e.g. *Petrotilapia* species; members of the *Pseudotropheus zebra* species-complex) usually gather loose Aufwuchs; those which nip and jerk are usually plucking filamentous strands from the rocks (e.g. members of the *Pseudotropheus tropheops* species-complex), those which nibble are 'mowing' the filamentous strands and also collecting loose Aufwuchs (e.g. *Labeotropheus* species); those which pick at the Aufwuchs are likely to be gathering Invertebrata (e.g. some *Labidochromis* species).

Additional trophic groups among rocky-zone fishes are those which feed mainly upon plankton (e.g. *Cynotilapia* species), scales and fins (*Genyochromis mento*), and the fry of other fishes (*Melanochromis* species and a number of *Cyrtocara* species). Inferences obtained from observations of feeding behaviour were supported in many instances by examination of stomach contents. Nine principal food categories were recorded: C1, C2, C3, loose Aufwuchs, zooplankton, phytoplankton, benthic Invertebrata, fish fry and fins/scales. Stomach contents of herbivorous and planktivorous species were spread under a coverslip on a slide and scanned thoroughly across the microscope field

to estimate the percentage cover of each food category and hence its relative abundance. The stomach contents of predatory fishes were identified and counted as individual items.

There is little doubt that the categorization of the food items is too broad to develop a detailed picture of resource subdivision, but as so little is known about the Aufwuchs, identification was a major problem and a collective grouping proved to be the only practical short-term solution.

## Terms and measurements

### Rock size

Reference is made to rock size as follows: Pebbles: 20 cm or less in diameter; small rocks: 20–50 cm diameter; medium rocks: 50–150 cm diameter; large rocks: 150–400 cm diameter; boulders: rounded or angular rocks greater than 400 cm diameter; slabs: flat rock surfaces from one or two square metres to several hundred square metres.

Nowhere are there rocks of uniform size so these categories refer to the size of rock which predominates in the area being discussed.

### Depth

Depth is expressed in metres or in descriptive terms as follows: Extreme shallows: less than 1 m depth; shallows: less than 10 m depth; middle depth: from 10 to 25 m depth; deep: from 25 to 40 m depth; extremely deep: beyond 40 m.

These terms are used to describe the distribution of the majority of individuals of a species or a group. For example, 'a fish of the shallows' must be interpreted to mean that most individuals are found in the shallows, but the normal distribution may extend beyond this.

### Length of fishes

All measurements of length are given in millimetres and refer to the standard length only. The letters which designate standard length (SL) are omitted from the text.

### Abundance

Although data on numerical abundance of species at particular stations are given in the text, the abundance of fishes is referred to more generally in the descriptive section (p.157–249) as follows:

Abundant (A), normally a dominant species in the zone being studied and usually more than 150 individuals are visible from a single point in visibility of 8–10 m;

Numerous (N), about 30–150 individuals are visible from a single point in a visibility of 8–10 m;

Common (C), fishes which are easily found within their preferred habitat, usually fewer than 30 individuals can be seen from a single point in visibility of 8–10 m;

Uncommon (U), fishes which will be found after careful looking within the preferred habitat;

Rare (R), fishes which are known to be present, but which are difficult to find.

### Intermediate habitat

Fryer (1959a) introduced the term 'intermediate habitat' to describe regions in which sand and rock are mixed. We also use this term for such habitats, but in addition we include areas in which aquatic macrophytes and sand occur among rocks. Most intermediate zones studied by us were at the sand-rock interface at the base of rocky shores, though some gradually shelving areas of mixed habitat were also found.

## RESULTS

### Cichlid fishes of rocky habitats

#### THE MBUNA

Most Mbuna genera were described by Regan (1921) and Trewavas (1935) and are distinguished from one another principally by anatomical differences resulting from the evolution of trophic specializations. The classification is based upon differences in gross morphology, in jaw structure and in differences in the pattern and anatomy of the oral and pharyngeal dentition. The resulting generic diagnoses separated reasonably the 23 Mbuna species known in 1935. Since Trewavas's study, however, many more species have been discovered (we list 196 Mbuna taxa below) and, as a fairly high proportion of these do not conform to the original generic diagnoses, a revision of Mbuna systematics is necessary. Although the present study is not principally concerned with taxonomy the results provide data on coloration, behaviour and the habitat preference characteristic of each species. These data are valuable aids to identification and hence useful taxonomic tools.

In addition to the 10 described genera we recognize several different species-groups within the genera *Pseudotropheus* and *Melanochromis*. Some of these, such as the sibling species-complexes, are closely related and represent natural groups which are undoubtedly monophyletic. These monophyletic assemblages are referred to as species-complexes. Other species are grouped because they share a number of behavioural or morphological features though they are apparently polyphyletic; these are referred to as species-groups. Since these are probably polyphyletic groups there is little doubt that members of each will be assigned eventually to different taxonomic groups. The Mbuna group is a monophyletic species-flock (Trewavas 1935; Fryer 1959a; Fryer & Iles 1972), but a number of different branches from the monophyletic stem have contributed to some of the currently recognized genera and species-groups. The term polyphyletic is used below when referring to those groups which comprise several lineages.

This survey records 196 Mbuna taxa which have been assigned to the genera and species-groups as listed in Table 1. Of these 196 taxa only 49 are previously described, but there are described species which have not been included here either because they do not occur in the area studied or their descriptions are so inadequate that we were unable to match

**Table 1** The number of species of Mbuna in each genus, species-complex and species-group

	Number of species
Genus <i>Pseudotropheus</i>	
<i>P. zebra</i> species-complex	27
<i>P. tropheops</i> species-complex	34
<i>P. williamsi</i> species-complex	8
<i>P. elongatus</i> species-group	24
<i>P.</i> 'aggressive' species-group	12
<i>P.</i> 'miscellaneous' species-group	20
Genus <i>Melanochromis</i>	
<i>M. melanopterus</i> species-complex	15
<i>M.</i> 'heterogeneous' species-group	5
Genus <i>Petrotilapia</i>	17
Genus <i>Labidochromis</i>	17
Genus <i>Cynotilapia</i>	10
Genus <i>Gephyrochromis</i>	2
Genus <i>Labeotropheus</i>	2
Genus <i>Iodotropheus</i>	1
Genus <i>Cyathochromis</i>	1
Genus <i>Genyochromis</i>	1
Total	196

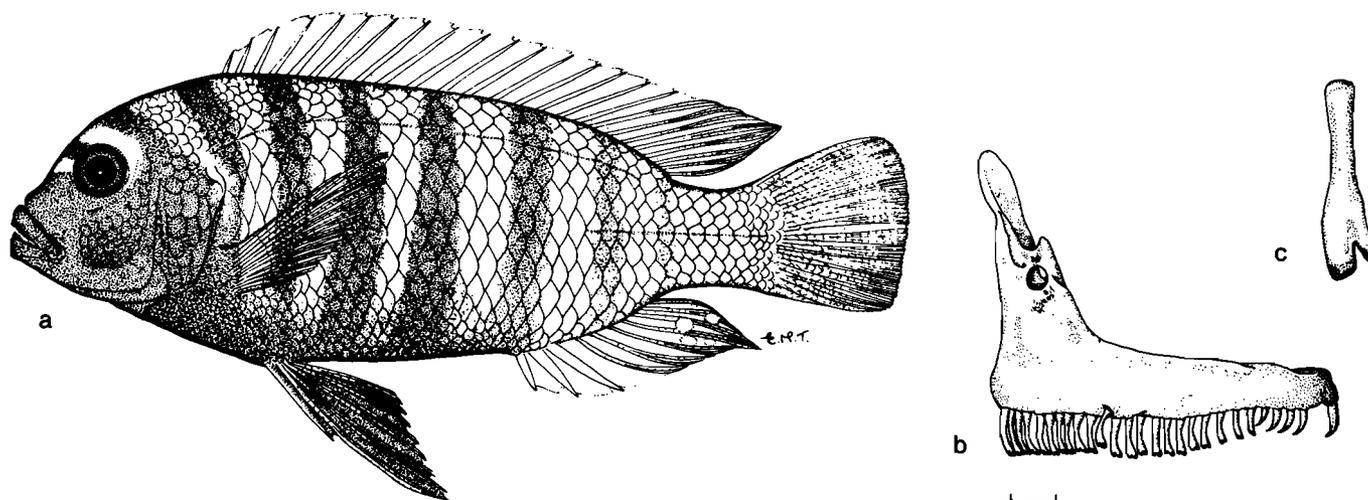
them with species which we found. These additional Mbuna are discussed in the appropriate sections below.

#### Genus *Pseudotropheus* Regan 1921

Fryer (1957: 350) considers that the genus *Pseudotropheus* is 'rather ill-defined' since it is so very similar to the genus *Gephyrochromis*. He also notes (Fryer 1956a: 88) that the distinction between some of its members and fishes of the genus *Melanochromis* is very tenuous. With the increasing number of Mbuna discovered since 1957 the need for a taxonomic revision of the genus has grown. Our division of the genus into three species-groups and three species-complexes may provide taxonomic pointers to at least some of the divisions necessary within the genus.

#### The *Pseudotropheus zebra* species-complex (Figure 6a)

All species which resemble *Pseudotropheus zebra* anatomically are included in this species-complex. These



**Figure 6** (a) *Pseudotropheus zebra*, Monkey Bay, 95 mm SL. (b) Lateral aspect of left premaxilla of *P. zebra* (Scale = 1 mm). (c) Anterior outer row tooth of *P. zebra*.

fishes have terminal mouths which they press against the rocks during feeding to collect loose Aufwuchs in the manner described by Fryer (1959a) and Holzberg (1978). Although their feeding behaviour is similar to that of *Petrotilapia* spp. and *Cyathochromis obliquidens* Trewavas, 1935, these genera differ anatomically, particularly in dentition. *P. zebra* as defined by Boulenger (1899), Trewavas (1935) and Fryer (1959a), has several rows of teeth of which the outermost are close-set and bicuspid (Figure 6b & 6c). The inner rows, three or four in number, are composed of tricuspid teeth which are long, rather mobile and widely separated. A few of the lateral teeth are conical (Figure 6b). A superficial examination of the dentition of several different members of this species-complex indicates that the teeth are not identical in all species. These differences in dentition are likely to be important anatomical features which may be used in the future to distinguish between at least some species of this complex.

Only 5 of the 27 species listed in Table 2 are described. *Pseudotropheus lanisticola* Burgess 1976 is not included in the list as it is considered to be conspecific with *Pseudotropheus livingstonii* Boulenger 1899.

### 1. *Pseudotropheus zebra* (Boulenger, 1899) (Plate 1a)

**Synopsis.** *P. zebra* is a blue and black barred species which is numerous among small and medium-sized rocks at many areas of the lake. It apparently prefers sediment-free zones of the shallow and middle depths. It exhibits

polychromatism.

**Distribution.** Nkopola (C), Nkudzi (N), Boadzulu I. (N–A), Kanchedza I. (N), Monkey Bay (N–A), Nankumba (N–A), Domwe I. (N), Zimbabwe I. (N), Thumbi West I. (N–A), Otter Point (C), Mumbo I. (N), Namalenje I. (N), West Reef (N), Eccles Reef (N), Makanjila (C), Masinje (C), Likoma I. (N–A), Chisumulu I. (N–A), Nkhata Bay (N–A), Lion's Cove (N–A), Dankanya Bay (N).

**Coloration. Monkey Bay BB males:** Body powder-blue with 8–10 black bars. Head light blue dorsally with black occipital and interorbital bars; lower half of snout as well as cheeks and opercula black, but chin blue and branchiostegal membranes light blue, almost white. Dorsal fin pale blue with yellow-orange spots on trailing edge. Caudal fin blue with yellow trailing edge. Anal fin dark blue anteriorly, pale blue posteriorly with variable number of yellow egg-dummies, but usually 3–7. Pelvic fins blue with black submarginal bands and white leading edges.

**Monkey Bay BB females:** Body and head pale blue almost white with darker blue blotches. Fins pale blue, 2–9 yellow-orange egg-dummies.

**Monkey Bay OB females:** Body and head yellow-orange though whitish-yellow in some individuals, with a variable number of black blotches and orange spots. A few orange individuals were found which did not have any black markings.

**Table 2** The members of the *Pseudotropheus zebra* species-complex. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (–), introduced (i)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	Ila	Iib	Iic	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Pseudotropheus zebra</i>	113	Likoma I.	+	+	+	+	–	+	+	–	+	–	+	+	–	–
2. <i>P. livingstonii</i>	121	SE Arm Trawl	+	+	+	+	–	+	+	–	+	–	–	–	–	–
3. <i>P. zebra</i> 'mazinzi'	94	Mazinzi	–	+	–	–	–	–	–	–	–	–	–	–	–	–
4. <i>P. elegans</i>	132	SE Arm Trawl	+	+	+	+	–	–	–	–	–	–	–	–	–	–
5. <i>P. zebra</i> 'fusco'	82	Maleri I.	–	+	–	–	–	i	–	+	–	+	–	–	–	–
6. <i>P. zebra</i> 'masinje'	77	Masinje	–	–	–	+	–	–	–	–	–	–	–	–	–	–
7. <i>P. heteropictus</i>	86	Thumbi West I.	–	–	–	–	–	+	–	–	–	–	–	–	–	–
8. <i>P. zebra</i> 'mumbo'	84	Mumbo I.	–	–	–	–	–	–	+	–	–	–	–	–	–	–
9. <i>P. zebra</i> 'blue'	82	Maleri I.	–	–	–	–	–	–	–	+	–	–	–	–	–	–
10. <i>P. zebra</i> 'red dorsal'	78	Nakantenga I.	–	–	–	–	–	–	–	+	–	–	–	–	–	–
11. <i>P. zebra</i> 'yellow throat'	102	Maleri I.	–	–	–	–	–	–	–	+	–	–	–	–	–	–
12. <i>P. zebra</i> 'black dorsal'	94	Maleri I.	–	–	–	–	–	–	–	+	–	–	–	–	–	–
13. <i>P. zebra</i> 'patricki'	74	Mbenji I.	–	–	–	–	–	–	–	+	–	+	–	–	–	–
14. <i>P. zebra</i> 'mbenji'	100	Mbenji I.	–	–	–	–	–	–	–	–	–	+	–	–	–	–
15. <i>P. lombardoi</i>	84	Mbenji I.	–	–	–	–	–	–	–	–	i	+	–	–	–	–
16. <i>P. livingstonii</i> 'likoma'	96	Likoma I.	–	–	–	–	–	i	–	–	–	–	+	–	–	–
17. <i>P. zebra</i> 'bevous'	88	Likoma I.	–	–	–	–	–	–	–	–	–	–	+	–	–	–
18. <i>P. aurora</i>	87	Likoma I.	–	–	–	–	–	i	–	–	–	–	+	–	–	–
19. <i>P. zebra</i> 'greberi'	94	Chisumulu I.	–	–	–	–	–	–	–	–	–	–	+	–	–	–
20. <i>P. zebra</i> 'cobalt'	85	Nkhata Bay	–	–	–	–	–	i	–	–	i	–	i	+	–	–
21. <i>P. zebra</i> 'gold'	94	Lion's Cove	–	–	–	–	–	–	–	–	–	–	–	+	–	+
22. <i>P. zebra</i> 'ruarwe'	79	Ruarwe	–	–	–	–	–	–	–	–	–	–	–	–	–	+
23. <i>P. zebra</i> 'chilumba'	115	Mpanga Rocks	–	–	–	–	–	–	–	–	–	–	–	–	+	+
24. <i>P. zebra</i> 'mpanga'	102	Mpanga Rocks	–	–	–	–	–	–	–	–	–	–	–	–	–	+
25. <i>P. zebra</i> 'chitande'	82	Chitande	–	–	–	–	–	–	–	–	–	–	–	–	–	+
26. <i>P. zebra</i> 'pearly'	89	Mpanga Rocks	–	–	–	–	–	–	–	–	–	–	–	–	–	+
27. <i>P. zebra</i> 'ianth'	82	Mpanga Rocks	–	–	–	–	–	–	–	–	–	–	–	–	–	+

**Geographical variation.** *P. zebra* is widespread and shows considerable geographical variation on coloration and markings. Some populations discussed here may be better categorized as subspecies or even as species if the specific mate recognition hypothesis of Paterson (1978) could be strictly and sensitively applied to these populations. For the time being, however, the populations grouped here are considered to be conspecific since they have in common a number of morphological, ecological and behavioural characteristics.

The differences in coloration of members of various populations from those of the Monkey Bay individuals are given for sexually active males, and where appropriate, for adult females.

The Zimbabwe Island form is darker than any other *P. zebra* population. The black vertical bars are broad and run into the dorsal fin where they merge to produce an almost entirely black fin (Plate 1b). The caudal anal and pelvic fins as well as the head are predominantly black. Females are almost entirely black with indistinct barring.

At Nkopola, Nkudzi, Mpandi Island and Kanchedza Island the dorsal fin is lime-yellow and the caudal and anal fins have a yellow cast (Plate 1c).

At Boadzulu Island the rayed portion of the dorsal fin is yellow. At Masinje Rocks the rayed portion of the dorsal fin has yellow spots.

At West Reef the black bars of the flanks run into the dorsal fin which has an orange rayed portion (Plate 1d).

Along the Nankumba Peninsula and at the islands of Domwe and Thumbi West the *P. zebra* populations appear identical to those of Monkey Bay, except at Mitande Rocks, off Thumbi West Island, where 40% to 60% of females are pinkish-yellow and unbarred.

At Otter Point the populations along the mainland rocky zones appear identical to those of Monkey Bay, but at Otter Island the head of males has a light blue lower half.

At Mumbo Island the dorsal fin has a yellowish tinge and a yellow-orange trailing portion. The vertical bars on the flanks penetrate a short distance into the dorsal fin.

Both sexes of the Namalenje Island population appear identical in coloration to the Monkey Bay forms.

At Likoma Island males are paler blue and at Ndumbi Rocks they are almost white.

Around the southern regions of Chisumulu Island (Same Bay, Membe Islet, Liwelo Bay) *P. zebra* males are so faintly barred that they appear almost uniformly pale blue, but the anal and pelvic fins have conspicuous black markings. Around the northern sector, at Machili Islet and Mkanila Bay, *P. zebra* males are distinctly barred. The upper half of the head is light blue and sharply divided from the lower black half. The diving stations at Chisumulu Island were too far apart to ascertain whether a colour gradation occurs or whether the differently coloured populations are abruptly divided at some intervening point.

From Chirombo Point to Dankanya Bay, the populations appear indistinguishable from those of Monkey Bay.

**Habitat.** This species lives in a variety of rocky habitats and is occasionally found over sand and among macrophytes, but it is most numerous among small-medium and medium-sized rocks where the sediment layer is thin. It is most common in 5–20 m, but its full depth range extends from the extreme shallows to at least 40 m. In many areas, however, its entire depth range is not used. For example at the point

of the Nkhata Bay peninsula *P. zebra* penetrates to 35 m, but within Nkhata Bay it is seldom seen below 20 m (p.920). One possible reason for this difference is that within Nkhata Bay the sediment layer covering the rocks below 20 m is thicker than at the point of the peninsula.

**Territoriality.** Males defend areas of about 100–200 cm diameter at Nkhata Bay (Holzberg 1978). These territories are usually centred around a hole among the rocks in which the resident spawns or takes refuge. Females, juveniles and non-territorial adult males occur in large schools, frequently numbering hundreds of individuals as well as singly or in small groups.

**Feeding.** The way in which *P. zebra* brushes loose Aufwuchs from the rocks was described by Fryer (1959a) and Holzberg (1978). Fryer (1959a) found that at Nkhata Bay *P. zebra* subsists entirely upon loose Aufwuchs. The stomachs of 36 territorial individuals caught in Monkey Bay contained on average 81% loose Aufwuchs, 16% benthic Invertebrata, 3% phytoplankton and tiny amounts of filamentous algae. Non-territorial fishes feed in the water column and their stomach contents were dominated by plankton. At times when plankton is abundant in Monkey Bay, territorial males also feed in the water column, taking large amounts of plankton. Indeed, at most areas we visited *P. zebra* fed upon plankton when it was available.

## 2. *Pseudotropheus livingstonii* (Boulenger 1899)

**Synopsis.** *P. livingstonii* lives mainly over sand where it finds refuge in the empty shells of the gastropod, *Lanistes nyassanus* (Plate 1e).

**Distribution.** Trawl samples of the Malawi Fisheries Department show that the species is common over much of the south-eastern and south-western arms of the lake. We found it at Makanjila (U), West Reef (U), Chemwezi (R), Crocodile Rocks (C), Boadzulu I. (R), Nkudzi (R), Mphandi I. (U), Kanchedza I. (U), Monkey Bay (Zambo) (C), Mvunguti (U), Otter Point (U), Thumbi West I. (R), and the Maleri Is. (R). We did not find *P. livingstonii* at Nkhata Bay and believe that Fryer (1959a) misidentified a fish we have called *P. zebra* 'gold' (its colours are given in Fryer & Iles 1972: 540).

**Coloration. Monkey Bay males:** Body violet-blue with 5 to 6 faint brownish-blue bars running across the flanks, but not onto the belly or chest; belly pale blue posteriorly, yellowish-blue anteriorly; chest golden-yellow. Head grey-blue dorsally, light blue ventrally with yellow chin and light blue interorbital bar. Dorsal fin violet-blue along its base, yellowish-orange distally with bright orange tips to the lappets. Caudal fin orange-yellow with light blue longitudinal streaks and light blue upper and lower edges. Anal fin grey-blue antero-dorsally, yellowish postero-ventrally with 1–3 yellow egg-dummies. Pelvic fins grey with black submarginal bands and white leading edges.

**Monkey Bay females:** Body pale brown basic colour with an overall blue tinge; the dorso-medial ridge, upper aspect of caudal peduncle and particularly the region above the shoulder dark brown frequently with magenta tinge; belly pale brown almost white in some individuals; 6–7 dark brown bars running about half-way across flanks from dorsum. Head grey-brown dorsally, light brown ventrally with iridescent purple-blue around the

mouth and along the edges of the opercula; chin and gular regions whitish-brown. Dorsal fin orange-yellow with blue tinge and orange lappets; rayed portion pale blue with pattern of orange and white streaks. Caudal fin pale blue with longitudinal orange and white streaks. Anal fin bright orange-yellow anteriorly, blue posterodorsally with a yellow egg-dummy. Pelvic fins hyaline posteriorly, black submarginally with white leading edges.

**Geographical variation.** The species probably forms a continuous series of local populations throughout its distribution along the sandy regions of the south-eastern and south-western arms of the lake. Nevertheless those populations in the south-eastern arm south of Nkudzi appear larger, deeper bodied and a darker blue than the other populations (unquantified observations).

**Habitat.** Lives principally over sand, but also in intermediate habitats and rarely over rock. *P. livingstonii* has been seen from 2,5–40 m depth and it has been caught in trawl samples to depths of 50 m.

**Territoriality.** The foci of *P. livingstonii* territories are the empty shells of the gastropod *Lanistes nyassanus* (Dr K. McKaye, pers. comm.). The shells are occupied by adults of both sexes, but we also found juveniles, some of which were very small, in these shells which indicates that shells are used as refuge sites from early in the lives of these fishes. When they are found away from shells, *P. livingstonii* are usually solitary or in small groups comprising fewer than five individuals.

**Feeding.** *P. livingstonii* feeds from sand, presumably taking epipelagic algae.

### 3. *Pseudotropheus zebra* 'mazinzi'

**Synopsis.** Pale blue males and brown females which inhabit a submerged rocky reef.

**Distribution.** Mazinzi Reef (N).

**Coloration. Males:** Body, head, dorsal and caudal fins pale blue. Anal and pelvic fins black with 1–3 yellow egg-dummies on anal fin.

**Females:** Body and head uniformly brown. Dorsal and caudal fins pale brown, but anal and pelvic fins dark brown to black.

**Habitat.** Over both rock and sand at the reef.

**Territoriality.** Males exclude all intruders from their territories, but appear a little more tolerant of heterospecifics than they are of conspecifics. Females, juveniles and non-territorial adult males form large schools above the reef.

**Feeding.** At the time of our visit to Mazinzi (November) virtually the entire population was feeding on plankton; a few individuals were seen to feed on epilithic Aufwuchs and from the sand.

### 4. *Pseudotropheus elegans* Trewavas, 1935

**Synopsis.** A large sand-dwelling species common in trawl samples.

**Distribution.** It has been caught in trawl samples in the south-east and south-west arms of the lake, at Nkhotakhota and at Bandawe. Jackson (1961a) reports that the type specimen was caught by Christy at Chilumba. We found

*P. elegans* at West Reef (R), Chemwezi (C), Crocodile Rocks (C), Boadzulu I. (R), Nkudzi (R) and Mazinzi (U).

**Coloration. Mazinzi males:** Body bluish with a brown tinge, but grey along dorsal ridge; chest and belly whitish with yellow tinge in some individuals; 5–6 broad grey-brown bars; caudal peduncle yellowish-brown. Head grey-blue dorsally, grey-brown below the level of the orbit; chin whitish; branchiostegal membranes yellow; interorbital bar light blue; opercular patch black. Dorsal fin whitish-grey with yellow spines and rays, lappets white with orange tips; inter-ray membranes white basally and yellow-orange distally; in some individuals the entire rayed portion yellow-orange. Caudal fin orange-yellow with pale blue inter-ray membranes. Anal fin grey-yellow with black submarginal band and white leading edge; 1–6 yellow egg-dummies. Pelvic fins orange-yellow with black submarginal bands and white leading edges. Pectoral fins bright yellow.

**Females.** Not known.

**Habitat.** Trawl samples and diving observations indicate that *P. elegans* is a sand-dweller. It also occurs at the sand-rock interface. At Chemwezi it was one of the more common Mbuna on the rocks. We found it at 6 m depth and it has been recorded to 76 m in trawl samples.

**Feeding.** Stomach contents of 58 specimens taken from a trawl sample off Nkudzi at 30 m depth contained on average, 78% benthic Invertebrata, 12% phytoplankton, 6% zooplankton and 4% loose Aufwuchs, mainly diatoms.

**Note:** Colour notes were made from a sample of more than 250 freshly caught males. Strangely, not one of the specimens taken in the trawl sample was a female.

### 5. *Pseudotropheus zebra* 'fusco' (Plate 1f)

**Synopsis.** Bright yellow males are conspicuous fishes of the intermediate zones, females are brown.

**Distribution.** All three Maleri Is. (C–N), Mbenji I. (C), Thumbi West I. (R), Nkudzi (U) and Mazinzi Reef (U).

**Coloration. Maleri Island males:** Body and head golden-yellow. Dorsal fin pale blue with yellowish tinge. Caudal fin yellow with blue cast. Anal fin pale blue with a single bright yellow egg-dummy (occasionally two egg-dummies). Pelvic fins yellow, but black submarginally with white leading edges.

**Maleri Island females:** Body and head brown, fins pale brown.

**Geographical variation.** *P. zebra* 'fusco' at Thumbi West Island (only one individual found), Mazinzi Reef and Nkudzi are superficially indistinguishable from the Maleri Island populations. Males at Mbenji Island are a brighter yellow and the dorsal and anal fins are lighter in colour with white dorsal fin lappets. Females in all populations appear identical.

**Habitat.** This species inhabits intermediate zones and lives over sediment-covered slabs. Depth distribution is dependent on the presence of intermediate zones which it follows from 3–27 m.

**Territoriality.** Males are aggressively territorial and ritualized intraspecific fights were common in the population at the north-western shore of Maleri Island. Sand-scrape nests

were found in many territories. Females are not territorial and are evenly dispersed over the intermediate habitats tenanted by territorial males.

**Feeding.** Members of this species feed in a manner typical of the *P. zebra* group. Surprisingly therefore, stomachs of 15 individuals caught at 6 m depth at Maleri Island contained on average, 44% insect larvae, 27% zooplankton, 14% phytoplankton and only 13% loose Aufwuchs with small proportions of filamentous algae. At the time we visited Mbenji Island (March 1980) zooplankton were common and the species spent a considerable amount of time feeding in the water column.

#### 6. *Pseudotropheus zebra* 'masinje'

**Synopsis.** A small member of the *P. zebra* species-complex which inhabits the intermediate zone. Males are blue and yellow, females are brown.

**Distribution.** Masinje Rocks (U).

**Coloration. Males:** Body and head pale blue with faintly yellow belly, chest, gular region, chin and branchiostegal membranes. Fins pale blue with a yellow egg-dummy on the anal fin.

**Females:** Body and head uniformly brown with pale brown fins.

**Habitat.** Intermediate zones in 2–7 m depth.

**Territoriality.** Males hold territories over rocks and less frequently over sand where nests are usually excavated. Females form schools with juveniles and non-territorial adult males.

**Feeding.** This species was seen to feed from the rocks and to take plankton from the water column.

**Note:** This species is superficially similar to *P. zebra*, but it is smaller and not as vividly coloured.

#### 7. *Pseudotropheus heteropictus* Staeck, 1980 (Plate 1g)

**Synopsis.** A fish of the rock-sand interface at the island of Thumbi West. It resembles *P. zebra*, but is not as deep-bodied.

**Distribution.** Thumbi West I. (C–N).

**Coloration. Males:** Body pale blue with 6–8 black bars traversing the flanks anterior to the vent and 4–6 faint bars crossing the body posterior to the vent; ventral part of chest and the belly dark grey. Head pale blue occipital region, but interorbital region black with two light blue bars; mouth, cheeks, opercula and gular region dark grey-blue. Dorsal fin pale blue with a broad black submarginal band; lappets white. Caudal fin blue at base with black upper and lower borders and white edges; trailing edge black. Anal fin black with white leading edge and 3–9 bright yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Body beige with 8–9 grey-blue vertical bars, belly whitish with faint bars. Head grey-brown with blue tinge and 2 prominent light blue interorbital bars; opercular spot black; chin and branchiostegal membranes whitish-yellow, though bright yellow in some individuals. Dorsal fin grey-brown with a black submarginal band; lappets and trailing edge yellow-orange; numerous orange ocelli. Caudal fin grey-brown with dark grey up-

per and lower borders and yellow-orange trailing edge. Anal fin orange, but hyaline along its base. Pelvic fins orange with black submarginal bands and white leading edges.

**Habitat.** *P. heteropictus* lives at the sand-rock interface, over slabs, over pockets of sand among the rocks and occasionally over broken rock. It is most numerous at 15 to 25 m, but occurs from 4 m to at least 40 m depth.

**Territoriality.** Males usually hold territories over sand and dig sand-scrape nests alongside or beneath rocks. They also defend territories over slabs and occasionally over purely rocky substrata. Territories are defended mainly against conspecifics, but heterospecific intruders are not tolerated in the vicinity of the nest. Females, juveniles and non-territorial adult males occur singly, in pairs, or in small groups of 3–8 individuals.

**Feeding.** Feeding behaviour is similar to that of *P. zebra*, but takes place in sediment-rich areas.

#### 8. *Pseudotropheus zebra* 'mumbo' (Plate 1h)

**Synopsis.** A brown and beige species of the intermediate zones of Mumbo Island.

**Distribution.** Mumbo I. (C).

**Coloration. Males and females:** Body beige with 6–7 brown, wedge-shaped bars that taper towards the belly. Head beige with brown occipital and interorbital bars. Dorsal fin beige, but brown bars from the body extend across its base. Caudal fin grey-brown with a darker grey along the upper and lower borders. Anal and pelvic fins light brown with dark brown submarginal bands and white leading edges; 1–3 yellow egg-dummies on anal fin of males.

**Habitat.** This species inhabits the intermediate zone where its distribution follows the rock-sand interface in 3–25 m depth.

**Territoriality.** Males hold territories which they defend against conspecifics. Females and juveniles are usually solitary, though they occasionally occur in groups of 2–5 individuals.

**Feeding.** Members of this species were seen to feed from the Aufwuchs mat and from sandy substrata.

#### 9. *Pseudotropheus zebra* 'blue' (Plate 1i)

**Synopsis.** A small lithophilous species. Males are pale blue. Females are light brown.

**Distribution.** Maleri I. (N) and Nankoma I. (C).

**Coloration. Maleri Island males:** Body and head pale powder-blue usually without a trace of barring. Dorsal, caudal and anal fin pale blue, almost white; 1–5 yellow egg-dummies. Pelvic fins pale blue with black submarginal bands.

**Maleri I. females:** Body and head light brown, fins yellow. 2–5% females of the OB colour morph.

**Habitat.** Common among small-medium rocks between 5 and 15 m, but the depth distribution extends from 0 to 25 m.

**Territoriality.** Males are territorial and while they frequently share space with other members of the *P. zebra* species-complex, their aggression is directed almost exclusively at

conspecifics. Females, juveniles and non-territorial adults form large schools.

**Feeding.** Stomach contents of 17 territorial males contained on average 76% loose Aufwuchs, 17% phytoplankton, 5% zooplankton and 2% benthic Invertebrata. Four non-territorial fishes had their stomach contents dominated by plankton (about 60% phytoplankton and 30% zooplankton) and the remaining 10% was loose Aufwuchs.

#### 10. *Pseudotropheus zebra* 'red dorsal' (Plate 1j)

**Synopsis.** A distinctly barred, lithophilous species with a red dorsal fin.

**Distribution.** Endemic to Nakantenga I. (N) but a small population has been introduced to Maleri I. (R) by an exporter of aquarium fishes.

**Coloration. Males:** Body pale blue with 5 pitch-black bars anterior to the vent and 3–4 faint bars posterior to the vent; chest and belly black. Head black with two pale blue interorbital bars and a pale blue occipital bar. Dorsal fin orange-red and penetrated along its base by black vertical bars from the body. Caudal fin yellow-orange with blue inter-ray membranes. Anal fin light blue with 1–4 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Body blue-grey with black barring. Head black with blue-grey interorbital and occipital bars. Dorsal and caudal fins brownish-red. Anal and pelvic fins black.

**Habitat.** Occurs from 2 to 27 m over small to medium-sized rocks. It occupies essentially the same habitat as that used by *P. zebra* 'maleri-blue' at Maleri and Nankoma Islands.

**Territoriality.** Males defend territories against conspecific males only. Females, juveniles and non-territorial adult males occur in schools in the water column, but were also found singly among the rocks.

**Feeding.** Stomach contents of 12 individuals caught at 4–8 m depth indicated that this species had been feeding on loose Aufwuchs (43%), plankton (40%), benthic Invertebrata (12%) and filamentous algae (5%).

#### 11. *Pseudotropheus zebra* 'yellow throat' (Plate 2a)

**Synopsis.** A large, lithophilous blue species of shallow waters with a yellow gular region.

**Distribution.** All three Maleri Is. (C–N).

**Coloration. Males:** Body sky-blue with 7–9 broad, blue bars; chest yellow ventrally. Head sky-blue with a darker blue occipital and interorbital bar; chin, gular region and branchiostegal membranes yellow. Dorsal and caudal fins pale blue with yellow tinge. Anal fin pale blue with black leading edge and 1–5 yellow egg-dummies. Pelvic fins yellow posteriorly, black anteriorly.

**Females:** Body dark brown sometimes almost black, with darker bars and yellowish chest. Head dark brown with yellow chin, gular region and branchiostegal membranes. Fins pale brown, but pelvics with black submarginal bands and an orange-yellow tinge.

**Habitat.** The preferred habitat is among small to medium-sized rocks in sediment-free zones. Members of this species are most numerous between 2 and 8 m, but rare beyond 12 m depth.

**Territoriality.** Only males hold territories, but they do not appear to be as aggressive in territorial defence as other lithophilous members of the *P. zebra* species-complex at the Maleri Islands. Females, juveniles and non-territorial males usually occur singly or in small groups.

**Feeding.** Observations of feeding behaviour suggest that this species feeds on Aufwuchs and plankton.

#### 12. *Pseudotropheus zebra* 'black dorsal' (Plate 2b)

**Synopsis.** A lithophilous fish of deep, sediment-rich habitats. Males are heavily barred with a prominent black band in the dorsal fin; females are light yellow.

**Distribution.** All three Maleri Is. (C).

**Coloration. Maleri Island males:** Body light blue with 7 conspicuous black bars anterior to the vent and 3 faint bars posterior to the vent; belly dark brown or black. Head pale blue except for a black patch on the forehead which is divided by a bright blue interorbital bar; cheek and chin rusty-red. Dorsal fin blue, but black bars of the body enter the fin to merge with the prominent black submarginal band; lappets white. Caudal fin pale blue with black margins. Anal fin black anteriorly, dusky-blue posteriorly, with 1–4 yellow egg-dummies. Pelvic fins black with white leading edges.

**Maleri Island females:** Body and head pale yellow, sometimes beige. Fins bright yellow.

**Geographical variation.** Males at Nakantenga are identical to those of Maleri Island except cheek and chin pale blue, not rusty-red. No variation of female coloration was noted.

**Habitat.** This species lives in deeper water than the other lithophilous members of the *P. zebra* species-complex at the Maleri Islands, occurring from 5 m down to the limit of the rocky zone (27 m), sometimes extending a few metres onto sand. The greatest numbers of this species are found between 15 and 20 m among broken medium-sized rocks. It also occurs over featureless slabs and occasionally over sand patches among rocks.

**Territoriality.** Males are aggressively territorial chasing both conspecifics and heterospecifics from their territories. Saucer-shaped nests are dug by those males which hold territories over sand. Females and other non-territorial members of this species are usually solitary.

**Feeding.** By virtue of the depth at which it lives, the rocks from which members of this species feed are normally covered by a layer of sediment. The stomach contents of eight individuals caught in 10 to 12 m depth at Nakantenga Island contained on average 35% loose Aufwuchs, 27% benthic crustaceans, 26% plankton, 6% insects and the remainder C<sub>1</sub> and C<sub>2</sub>.

#### 13. *Pseudotropheus zebra* 'patricki' (Plate 2c)

**Synopsis.** A shallow-water fish which lives over sand in close proximity to rocks.

**Distribution.** Maleri I. (U), Nankoma I. (U), Namalenje I. (U) and Mbenji I. (C).

**Coloration. Mbenji males:** Body pale brownish-yellow with a mustard-yellow patch on the shoulder; 5–6 brown bars traverse the flanks. Head pale brown with mustard-yellow occipital region and grey snout; two bright silvery-

blue inter-orbital bars are conspicuous features of this species. Dorsal fin yellowish-blue with yellow lappets. Caudal fin yellow-brown with longitudinal pale blue streaks and narrow, black upper and lower borders. Anal fin black anteriorly, lilac-blue posteriorly with 1–2 large, yellow egg-dummies. Pelvic fins dusky-yellow, black submarginally with white leading edges.

*Mbenji females:* The same colours as males but relatively drab.

*Geographical variation.* The populations at Namalenje Island and at the two northern Maleri Islands are a sandy-brown with faint yellow shoulders and occipital regions; they are not as intensely marked as the Mbenji Island population.

*Habitat.* Inhabits sandy areas among rocks or near to rocks in sediment-rich areas. Although it is seldom found over purely rocky habitats, it is not found more than 5 to 7 m from the rocks. *P. zebra* 'patricki' is most numerous at 3–7 m depth, but its depth distribution extends from 1–12 m.

*Territoriality.* Males are territorial and normally excavate sand-scrape nests, most frequently alongside or beneath rocks, but also in sand several metres from the nearest rocks. They are vigorous in the defence of their territories, usually directing aggression conspecifically. Females, juveniles and non-territorial adult males are normally solitary.

*Feeding.* This species feeds from sand and rock substrata and on plankton in the water column.

#### 14. *Pseudotropheus zebra* 'mbenji' (Plates 2d & 2e)

*Synopsis.* A large deep-bodied lithophilous species of Mbenji Island which exhibits polychromatism.

*Distribution.* Mbenji I. (C).

*Coloration. Males:* Body pale powder-blue with very faint traces of vertical barring. Head powder-blue with a dark blue interorbital bar. Dorsal fin yellow-orange. Caudal fin blue, usually with orange borders. Anal and pelvic fins pale blue. OB forms marbled blue on white.

*Females:* Body and head dark brown with orange-brown unpaired fins. Pelvic fins orange with thin black submarginal bands and white leading edges. OB forms whitish-yellow with black blotches.

*Habitat.* It is more common on exposed, wave-washed shores than in sheltered sediment-rich regions which suggests that it prefers sediment-free zones. Inhabits predominantly medium-sized rocks from 1 to 19 m depth, and is most numerous between 5–15 m.

*Territoriality.* Territorial aggression of males is confined almost entirely to conspecific male intruders. Females and other non-territorial individuals form schools of 10–50 fishes, often in mixed groups with *Cynotilapia* spp. and *P. lombardoi*.

*Feeding.* Territorial males do feed principally from the Aufwuchs mat within their territories, but at the time of the survey (May 1980) zooplankton was abundant and many individuals joined feeding females and juveniles in the water column.

#### 15. *Pseudotropheus lombardoi* Burgess, 1976.

*Synopsis.* Yellow males and blue females of sediment-rich areas.

*Distribution.* Endemic to Mbenji I. (C) but introduced to Namalenje I. (R) by an exporter of aquarium fishes.

*Coloration. Males:* Body bright golden-yellow with black barring which may disappear completely in highly motivated fishes. Head golden-yellow. Dorsal fin yellowish-blue, darker yellow in rayed portion; lappets whitish. Caudal fin yellow with pale blue longitudinal streaks. Anal and pelvic fins yellow. Egg-dummy bright yellow.

*Females:* The entire fish pale blue with 5 black vertical bars that extend from immediately below the dorsal fin lappets across the flanks and taper off before reaching the belly. Black occipital and interorbital bars present and black markings in the rayed part of the dorsal fin and on the caudal fin.

*Habitat.* *P. lombardoi* is usually found in areas rich in sediment and is most numerous at the sand-rock interface and over large flat rocks. However, it also occurs among medium-sized rocks. It lives from 2 to 25 m depth and is most numerous in water deeper than 10 m.

*Territoriality.* Males are strongly aggressive intraspecifically, but weakly aggressive towards heterospecific intruders. Those individuals which hold territories over sand in the intermediate zone excavate nests, usually digging beneath rocks. Females, juveniles and non-territorial adults occur singly or in small groups.

*Feeding.* *P. lombardoi* feeds on plankton and from both rocky and sandy substrata.

*Note:* Males of most haplochromines of Lake Malawi are blue when sexually active, but *P. lombardoi* is unusual in that females are blue with black barring while males are golden-yellow with black barring.

#### 16. *Pseudotropheus livingstonii* 'likoma' (Plate 2f)

*Synopsis.* Superficially resembles *P. livingstonii* and also inhabits sandy zones and intermediate areas. Juveniles take refuge in snail shells.

*Distribution.* Endemic to the southern half of Likoma I. (N), but an introduced population occurs at Thumbi West I. (R).

*Coloration. Likoma males:* Body light brown with mauve-blue flecks of colour on the scales; 6–7 mauve-brown bars of equal intensity traversing flanks, but not extending onto belly. Head light brown with iridescent mauve cheeks, lips and edges to the opercula; interorbital bar bright blue-mauve. Dorsal fin pale brown with a poorly defined narrow blue submarginal band and orange lappets; rayed portion yellowish-brown. Caudal fin light brown with pale blue rays, and an overall blue tinge. Anal fin black, with white leading edge, a hyaline area postero-dorsally and 2–3 yellow egg-dummies. Pelvic fins black with white leading edges.

*Likoma females:* Body beige with 6–7 grey-brown bars traversing flanks, but not extending onto belly. Head dark grey-brown dorsally and light brown ventrally with a blue tinge on the lips, around the mouth, on the opercular spot and on the posterior edge of the operculum. Dorsal fin hyaline with a hint of blue; lappets whitish; rayed portion pale brown. Caudal fin pale brown with light blue rays. Anal fin black with white leading edge

and 2–3 yellow egg-dummies. Pelvic fins black with white leading edges.

**Habitat.** Common in intermediate habitats and over sand, but uncommon in purely rocky environments. Usually found in water less than 15 m deep, but juveniles have been seen inhabiting the shells of *Lanistes nyassanus* down to a depth of 23 m.

**Territoriality.** Throughout most of its distribution range this species appeared to be non-territorial, normally being found in mixed schools comprising adults and subadults of both sexes. These schools usually numbered between 15 and 60 individuals, but occasionally schools of about 200 members were seen. A large group of territorial fish was found in 4–12 m depth at Ponyemba, where parallel ridges of rock run out towards Masimbwe Islet. The territorial fishes were about 2 m apart, were highly aggressive intraspecifically and their defended areas were usually at the base of the rocks and centred around sand-scrape nests. Approximately 25% of the territorial fishes defended areas which were entirely on the rocky ridges. Associated with these males were numerous females and non-territorial males which remained 2–3 m above the males in the water column, apparently feeding on plankton.

**Feeding.** *P. livingstonii* 'likoma' feeds from rock and sand substrata. The stomach contents of 13 individuals caught at Khuyu Bay contained on average, 68% benthic invertebrates, 20% loose Aufwuchs, 8% plankton and 4% C1. However, they have been seen to orientate themselves to plankton-bearing currents where they fed exclusively upon plankton. Also, during the construction of an artificial reef at Khuyu Bay this species was seen to tear wads of filamentous algae from rocks which had been collected in the extreme shallows and placed on the reef.

#### 17. *Pseudotropheus zebra* 'bevous' (Plate 2g)

**Synopsis.** An elongate member of the species-complex which inhabits the rock-sand interface.

**Distribution.** Likoma I. (U) and Chisumulu I. (U).

**Coloration.** *Likoma males:* Body blue with 8–9 narrow black bars, but belly uniformly grey-blue. Head greyish-blue with a dark grey opercular patch. Dorsal fin pale blue with a narrow black submarginal band and white lappets that are yellow-tipped. Caudal fin blue with black upper and lower borders and white edges. Anal fin blue-grey with a black submarginal band and a white leading edge, 1–4 yellow egg-dummies. Pelvic fins grey-blue with black submarginal bands and white leading edges. *Likoma females:* Body light grey with darker grey barring. Head dark grey. All fins light grey, but black submarginal bands on anal and pelvic fins.

**Geographical variation.** The males at Chisumulu Island differ from those at Likoma Island by having a yellowish chest, inconspicuous barring, a bright blue opercular patch and blue lips. The rayed portion of the dorsal fin yellow-orange. Caudal fin yellowish-blue with orange trailing edge. In some individuals the rayed portion of the dorsal fin may be darkened by a dorsal fin-spot. Pelvic fins have yellowish-white leading edges. Females resemble those of Likoma Island.

**Habitat.** Inhabits the rock-sand interface zone from 6 to

36 m, but is most numerous between 10 and 25 m.

**Territoriality.** Males defend territories over sand, among rocks, and occasionally in purely rocky environments in proximity to sandy areas. Sand-scrape nests are dug. Most aggression is directed towards conspecifics. Females are not territorial, usually occurring singly or in small groups (2–8 individuals) with other non-territorial conspecifics.

**Feeding.** Members of this species were seen to brush the Aufwuchs in a *P. zebra*-like manner. Occasionally individuals gripped the algae and jerked it from the rocks. *P. zebra* 'bevous' was also observed feeding upon zooplankton.

#### 18. *Pseudotropheus aurora* Burgess, 1976

**Synopsis.** An inhabitant of the intermediate zones of shallow water. Males blue and yellow, females brown.

**Distribution.** Endemic to the southern half of Likoma I. (C) occurring from Madimba Bay to Ulisa (Figure 55). It has also been introduced to Otter Point (U) and Thumbi West I. (U) by exporters of aquarium fishes.

**Coloration.** *Likoma Island males:* Body violet-blue dorsally, powder-blue lower flanks and belly; chest and anterior part of belly golden-yellow; 6–7 blue-grey bars present, but usually very faint in sexually active individuals. Head violet-blue dorsally with the occipital region tending to grey in some individuals; cheeks, chin, gular region and branchiostegal membranes golden-yellow; interorbital bar indistinct pale blue. Dorsal fin yellow with light blue rayed portion and an indistinct narrow, blue submarginal band. Caudal fin yellow with blue cast. Anal fin pale blue, tending to yellow posteriorly with a bright yellow egg-dummy. Pelvic fins yellow with white leading edges.

*Likoma Island females:* Body and head brown; fins beige.

**Habitat.** *P. aurora* inhabits the intermediate zones being particularly common along the rock-sand interface. Occasionally it occurs in purely rocky habitats which are close to sand. It has never been found below 8 m depth and is most numerous between 2 and 5 m.

**Territoriality.** Territories are held by males, usually over the upper surfaces of medium-sized and large rocks, but a small proportion of males occupy less prominent sites and some defend areas at the base of rocks where they dig sand-scrape nests. Females, juveniles and non-territorial adult males occur singly or in groups of up to 30 individuals.

**Feeding.** Frequently *P. aurora* were seen in schools with Utaka, *Cynotilapia afra* and *P. zebra* in the water column above the rocks where they fed on plankton. Normally, however, they fed from the rock and sand substrata.

#### 19. *Pseudotropheus zebra* 'greberi' (Plate 2h)

**Synopsis.** A deep-bodied fish of sediment-rich zones in deeper water.

**Distribution.** Chisumulu I. (C).

**Coloration.** *Males:* Body pale blue with 8–9 golden-brown bars; chest golden. Head golden with blue tinge dorsally; occipital bar golden-brown and interorbital bars light blue. Dorsal fin pale blue with white lappets and a lime-

yellow trailing edge. Caudal fin pale blue suffused with yellow. Anal fin blue with 2–7 yellow egg-dummies. Pelvic fins yellowish with narrow black submarginal bands and white leading edges.

*Females:* Body grey-blue with darker grey barring and pale grey fins.

*Habitat.* It is most numerous in sediment-rich areas between 10 and 35 m depth where it lives among small and medium-sized rocks, occasionally venturing onto slabs and large rocks.

*Territoriality.* Males defend territories against conspecifics. Females, juveniles and non-territorial adult males are usually solitary.

*Feeding.* Feeds on plankton and Aufwuchs.

### 20. *Pseudotropheus zebra* 'cobalt'

*Synopsis.* Anatomically identical to *P. zebra*, but differs in that individuals are either uniformly cobalt-blue or pure white.

*Distribution.* Endemic to the Nkhata Bay area (N) where it inhabits the rocky zone from Chirombo Point to the southern shores of Dankanya Bay. Mara Rocks (U). It has also been introduced to the islands of Likoma (R), Namalenje (R) and Thumbi West (C–N) by exporters of aquarium fishes.

*Coloration.* Most males uniformly cobalt-blue and some individuals with 6–8 faint, incomplete bars. Rarely, white individuals defend territories and, although white is the female coloration, Holzberg (1978) believes that these territorial individuals are white males. Most females pure white, but blue females also occur though they are never the brilliant blue of males (Holzberg 1978).

*Habitat.* *P. zebra* 'cobalt' inhabits areas of small and medium-sized rocks within a depth range of 0–25 m. It is most common from 3 to 10 m and appears to avoid sediment-rich areas.

*Territoriality.* Males are territorial (Holzberg 1978). Females, juveniles and non-territorial adult males usually form schools, but also occur singly among the rocks.

*Feeding.* It is assumed that, since these fishes feed in the same manner as *P. zebra* and since Fryer (1959a) considered them to be conspecific with *P. zebra* in his analysis of stomach contents, *P. zebra* 'cobalt' feeds principally upon loose Aufwuchs.

*Note:* In his study of the Mbuna at Nkhata Bay, Fryer (1959a) considered *P. zebra* to show a higher degree of polychromatism than it actually has for he believed *P. zebra* 'cobalt' to be conspecific with *P. zebra*. Holzberg (1978) showed that the BB, OB and O forms of *P. zebra* did not spawn with the white (W) and blue (B) forms of *P. zebra* 'cobalt'. He also found behavioural and ecological differences between the two species.

### 21. *Pseudotropheus zebra* 'gold' (Plate 2i)

*Synopsis.* A golden member of the species-complex. It occurs in sediment-rich areas of deeper water.

*Distribution.* Chirombo Point to Ruarwe (C) along north-western shores, but absent from Mara Rocks, Mpanga

Rocks and Chitande.

*Coloration. Nkhata Bay males:* Body gold with 8–9 brownish-blue bars. Head gold with a grey-brown snout and occipital region; two light blue interorbital bars. Dorsal and caudal fins yellow. Anal fin golden with pale blue edges and a bright yellow egg-dummy. Pelvic fins golden-yellow with black submarginal bands and light blue, almost white, leading edges.

*Nkhata Bay females:* Similar to males but dull brownish-yellow.

*Geographical variation.* Males at Lion's Cove are brighter yellow with fainter barring. At Ruarwe the bars are dark brown and the belly, chest, pelvic fins and head are black. The anal fin of the Ruarwe form is predominantly black, but retains its light blue edging.

*Habitat.* Occurs over rocks of a variety of sizes and in intermediate zones, but is most common among medium-sized and medium-large rocks of sediment-rich areas. Its full depth range is from 5 to at least 40 m and it is most numerous between 12 and 25 m.

*Territoriality.* Territorial males direct their aggression principally at conspecifics. Where territories are in the intermediate zones, sand-scrape nests are excavated. Non-territorial fishes are usually solitary but also form small groups of up to 15 individuals.

*Feeding.* This species was seen to feed from the rock surface and on plankton in the water column. Fryer (1959a) reports that its stomach contents contained loose Aufwuchs (Fryer 1959a identified this fish as *P. livingstonii*).

### 22. *Pseudotropheus zebra* 'ruarwe'

*Synopsis.* An elongate member of the *P. zebra* species-complex which inhabits the intermediate zone.

*Distribution.* Ruarwe (C).

*Coloration. Males:* Body sky-blue with 4 dark blue bars on the anterior half of the flanks and 3–4 lighter bars posteriorly. Head dark grey along the occipital region and snout; two light blue interorbital bars and a light blue occipital bar. Dorsal fin pale blue with a prominent black submarginal band which is narrow anteriorly, but broadens posteriorly; lappets light blue to almost white. Caudal fin pale blue with black upper and lower borders and white edge; rays black. Anal fin hyaline posteriorly, black submarginally with a white leading edge; 3–6 yellow egg-dummies. Pelvic fins black with white leading edges.

*Females:* Colours not recorded.

*Habitat.* Lives in the intermediate zone particularly along the rock-sand interface, but also in other regions where sand occurs between the rocks. It was found from 5 to 35 m depth, but was most common at about 20 m depth.

*Territoriality.* Males hold territories over sand where nests are dug alongside or beneath rocks. Females and other non-territorial individuals form schools of 5–30 members.

*Feeding.* This species was seen to feed from the sand, from rocks and from the water column.

### 23. *Pseudotropheus zebra* 'chilumba' (Plate 2j)

*Synopsis.* A large, deep-bodied member of the *P. zebra*

species-complex which lives among rocks in sediment-free zones. A characteristic of the species is the black submarginal band in the dorsal fin.

**Distribution.** Chilumba at Mpanga Rocks (C), Chitande (C–N) and at the base of the harbour wall (U); Ruarwe (C), Mpandi Point (U), Usisya (C) and Mara Rocks (C).

**Coloration.** *Chitande males:* Body pale blue with 4 pitch-black bars on the anterior half of the body and 4–5 faint bars on the posterior half; belly unbarred. Head pale blue with two black interorbital bars, a black occipital bar and a black line above the upper lip; gular region and branchiostegal membranes yellow. Dorsal fin pale blue with pitch-black, prominent submarginal band and light blue, almost white, lappets; trailing portion pale blue with yellow ocelli. Caudal fin pale blue. Anal fin pale blue with 1–5 yellow egg-dummies. Pelvic fins black with light blue almost white leading edges.

*Chitande females:* Body and head grey with black barring similar to that of males; gular region and branchiostegal membranes off-white, tinged with yellow. Unpaired fins light grey with a black submarginal band in the dorsal fin. Pelvic fins black with white leading edges.

**Geographical variation.** This species shows considerable geographical variation. The form at the harbour wall at Chilumba appears the same as that found at Chitande, but that at Mpanga Rocks has pale yellow, almost white chest, gular region and chin (not bright yellow); its submarginal band in the dorsal fin is narrower and does not run the entire length of the fin. At Ruarwe the species is similar to the Chitande form. At Usisya and Mpandi Point it resembles the Chitande form, but the posterior half of the dorsal fin is red. At Mara Rocks the barring is very faint, as is the submarginal band in the dorsal fin. Females are similar to the Chitande form at all sites, except Mara Rocks where the barring is inconspicuous.

**Habitat.** It is a lithophilous fish favouring medium-sized rocks in sediment-free zones; it does occur over large rocks (Mara Rocks and Mpanga Rocks) and also over small rocks (Usisya and Mpandi Point) close to sandy areas. Common between 2 and 15 m but found from the extreme shallows to at least 21 m.

**Territoriality.** Males are territorial, exhibiting mainly intraspecific aggression. Females and other non-territorial individuals usually occur in small schools, but some individuals are solitary.

**Feeding.** Seen to feed on Aufwuchs and from plankton.

#### 24. *Pseudotropheus zebra* 'mpanga' (Plate 3a)

**Synopsis.** A member of the *P. zebra* species-complex which has an orange dorsal fin and is found at Mpanga Rocks.

**Distribution.** Mpanga Rocks (C).

**Coloration.** *Males:* Body pale blue with 7–8 black bars, becoming fainter posteriorly; belly and chest black. Head black with pale blue interorbital and occipital bars. Dorsal fin orange with white lappets. Caudal fin blue basally, yellowish-blue distally with white upper and lower edges. Anal fin black, but with hyaline trailing edge and 3–8 yellow egg-dummies and a white leading edge. Pelvic fins black with white leading edges.

*Females:* Same as males, but relatively drab.

**Habitat.** It lives among medium-sized and large rocks as well as over boulders in sediment-free zones. This species is common between 2 and 25 m, but may be found in the extreme shallows and to a depth of at least 31 m.

**Territoriality.** Males are territorial, defending their territories principally against conspecifics. Females are not territorial and usually occur in schools, but may also be solitary.

**Feeding.** They were seen to feed upon Aufwuchs and plankton.

**Note:** *P. zebra* 'mpanga' is very similar to *P. zebra* and could be conspecific with it. However, it co-exists with a sibling species (*P. zebra* 'chilumba') which might have equally valid claims to conspecificity with *P. zebra*, and it inhabits a region in which the rocks are larger than those normally frequented by *P. zebra* (except for the *P. zebra* population on Zimbabwe which lives over large rocks and boulders). For the time being, therefore, the Mpanga Rocks population is categorized separately.

#### 25. *Pseudotropheus zebra* 'chitande'

**Synopsis.** A small lithophilous member of the *P. zebra* species-complex which exhibits polychromatism.

**Distribution.** Chitande (C).

**Coloration.** *Males:* Body and head sky-blue, with faint grey-blue barring on the flanks. Dorsal, caudal and anal fins pale blue with 2–5 yellow egg-dummies on the anal fin. Pelvic fins black. No OB males seen.

*Females:* Body and head grey, fins pale grey with black blotches.

**Habitat.** The preferred habitat appears to be among small and medium-sized rocks in 5–15 m depth. The total depth range of this species is from the extreme shallows where rocks are sediment-free down to at least 30 m where a heavy sediment mantle covers the rocks.

**Territoriality.** Males defend territories principally against conspecifics. Females are not territorial.

**Feeding.** It feeds from the rocks and on plankton.

#### 26. *Pseudotropheus zebra* 'pearly' (Plate 3b)

**Synopsis.** A small lithophilous member of the *P. zebra* species-complex; both sexes white.

**Distribution.** Mpanga Rocks (U) and Ruarwe (U–C).

**Coloration.** *Males:* Pearly white with bluish-white fins.  
*Females:* Creamy white.

**Habitat.** It is most common among small and medium-sized rocks, where territories are held. However, the members of this species appear to range widely to feed and are found in other rocky habitats. It occurs from the surface waters down to at least 35 m depth, but is most numerous in 4–18 m.

**Territoriality.** *P. zebra* 'pearly' is probably the least aggressive member of the *P. zebra* species-complex. Although males defend territories against conspecifics, they may leave their territories to feed. Females and other non-territorial individuals are usually solitary, but were occasionally seen

in small groups numbering less than five.

**Feeding.** Members of this species feed on Aufwuchs and plankton. *P. zebra* 'pearly' appears to be more closely tied to the rocks than other members of the *P. zebra* species-complex and does not rise more than about 0,5 m above the bottom to catch plankton.

### 27. *Pseudotropheus zebra* 'ianth' (Plate 3c)

**Synopsis.** A small lithophilous violet-grey member of the *P. zebra* species-complex.

**Distribution.** Mpanga Rocks (U).

**Coloration. Males:** Body off-white with violet tinge, 7–8 purple-brown bars. Head pale brown with violet-tinged cheeks, a grey-brown snout and occipital region and a pale bluish-white interorbital bar. Dorsal fin yellowish-brown, but rayed portion grey-brown with blue-tinged inter-ray membranes; lappets white. Caudal fin grey-brown with dark grey, almost black upper and lower borders. Anal fin black with light blue leading edge and a single large, yellow egg-dummy. Pelvic fins hyaline posteriorly, black submarginally with white leading edges.

**Females:** Similar to males, but without the violet and purple sheen.

**Habitat.** This species was found in regions where small rocks had collected among the large rocks and boulders that characterize Mpanga Rocks and were seldom seen away from these areas. It occurs from 4 to 16 m depth.

**Territoriality.** Males are aggressively territorial chasing mainly conspecifics, but also heterospecifics, some of which were much larger than themselves.

**Feeding.** Seen to feed from the Aufwuchs mat and from the water column.

### *Pseudotropheus tropheops* species-complex

*Pseudotropheus tropheops* Regan, 1921 was one of the first Mbuna to be described. A similar species was described by Ahl (1927) as *P. macrophthalmus*, and Trewavas (1935) described a closely related species, *P. microstoma*, as well as a subspecies, *P. tropheops gracilior*, leaving Regan's

species as the nominal subspecies.

Fryer (1959a) did not recognize the species and subspecies previously described and assigned them all to *P. tropheops*, arguing that the morphological differences which had been used to distinguish them were merely expressions of an unusually large degree of intraspecific variability. It is now apparent that many members of the *P. tropheops* species-complex exist (Table 3). Members of this group are recognized by the profile of the snout which descends steeply (Figure 7a). The angle at which the snout descends varies slightly from one species to the next but is nonetheless a clear distinguishing feature of the group. The mouth in most species is slightly subterminal and feeding is usually effected at an angle of about 45° to the rock surface. Algae are nipped from the rocks with a sideways and upward jerk of the head.

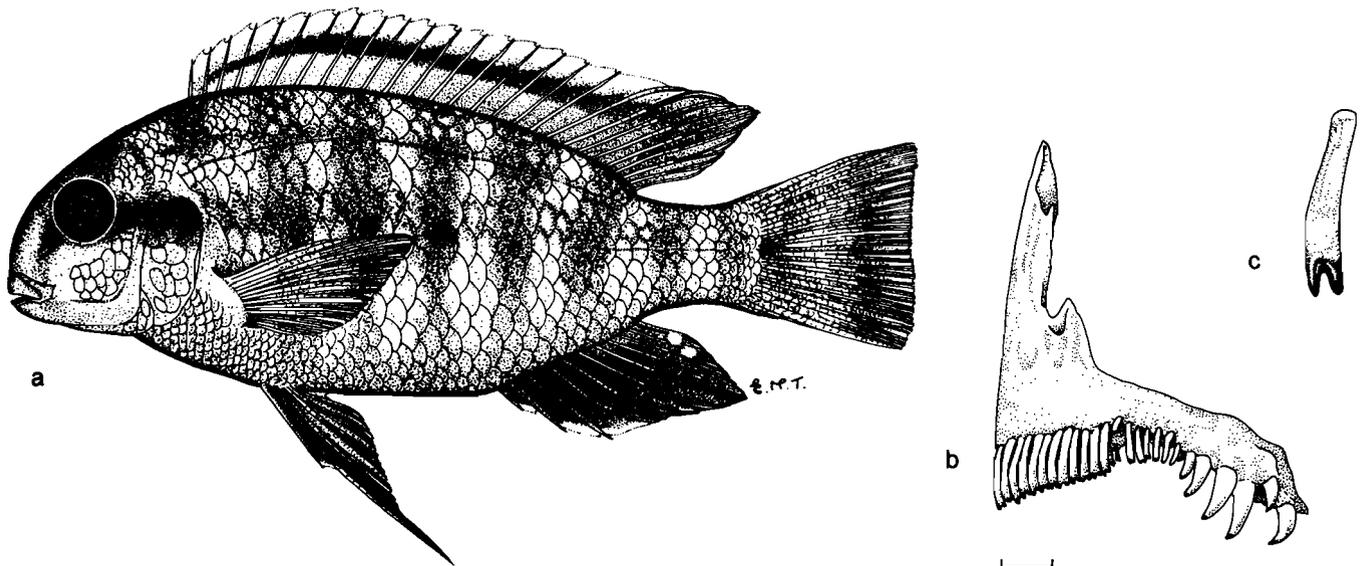
A superficial examination of the dentition of members of this species-complex indicates that all species are similar, each having an outer series of bicuspid teeth, several inner rows of tricuspid teeth and a series of large conical teeth on the lateral edges of the upper jaws (Figures 7b & c).

*P. tropheops romandi* Colombe, 1979 is reputedly from Likoma Island, though no such fishes were found there during this survey. We believe that the female is *P. tropheops* 'intermediate' from Thumbi West Island, but we are unable to identify the male (the holotype) from Colombe's description. As it is likely that two different species are included in the type series of *P. tropheops romandi* we do not use the name here. We have included in the *P. tropheops* species-complex a species which resembles *Pseudotropheus novemfasciatus* Regan, 1921 as it has a sloping head profile. This fish is referred to as *P. cf. novemfasciatus* as it has not been established positively that Regan's species and that which we recognize are the same.

### 1. *Pseudotropheus cf. gracilior* (Plate 3d)

**Synopsis.** This is an elongate broad-mouthed species of deeper waters favouring sediment-coated rocks in the south-western regions of the lake.

**Distribution.** Nkudzi (C), Kanchedza I. (U), Monkey Bay (C), Mvunguti (C), Domwe I. (C), Thumbi West I. (C) and Otter Point (C).



**Figure 7** (a) *Pseudotropheus tropheops* 'orange chest', Monkey Bay, 88 mm SL. (b) Lateral aspect of left premaxilla of *P. tropheops* 'orange chest' (Scale = 1 mm). (c) Anterior outer row tooth of *P. tropheops* 'orange chest'.

**Table 3** The members of the *Pseudotropheus tropheops* species-complex. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-), introduced (i)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	IIa	IIb	IIc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Pseudotropheus</i> cf. <i>gracilior</i>	91	Monkey Bay	+	+	-	-	-	+	-	-	-	-	-	-	-	-
2. <i>P. tropheops</i> 'orange chest'	118	Zimbabwe I.	+	+	+	-	-	+	-	+	-	-	-	-	-	-
3. <i>P. tropheops</i> 'broad mouth'	100	Chemwezi Rocks	+	+	-	+	-	+	-	+	+	-	-	-	-	?
4. <i>P.</i> cf. <i>microstoma</i>	98	Monkey Bay	+	-	-	-	-	+	-	-	-	-	-	-	-	-
5. <i>P. tropheops</i> 'red cheek'	101	Masimbwe Islet	+	-	-	-	-	i	-	-	-	-	+	-	-	-
6. <i>P.</i> cf. <i>novemfasciatus</i>	90	Monkey Bay	+	+	-	-	-	-	-	-	-	-	-	-	-	-
7. <i>P. tropheops</i> 'boadzulu'	102	Boadzulu I.	-	-	+	-	-	-	-	-	-	-	-	-	-	-
8. <i>P. tropheops</i> 'black dorsal'	98	West Reef	-	-	-	+	-	-	-	-	-	-	-	-	-	-
9. <i>P. tropheops</i> 'yellow gular'	103	Eccles Reef	-	-	-	+	-	-	-	-	-	-	-	-	-	-
10. <i>P. tropheops</i> 'chinyankwazi'	93	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
11. <i>P. tropheops</i> 'chinyamwezi'	105	Chinyamwezi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
12. <i>P. tropheops</i> 'lilac'	104	Thumbi West I.	-	-	-	-	-	+	-	-	-	-	-	-	-	-
13. <i>P. tropheops</i> 'lilac mumbo'	106	Mumbo I.	-	-	-	-	-	-	+	-	-	-	-	-	-	-
14. <i>P. tropheops</i> 'lilac maleri'	88	Maleri I.	-	-	-	-	-	-	-	+	+	-	-	-	-	-
15. <i>P. tropheops</i> 'intermediate'	89	Thumbi West I.	-	-	-	-	-	+	-	-	-	-	-	-	-	-
16. <i>P. tropheops</i> 'gold otter'	79	Otter Point	-	-	-	-	-	+	-	-	-	-	-	-	-	-
17. <i>P. tropheops</i> 'maleri blue'	91	Maleri I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-
18. <i>P. tropheops</i> 'maleri yellow'	101	Maleri I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-
19. <i>P. tropheops</i> 'mbenji blue'	92	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
20. <i>P. tropheops</i> 'mbenji yellow'	98	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
21. <i>P. tropheops</i> 'yellow chin'	115	Makulawe Point	-	-	-	-	-	-	-	-	-	-	+	-	-	-
22. <i>P. tropheops</i> 'membe'	88	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
23. <i>P. tropheops</i> 'dark'	112	Ndumbi Rocks	-	-	-	-	-	-	-	-	-	-	+	-	-	-
24. <i>P. tropheops</i> 'gold'	89	Mkanila Bay	-	-	-	-	-	-	-	-	-	-	+	-	-	-
25. <i>P. tropheops</i> 'mauve'	79	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	+	+
26. <i>P. tropheops</i> 'olive'	92	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	+	+
27. <i>P. tropheops</i> 'black'	103	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	+	+
28. <i>P. tropheops</i> 'rust'	87	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
29. <i>P. tropheops</i> 'deep'	85	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
30. <i>P. tropheops</i> 'band'	102	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
31. <i>P. tropheops</i> 'no band'	94	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
32. <i>P. tropheops</i> 'red fin'	89	Ruarwe	-	-	-	-	-	-	-	-	-	-	-	-	?	+
33. <i>P. tropheops</i> 'weed'	83	Chitande	-	-	-	-	-	-	-	-	-	-	-	+	+	+
34. <i>P. tropheops</i> 'chitande yellow'	99	Chitande	-	-	-	-	-	-	-	-	-	-	-	-	-	+

**Coloration.** *Monkey Bay males:* Body bronze-yellow at shoulder, along dorsum and on chest; flanks and caudal peduncle royal blue; barring usually not prominent though 4 anterior bars occasionally distinct, but 3 in the region of caudal peduncle normally inconspicuous. Head bronze-yellow with metallic-blue edges to operculum and chin. Snout and forehead dark blue, interorbital bars light blue. Dorsal fin yellowish-blue in spinous portion, grey-blue in rayed portion; submarginal band black, lappets yellow with white tips. Caudal fin dark blue at base, lighter blue distally, upper and lower edges white. Anal fin blue, with black submarginal band and a white leading edge; 1-3 yellow egg-dummies. Pelvic fins black with white leading edges.

*Monkey Bay females:* Two colour forms: body and head either yellow or grey-white. Black submarginal band running length of dorsal fin. Rayed part of dorsal fin and entire caudal fin covered by faint white dots.

**Geographical variation.** Little geographical variation was found. Thumbi West Island males have darker, almost

ochre-brown coloration on shoulder, dorsum and chest. The areas of blue are smaller and tend to lilac. Females at Nkudzi are brighter yellow; almost orange.

**Habitat.** This species prefers sediment-rich rocky areas and is accordingly most numerous in sheltered zones, such as Monkey Bay and Nkudzi Bay. When on exposed shores it is usually at depths beyond which the cleansing effects of wave action and surface currents are felt. It favours slabs, boulders and large rocks, but also occurs at the rock-sand interface. Its depth distribution is from the surface down to at least 40 m, but it is most numerous between 6 and 25 m.

**Territoriality.** Males defend territories among rocks. Frequently these territories are at the edge of slabs at sites where other rocks provide refuges for spawning. Some territories were also found over sand in the intermediate zones. Most of these territories centred around sand-scrape nests which had been excavated alongside or beneath rocks. Females and juveniles are not territorial, but occur singly or in small

groups. Occasionally groups of 30 individuals were seen feeding together over slabs.

**Feeding.** Stomachs of 42 specimens caught in Monkey Bay contained on average 53% loose Aufwuchs, 38% benthic Invertebrata, 7% plankton and small proportions of C1, C2, and C3. Considerable individual variation was found in the stomach contents, some fishes had eaten loose Aufwuchs exclusively while stomachs of others caught at the same time and in the same area were crammed to capacity with benthic Invertebrata, particularly copepods and insect larvae.

## 2. *Pseudotropheus tropheops* 'orange chest' (Plate 3e)

**Synopsis.** A common lithophilous species of the south-western areas of the lake.

**Distribution.** Monkey Bay (C–N), Nankumba (C), Domwe I. (C), Zimbabwe I. (C), Kanchedza I. (C), Chigubi (U), Nkudzi (C), Mpandi I. (C), Crocodile Rocks (C), Boadzulu I. (C), Chemwezi I. (C), Thumbi West I. (C), Otter Point (C), Maleri Is. (C).

**Coloration. Monkey Bay males:** Body purple-grey, sometimes with brownish cast, ground colour with 7–8 grey bars faintly visible; chest and anterior part of belly orange-yellow. Head purple-grey dorsally, with orange-yellow opercula and chin; in some individuals the orange-yellow coloration extending onto the snout. Dorsal fin yellow with a blue cast; prominent black submarginal band; lappets yellow; rayed portion yellow-grey. Caudal fin bluish-grey with yellow cast, yellow upper and lower edges and yellow trailing edge. Anal fin blue with black submarginal band and white leading edge; 1–3 yellow-orange egg-dummies. Pelvic fins yellow-blue with black submarginal bands and white leading edges.

**Monkey Bay females:** Body grey-brown with 7–8 grey bars. Head grey-brown. Dorsal fin pale grey-brown with a prominent submarginal band and yellow lappets. Caudal, anal and pelvic fins grey-brown with narrow black submarginal bands on the anal and pelvic fins. This species also has an orange-blotch form which is uncommon in Monkey Bay.

**Geographical variation.** The populations of male *P. tropheops* 'orange chest' at Nankumba, Domwe I., Kanchedza I. and Chigubi are very similar in coloration and markings to that of Monkey Bay. At Mpandi I., Nkudzi and Crocodile Rocks the yellow in the fins of males is brighter and the orange-yellow of the cheeks, chin and chest is more intense than in the Monkey Bay form. The Boadzulu I. form is dark purple-brown with an ochre-red chest, chin and shoulder. The Zimbabwe form is a very dark purple-brown. The populations at Thumbi West I., Otter Point and the Maleri Islands are generally lighter in colour than that at Monkey Bay, and they have more yellow in the fins.

In addition to the chest markings and coloration, a characteristic feature of these fishes is the conspicuous yellow or orange of the dorsal fin lappets and usually at least part of the fin's basal region. Females of all populations are similar, except those of Boadzulu I. and Zimbabwe I. which are almost black.

**Habitat.** *P. tropheops* 'orange chest' is particularly numerous among medium and medium-large rocks, in areas

which are relatively free of sediment. Its depth distribution extends from the extreme shallows to at least 33 m. The maximum numerical abundance of adults is between 5 and 18 m, but juveniles are abundant in the extreme shallows and rare beyond 8 m.

**Territoriality.** Adults of both sexes, but particularly males, hold territories on the upper surfaces of rocks, preferring sites where crevices, holes or cracks provide some refuge. Territories are so aggressively defended that algal gardens (defined on p.184) develop. Juveniles are not territorial, but form large groups which feed in the shallows.

**Feeding.** The stomach contents of 210 adults caught in Monkey Bay, contained on average 71% C2, 11% C1, 8% loose Aufwuchs. Small quantities of benthic Invertebrata and plankton comprised the remaining 10%. However, when plankton is plentiful, stomachs of members of this species may be filled with it.

## 3. *P. tropheops* 'broad mouth' (Plate 3f)

**Synopsis.** A deep-bodied species with a steeply descending snout and a wide mouth. It frequents shallow, sediment-rich rocky zones and intermediate habitats of southern Lake Malawi.

**Distribution.** Nkopola (C), Nkudzi (C), Mpandi I. (C), Chigubi (C), Kanchedza I. (C), Monkey Bay (C), Nankumba (C), Domwe I. (C), Chemwezi I. (C), Makanjila (U), Masinje (U), Thumbi West I. (U), Otter Point (U), Maleri I. (U), Nankoma I. (C), Senga Point (R), Rifu (R).

**Coloration. Monkey Bay males:** Body bluish with golden-yellow cast; shoulder and chest tarnished gold; 5 prominent black bars running from the base of the dorsal fin to the belly, but usually not onto the belly, 2–4 faint bars posterior to the vent. Head tarnished-yellow on cheek, upper operculum and the sub-occipital region; opercular spot black with iridescent green-blue anterior edge; edges of opercula lilac-blue; gular region and branchiostegal membranes yellow; snout and occipital region dark blue-grey with two conspicuous light blue interorbital bars and a faint bar traversing the snout; eye bar black (lachrymal stripe, Barel *et al.* 1977). Dorsal fin blue-grey with a black submarginal band running its full length; lappets white with orange tips; trailing portion orange tinged. Caudal fin dark blue-grey at base, lighter distally with orange tinge to trailing edge. Anal fin black anteriorly, grey distally with 2–4 yellow egg-dummies. Pelvic fins grey to hyaline with black submarginal bands and white leading edges.

**Monkey Bay females:** Body yellow-orange at chest and shoulder, otherwise grey-white with yellowish hue; a mid-lateral row of 9–12 black patches running from behind the eye onto the base of the caudal fin; a dorso-lateral row of 8–9 black patches running from the occipital region to the caudal peduncle. Head yellowish-white ventrally, greyish dorsally; branchiostegal membranes and gular region yellow; 2 blue interorbital bars. Dorsal fin hyaline with blue cast; a black submarginal band and white lappets with yellow tips; trailing edge faintly yellow with numerous small white dots. Caudal fin grey with hyaline inter-ray membranes and faintly yellow trailing edge. Anal fin dusky with a black submarginal band and a single yellow egg-dummy. Pelvic

fins faintly yellow with white leading edges and black submarginal bands.

**Geographical variation.** Males at Masinje, Makanjila and Chemwezi have a greenish hue on the body and the vertical bars are dark green, tending to black. Other than this, geographical variation is minimal. Females appear unchanged throughout their range.

**Habitat.** *P. tropheops* 'broad-mouth' occurs in water less than 8 m deep in sediment-rich areas. It is predominantly lithophilous, but also lives over sand and among plants close to rocky zones.

**Territoriality.** Males are aggressively territorial excluding all intruders, particularly conspecifics. Territories are usually at 2 to 5 m depth, on horizontal upper surfaces of large rocks and slabs, normally where a narrow groove or depression in the rock may serve as a refuge and spawning site. Occasionally, territories were found among smaller rocks and also over sand. At Nkudzi territories over sand in the intermediate zone are common. Most females are not territorial, but a small proportion do defend territories.

**Feeding.** Stomachs of 22 specimens caught in Monkey Bay contained on average 72% C1 and 18% loose Aufwuchs. Small proportions of C2, benthic Invertebrata and plankton comprised the remaining 10%.

#### 4. *Pseudotropheus cf. microstoma* (Plate 3g)

**Synopsis.** A large, deep-bodied species with a sharply curved head profile. It inhabits the rock-sand interface.

**Distribution.** Monkey Bay (C), Mvunguti (C), Domwe I. (C), Otter Point (C). Despite its presence at the nearby Domwe Island, along the rocky areas from the Ilala Gap to Chembe, at Otter Point and even over Chembe Beach, it was not found at Thumbi West Island.

**Coloration.** *Monkey Bay males:* Body royal blue traversed by 5 prominent, black bars which extend across flanks from dorsum to belly; 2 additional, but inconspicuous bars situated immediately anterior to the caudal peduncle; chest and belly black. Head black except for a blue patch on the upper operculum that extends onto the dorsal part of the head; 2 light blue interorbital bars. Dorsal fin blue with a broad black submarginal band that runs the full length of the fin and merges at the base of the fin with the vertical body bars; lappets light blue with yellow flecks; rayed portion yellowish with orange trailing edge. Caudal fin black at base, trailing edge yellow-orange. Anal fin black with grey to hyaline trailing portion and 2 large orange-yellow egg-dummies. Pelvic fins dark grey.

*Monkey Bay females:* Body grey-brown with barring similar to that of males. Head brown. Fins brown with yellowish tinges.

**Habitat.** Greatest numbers of *P. cf. microstoma* occur at the rock-sand interface and in areas where patches of sand are interspersed among rocks. It also occurs over boulders and slabs, and is rare in purely rocky habitats. It does cross sand and was one of the Mbuna species to colonize an artificial reef built at Zambo at 3–5 m depth, 150 m from rocky shores (unpublished data). It inhabits a wide depth range, often following the rock-sand interface as it descends from the extreme shallows to at least 40 m.

**Territoriality.** Males are particularly active in the defence of territories in the mornings, but in afternoons several may be found feeding alongside one another. Defended areas are over rocks or alongside rocks over sand where small cup-shaped spawning sites (nests) are dug. Females are not territorial, occurring singly or in small groups which remain close to the substratum.

**Feeding.** *P. cf. microstoma* plucks Aufwuchs from the rocks. Stomach contents of 11 adults caught in Monkey Bay contained more C3 (47%) than any other species. The fish also ate on average 26% C1 and 17% loose Aufwuchs, and the remainder of the contents comprised benthic Invertebrata and plankton.

#### 5. *Pseudotropheus tropheops* 'red cheek' (Plate 3h)

**Synopsis.** A small-mouthed species of shallow, sediment-free rocky zones. Males are characterized by rusty-red patches on head, shoulder and chest. Females are apricot-yellow.

**Distribution.** Likoma I. (C), Chisumulu I. (C), Nankumba Peninsula between Tsano Rock and Zambo Point (U). An introduced population from Likoma I. has become established at Thumbi West I. (U).

**Coloration.** *Likoma males:* Body deep blue with 6–7 dark purple bars and rusty-red splashes of colour on the shoulder and pectoral region of chest. Head bluish-yellow with a grey-blue occipital region and snout; 2 light blue interorbital bars; a rusty-red splash on cheek and another on the subopercular region; branchiostegal membranes and gular region yellowish. The four rusty-red patches on the head and body sometimes merging but usually separated by intervening areas of bluish-yellow. Dorsal fin blue, but suffused with yellow; a prominent black submarginal band running the length of the spinous portion of the fin; lappets light blue, almost white with yellow tips; rayed portion of fin grey-blue, sometimes with faint yellow spots. Caudal fin blue-grey with darker upper and lower borders and yellowish trailing edge. Anal fin black anteriorly, grey distally with 2–4 yellow egg-dummies. Pelvic fins have white leading edges, black submarginal bands and yellowish-grey trailing portions.

*Likoma females:* Body apricot-yellow with two longitudinal rows of dark brown patches, one running dorso-laterally and the other mid-laterally. Head golden-yellow. All fins yellow.

**Geographical variation.** Chisumulu Island males have lighter blue bodies than those of Likoma Island. The Nankumba form has head patches which are more orange than those of the Likoma form. Females at all sites are similar.

**Habitat.** Medium-sized, rounded rocks in sediment-free areas are preferred by this species. *P. tropheops* 'red cheek' is most numerous from the surface to about 6 m, though an individual has been recorded at 19 m.

**Territoriality.** Males hold territories over the upper surfaces of rocks from which they chase all Mbuna intruders, but they treat conspecifics most aggressively. Females are not territorial, normally occurring singly.

**Feeding.** Males feed principally from within their territories plucking at the filamentous algae. Females feed from within

the same habitat, but are usually not permitted to feed from occupied territories. Stomachs of 20 individuals caught at Likoma Island contained on average 93% C2, 6% loose Aufwuchs and 1% of C1.

*Note:* The population found between Tsano Rock and Zamboni Point is small, probably numbering less than 500 individuals. It resembles the other populations in markings, habitat preference and behaviour, but its relationship to the Likoma and Chisumulu Island populations is unknown. As the populations appear superficially similar they are regarded as conspecific for the time being.

### 6. *Pseudotropheus cf. novemfasciatus*

*Synopsis.* An inhabitant of the vegetated areas in shallow, sediment-rich areas. Males are blue-grey and olive-yellow. Females are grey and olive-yellow.

*Distribution.* Monkey Bay (C), Kanchedza I. (C), Chigubi (U), Nkudzi (C), Mpandi I. (C), Nkopola (U).

*Coloration. Monkey Bay males:* Body blue-grey with an extensive olive-yellow overlay across the shoulder and back; a further olive-yellow patch covering the pectoral region of the chest; ventral region of chest and anterior belly black; 5 incomplete dark grey bars traversing mid-lateral part of flanks. Head blue-grey with olive-yellow occipital region; chin black; interorbital bar bright iridescent blue; opercular spot iridescent blue. Dorsal fin olive-yellow with a narrow submarginal band; lappets white with yellow tips. Caudal fin dark grey with light blue inter-ray membranes, white upper and lower edges and a yellow trailing edge. Anal fin black with a white leading edge and yellow egg-dummies. Pelvic fins black with contrastingly white leading edges.

*Monkey Bay females:* Body olive-yellow, tending to light grey ventrally; 5–6 dark grey bars conspicuous. Head olive-yellow, grey ventrally with blue interorbital bar. Dorsal fin yellowish-grey with narrow black submarginal band. Caudal, anal and pelvic fins grey.

*Habitat.* *P. cf. novemfasciatus* does not occur below 6 m. It is most abundant in intermediate habitats which comprise small and medium-sized rocks in vegetated areas. Usually the areas in which it lives are rich in sediment.

*Territoriality.* Territorial males defend areas which are usually less than 1 m in diameter. Saucer-shaped sand-scrape nests occur in most territories. Females and juveniles usually occur in groups of 3–15 individuals.

*Feeding.* This species appears to collect epiphytic growths from the surface of macrophytes. It also feeds from the Aufwuchs mat growing on rocks.

### 7. *Pseudotropheus tropheops* 'boadzulu' (Plate 3i)

*Synopsis.* This species is endemic to Boadzulu Island where it inhabits water deeper than 10 m.

*Distribution.* Boadzulu I. (C).

*Coloration. Males:* Body light blue with a yellowish tinge and 7–8 darker blue bars which become progressively paler ventrally so that the belly is unbarred. Head blue-grey dorsally, cheeks and chin pale blue and opercular patch black. Dorsal fin blue with prominent black submarginal band; lappets white with yellow tips. Caudal

fin blue with yellowish inter-ray membranes, yellow trailing edges and dark grey upper and lower borders. Anal fin dark blue tending to black anteriorly; leading edge white; 2–5 yellow egg-dummies. Pelvic fins black with white leading edges.

*Females:* Body silvery-grey with darker grey bars similar to those of males. Head grey. Fins greyish with darker grey markings corresponding to black markings of males.

*Habitat.* This species inhabits rocky and intermediate, sediment-rich zones of deeper water. It is most numerous between 20 and 25 m, is seldom found in less than 10 m and may go as deep as 40 m.

*Territoriality.* Males are weakly territorial, defending areas of about 1.5 m diameter. Non-territorial males and females remain in groups of 10–15 individuals.

*Feeding.* It was observed feeding from rock surfaces and from the water column where it presumably caught plankton.

### 8. *Pseudotropheus tropheops* 'black dorsal' (Plate 3j)

*Synopsis.* This species lives on rocky reefs in south-eastern Lake Malawi. The males are blue and the females yellow.

*Distribution.* Eccles Reef (C), West Reef (C).

*Coloration. West Reef males:* Body deep blue with 6–7 grey-blue vertical bars, which may be faint in some individuals. Head blue-grey dorsally tending to brownish-grey ventrally. Dorsal fin blue with prominent black submarginal band; lappets white. Caudal fin black with white edges and a few longitudinal blue streaks. Anal fin black anteriorly becoming hyaline posteriorly with 1–3 yellow egg-dummies. Pelvic fins black with white leading edges.

*West Reef females:* Body yellow with faint grey bars. Head greyish-yellow. Dorsal fin yellow with a black submarginal band. Caudal fin grey with a yellow cast. Anal and pelvic fins dark grey, almost black.

*Geographical variation.* The individuals at Eccles Reef are very similar in coloration, markings and size to those of West Reef, but males are paler blue and females are beige.

*Habitat.* This species occupies submerged reefs which comprise mainly large rocks as well as medium-sized rocks, boulders and slabs. While occurring over all these rock types it is most numerous among medium-large rocks at 8–12 m depth. The full depth range extends from 3 m to the rock-sand interface which occurs at a maximum depth of about 18 m.

*Territoriality.* Males hold territories over rocks of all sizes, including slabs. Females are not territorial.

*Feeding.* This species was observed feeding on Aufwuchs and from the water column.

*Note:* This species lives syntopically with *P. tropheops* 'yellow gular', the males of which are also blue. They may be distinguished, however, by the presence of the prominent black submarginal bar and the lack of a yellow gular region in *P. tropheops* 'black dorsal'. Females of the latter species are yellow, not grey-brown like those of *P. tropheops* 'yellow gular'.

### 9. *Pseudotropheus tropheops* 'yellow gular'

**Synopsis.** A small-mouthed species from reefs and shallow rocky areas of the south-eastern coast of Lake Malawi. Males are blue with a yellow gular region; females are grey-brown.

**Distribution.** Masinje (C), Makanjila (U), Eccles Reef (C), West Reef (C).

**Coloration.** *West Reef males:* Body blue with faint grey barring and a yellow chest. Head greyish-blue dorsally, lighter blue ventrally with a yellow chin and gular region; branchiostegal membranes whitish-yellow. Dorsal fin bluish-yellow. Caudal fin blue-grey. Anal fin blue-grey with a black submarginal band and a white leading edge; 2–4 yellow egg-dummies. Pelvic fins yellow-gold with black submarginal bands and white leading edges.

*West Reef females:* Body grey-brown, head dark grey dorsally, yellowish-grey ventrally. Fins pale grey with dark grey submarginal bands on anal and pelvics.

**Geographical variation.** Males of the populations at Makanjila and Masinje are a paler blue than those of West Reef and Eccles Reef and have a larger patch of yellow on the chest and belly. Females are darker grey at Makanjila and Masinje.

**Habitat.** At Eccles Reef and West Reef this species is found only in purely rocky habitats since it lives in water less than 7 m deep which is much shallower than the rock-sand interface. However, at Masinje and Makanjila it occupies rocky and intermediate zones of shallow water.

**Territoriality.** Males are territorial showing considerable aggression towards conspecifics. Females, non-territorial adult males and juveniles form schools of 20–50 individuals.

**Feeding.** It feeds from the rock surfaces, the water column and, where it lives in the intermediate zones, it has been seen to feed from sand substrata.

### 10. *Pseudotropheus tropheops* 'chinyankwazi'

**Synopsis.** The only member of the *P. tropheops* species-complex at Chinyankwazi Island.

**Distribution.** Chinyankwazi I. (C).

**Coloration.** *Males:* Body blue with silvery sheen, 6–7 black vertical bars of which the anterior 3–4 are broad and dark, but posterior bars faint; chest bronzed yellow. Head dark blue-grey with a light blue interorbital bar that is flanked by black bars; lower cheek, chin, gular region and branchiostegal membranes coppery-yellow. Dorsal fin mustard-yellow with a narrow black submarginal band running about half its length; rays black, inter-ray membranes light blue; lappets bright yellow; trailing edge orange. Caudal fin dark grey at base with light blue inter-ray membranes and black rays distally; upper and lower borders black with white edges; trailing edge orange. Anal fin black anteriorly, pale blue posteriorly with single large yellow egg-dummy. Pelvic fins black with white leading edges.

*Females:* Body grey-blue, almost black in some individuals with black barring. Head dark grey. Dorsal fin grey with yellowish tinge, a thin submarginal band and a white trailing edge. Caudal fin grey. Anal and pelvic fins dark grey with a trace of yellow on the pelvics.

**Habitat.** Occurs over rocks of all sizes, but is most numerous among small and medium-sized rocks in 3–10 m. It is rare beyond 14 m (deepest record is 16 m) and in the extreme shallows.

**Territoriality.** Territorial males favour broken rock but may be found over slabs where cracks or crevices provide refuge. Territories are so aggressively defended that algal gardens were discernible in some. Females are not territorial and occur in small groups or singly.

**Feeding.** This species has a narrow mouth and feeds by nipping and plucking at the Aufwuchs. It was also seen to feed upon plankton. Stomach contents of 8 specimens contained on average 60% C1, 25% phytoplankton (which was abundant in the water in Jan./Feb. 1980), 10% zooplankton and the remainder loose Aufwuchs and C2. A chironomid larva occurred in one stomach.

### 11. *Pseudotropheus tropheops* 'chinyamwezi' (Plate 4a)

**Synopsis.** The only member of the *P. tropheops* species-complex at Chinyamwezi Island.

**Distribution.** Chinyamwezi I. (C–N).

**Coloration.** *Males:* Body ochre-yellow tending to grey-brown dorsally and light yellow ventrally, particularly yellow at the chest region; 6–7 blue-brown vertical bars. Head dark grey dorsally; lower cheek, chin, gular region and branchiostegal membranes ochre-yellow. Dorsal fin black with a yellow base. Caudal fin black with pale blue longitudinal streaks. Anal fin black with white leading edges and a yellow egg-dummy. Pelvic fins black with white leading edges.

*Females:* This species exhibits polychromatism having both normal (N) and orange-blotch (OB) females. The N females are almost totally black with a brown-yellow patch on the chest.

**Habitat.** It lives all around Chinyamwezi Island which comprises broken rocks of varying sizes, but most individuals occur among medium-sized rocks. Its depth range is from surface waters to at least 30 m, but most individuals live between 5 and 20 m.

**Territoriality.** Males are highly aggressive in the defence of their territories. Algal gardens were found in about 25% of territories. Some females were also found defending territories, but most are not territorial.

**Feeding.** Stomach contents of 5 individuals were dominated by phytoplankton which was abundant in Jan./Feb. 1980 when the specimens were caught. Small quantities of C1, C2 and loose Aufwuchs were also present.

\* \* \*

The three species discussed next occur at the islands of Thumbi West, Mumbo and Maleri. All three populations have a similar basic coloration (lilac-blue in males) and all are essentially similar anatomically, but they do differ in details of coloration and preferred habitat (including depth distribution) and so they are considered as different species for the time being.

\* \* \*

### 12. *Pseudotropheus tropheops* 'lilac' (Plate 4b)

**Synopsis.** A shallow-dwelling species of sediment-free zones where it inhabits medium-sized rocks.

*Distribution.* Thumbi West I. (C).

*Coloration. Males:* Body lilac-blue with a metallic sheen and yellowish chest and shoulder; 5 broad dark blue bars traversing the flanks but not extending on to the belly and 2–3 faint bars crossing the caudal peduncle. Barring of variable intensity extremely faint in some sexually active individuals, but conspicuous in others. Head lilac-blue with a silvery sheen on forehead and 2 grey inter-orbital bars; chin, gular region and branchiostegal membranes yellow, opercular region golden-yellow. Dorsal fin lilac-blue with pale yellow blotches below a narrow, black submarginal band; lappets light blue, almost white with yellow tips; trailing edge orange. Caudal fin pale blue with dark grey rays; upper and lower borders black with white edges; trailing edge orange. Anal and pelvic fins pale blue with black submarginal bands and white leading edges; 2–3 yellow egg-dummies on anal fin. *Females:* Body pale brown, almost beige with a row of 7–8 black blotches running dorso-laterally and another row mid-laterally. Head brown with two faint grey inter-orbital bars. Dorsal fin yellowish with a narrow black submarginal band. Caudal fin pale blue with grey rays and brown trailing edge. Anal fin dark brown, almost black anteriorly, light brown posteriorly. Pelvic fins brown.

*Habitat.* *P. tropheops* 'lilac' seldom occurs beyond 5 m depth and is most numerous in 1 to 3 m among rounded, medium-sized rocks in sediment-free zones. It has not been seen in intermediate habitats.

*Territoriality.* Only males defend territories, usually over the upper surfaces of rocks. The territories have a diameter which is frequently dictated by the size of the rock, but is usually not more than about 1.75 m. Conspecific male intruders are treated aggressively, sometimes being chased for distances of about 3 m. Heterospecifics are not tolerated within the territories, but are not normally pursued beyond the territorial boundary. Females occur singly.

*Feeding.* Filamentous algae are plucked from the rocks, predominantly from the upper surfaces.

### 13. *Pseudotropheus tropheops* 'lilac mumbo' (Plate 4c)

*Synopsis.* The only member of the *P. tropheops* species-complex found at Mumbo Island.

*Distribution.* Mumbo I. (C).

*Coloration. Males:* Body lilac-blue with an opalescent sheen, 6–7 grey bars traversing the flanks but not extending onto the belly; chest and belly orange-yellow, though extent of this colour variable, being either confined to the chest or extending back to beyond the anal fin; a separate rusty-yellow patch covering the shoulder. Head blue with silvery sheen on occipital region and dorsal aspect of snout; mouth, lower part of cheek, chin, gular region and branchiostegal membranes yellow, tending to deep gold in some individuals. Dorsal fin light blue, suffused with yellow; black submarginal band narrow anteriorly, broadening posteriorly; lappets white with yellow tips. Caudal fin dark grey. Anal fin predominantly black with blue trailing edge and a yellow patch postero-dorsally; 1–2 yellow egg-dummies. Pelvic fins yellow-orange with black leading edges. *Females:* Body light brown with a single row of 6–8

large dark brown blotches running mid-laterally. Head light brown. Dorsal and caudal fin predominantly pale brown. Anal fin black, pelvic fins black anteriorly, but orange-brown posteriorly.

*Habitat.* This species lives principally over medium-sized and large rocks, though it is also found over slabs and boulders. It is rare among small rocks and in intermediate habitats. *P. tropheops* 'lilac mumbo' occurs from the surface to at least 25 m depth, being most common between 3 and 15 m.

*Territoriality.* Males are strongly territorial. Territories are usually held among medium-sized rocks where a refuge may be found and occasionally on open rock faces. Those individuals which tenant exposed areas have been seen to spawn in the open (once alongside a vertical rock face), but most individuals spawn while hidden from view. Females are not territorial.

*Feeding.* Feeds from the upper surfaces of rocks, where it appears to crop filamentous algae. It also feeds on plankton.

### 14. *Pseudotropheus tropheops* 'lilac maleri'

*Synopsis.* A wide-mouthed species which occurs in shallow rocky areas.

*Distribution.* All three Maleri Islands (C).

*Coloration. Males:* Body lilac-blue with silvery sheen which may become violet in sexually active individuals; barring faint; chest and anterior region of belly burnished yellow, tending to orange in some individuals. Head lilac, tending to violet with opalescent sheen; mouth, chin and lower opercular region burnished yellow. Dorsal fin light blue suffused with yellow, and with white and violet flecks; submarginal band lacking but the rayed portion of the dorsal fin black; lappets white, tipped with yellow. Caudal fin blue with black rays, black upper and lower borders and white edges. Anal and pelvic fins yellowish with black submarginal bands and white leading edges; 2–5 yellow-orange egg-dummies.

*Females:* Body buff-grey with broken vertical barring giving a blotched appearance. Head buff-grey. Dorsal fin buff with a conspicuous black blotch in rayed portion. Caudal fin light brown with darker brown rays and borders. Anal and pelvic fins yellowish-brown with black submarginal bands and white leading edges.

*Habitat.* The preferred habitat of this species is among small and medium-sized rocks, though it does occur on large rocks and rarely in intermediate habitats. It is most numerous in water shallower than 4 m and is rare beyond 10 m.

*Territoriality.* Males are territorial but do not usually display over prominent rocks, preferring to remain among smaller rocks which are sometimes set among large rocks. Aggression is directed strongly towards conspecifics, but heterospecifics are chased only when they penetrate deeply into the territory. Females are not territorial.

*Feeding.* Aufwuchs is collected by nipping and plucking which suggests that filamentous algae are ingested. This species has also been seen to feed on plankton.

### 15. *Pseudotropheus tropheops* 'intermediate' (Plates 4d & 4e)

*Synopsis.* Dark blue males and bright golden-yellow females

which breed in the intermediate zones.

**Distribution.** Thumbi West I. (C).

**Coloration. Males:** Body dark blue with 7–8 black bars on the flanks. Head black. Dorsal fin dark blue with a prominent, broad, pitch-black submarginal band; lappets whitish-blue with yellow tips; trailing edge orange. Caudal fin dark blue with white upper and lower edges and usually a light blue trailing edge, but in some individuals trailing edge yellow-orange. Anal fin black with a light blue trailing edge, a white leading edge and 1–3 yellow egg-dummies. Pelvic fins black with white leading edges, dusky brown posteriorly tending to orange in a few individuals.

**Females:** Uniformly golden-yellow with a conspicuous black submarginal band running the length of the dorsal fin. Thin black submarginal bands on the anal and pelvic fins.

**Habitat.** Males occur most commonly over patches of sand among rocks and are also found over sediment-covered slabs. They are rare in other habitats. Females and juveniles, however, range more widely and are usually found in purely rocky environs, in intermediate zones and in *Vallisneria aethiopica* beds. This fish occurs to at least 25 m depth. Males are rare in water shallower than 5 m, but females and juveniles occur in the extreme shallows.

**Territoriality.** Males establish territories over patches of sand occurring among rocks and over slabs. Nests are excavated beneath or alongside rocks and are 3–5 cm deep and 14–26 cm in diameter ( $N=34$ ). Territorial aggression is directed principally toward conspecifics. Females and juveniles are not territorial.

**Feeding.** Males feed from rock and sand substrata within their territories and on plankton in the water column. Non-territorial individuals feed in rocky areas, intermediate zones, from *V. aethiopica* fronds and on plankton. Stomach contents of 5 territorial males contained on average 70% loose Aufwuchs, 20% C1, 8% C2 and 2% benthic Invertebrata.

#### 16. *Pseudotropheus tropheops* 'gold otter'

**Synopsis.** A golden-yellow species which lives over the upper surfaces of rocks in shallow water.

**Distribution.** Otter Point (C).

**Coloration. Males and females:** Body and head golden-yellow with a dusky brown patch extending from the occipital region, along the back to the caudal peduncle. Fins yellow with narrow black submarginal bands in the anals and pelvics.

**Habitat.** It lives over the upper surfaces of large rocks in 1–5 m depth.

**Territoriality.** Males are territorial, defending areas over the upper surfaces of rocks. Females and juveniles are not territorial and are normally solitary.

**Feeding.** This species was seen to feed from the Aufwuchs mat.

**Note:** Although this species is superficially similar to *P. tropheops* 'gold' of Chisumulu Islands, it is considered to be a different species since it has a different preferred habitat.

#### 17. *Pseudotropheus tropheops* 'maleri blue'

**Synopsis.** An uncommon species found at the Maleri Islands in shallow water over large rocks.

**Distribution.** Maleri I. (U), Nankoma I. (R), Nakantenga I. (R).

**Coloration. Maleri Island males:** Body blue with 4–6 broad, grey bars. Head slate-grey with a bright blue interorbital bar. Dorsal fin blue-grey with a narrow black submarginal band and white lappets. Caudal fin grey-blue at base, lighter blue distally with black streaks. Anal fin black anteriorly, grey to hyaline posteriorly; 1–3 yellow egg-dummies. Pelvic fins dusky grey posteriorly, black submarginally with white leading edges.

**Females:** Not known.

**Habitat.** This species was found over the upper surface of large, flat rocks usually in less than 5 m depth.

**Territoriality.** Males defend territories on the upper surfaces of rocks.

**Feeding.** Feeds from the Aufwuchs mat.

#### 18. *Pseudotropheus tropheops* 'maleri yellow' (Plate 4f)

**Synopsis.** A shallow-water lithophilous species of the Maleri Islands. Males are predominantly yellow; females are brownish.

**Distribution.** Maleri I. (U–C), Nankoma I. (U–C), Nakantenga I. (U–C) and Namalenje I. (U–C).

**Coloration. Maleri males:** Body mainly yellow with bright yellow chest, shoulder, pectoral region and belly, but having a grey-blue cast over the yellow elsewhere. Head bright yellow on cheek, operculum, chin and branchiostegal membranes, but snout and occipital regions dark grey. Dorsal fin yellowish-blue with faint black markings in position of submarginal band; rayed portion grey dorsally, pale blue ventrally; lappets white. Caudal fin inter-ray membranes yellow and rays blue. Anal fin pale blue with a narrow black submarginal band and white leading edge; 1–3 yellow egg-dummies. Pelvic fins golden-yellow.

**Maleri females:** Body brownish with faint black markings in position of longitudinal bands. Head grey-brown. Fins pale brown with black submarginal bands on anal and pelvic fins.

**Geographical variation.** Sexually active males at Nankoma Island, at the north-western part of Maleri Island and at Namalenje Island are more yellow than those along the southern part of Maleri Island. Those at Nakantenga have a deeper blue coloration and less yellow. Females at all sites have the same coloration.

**Habitat.** It inhabits rocky zones of both sheltered and exposed regions, favouring large rocks in shallow water. It rarely occurs below 5 m depth.

**Territoriality.** Only the males are territorial and they display over the upper surfaces of prominent rocks.

**Feeding.** This species feeds mainly from the upper surfaces of large rocks.

**Note:** This species occurs syntopically with *P. tropheops* 'lilac maleri', but may be distinguished from it by dif-

ferences in coloration. Behaviourally too, the two species differ: territorial *P. tropheops* 'maleri yellow' frequents the upper surfaces of large prominent rocks, which rise above surrounding smaller rocks, whereas *P. tropheops* 'lilac maleri' defends areas among the smaller rocks (Table 4).

**Table 4** The number of territorial *P. tropheops* 'lilac maleri' and *P. tropheops* 'maleri-yellow' found over large prominent rocks and over small and medium-sized rocks over a distance of approximately 100 m at Maleri Island (Site C; Figure 47) at 2–5 m depth

	<i>P. tropheops</i> 'lilac maleri'	<i>P. tropheops</i> 'maleri yellow'
Over large rocks	3	33
Over medium-small rocks	25	4

#### 19. *Pseudotropheus tropheops* 'mbenji blue' (Plate 4g)

**Synopsis.** A species found among medium-large rocks in exposed areas of the Mbenji Islands. Males are predominantly blue, females are brown.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Body silvery-blue with 7–8 grey-blue bars, decreasing in intensity posteriorly; chest tarnished yellow. Head grey-blue dorsally, but tarnished yellow on cheek, chin and gular region. Dorsal fin pale blue with yellow cast; submarginal band black, narrow and faint; lappets white; trailing portion blue with black inter-ray membranes. Caudal fin grey-blue with a yellow tinge distally. Anal fin pale blue postero-dorsally, black submarginally with 1–4 yellow egg-dummies. Pelvic fins ochre-yellow posteriorly, black submarginally with white leading edges.

**Females:** Uniformly brown body and head; fins pale brown.

**Habitat.** This species frequents upper and vertical surfaces of medium-sized and large rocks in sediment-free areas. It seldom occurs over slabs, among smaller rocks or in intermediate zones. It is most common between 3 and 12 m at exposed sites, but may penetrate to at least 25 m depth.

**Feeding.** The species feeds from the Aufwuchs of upper and vertical rock surfaces and on plankton.

#### 20. *Pseudotropheus tropheops* 'mbenji yellow' (Plate 4h)

**Synopsis.** A fish of the Mbenji Islands which favours sheltered sediment-rich areas. Males are mainly yellow, but females are grey.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Body predominantly yellow tending to blue-grey dorsally; 5–6 narrow grey-brown vertical bars of which only the anterior 3 are darkly pigmented. Head yellow except for blue-grey occipital region and snout. Dorsal fin yellow with prominent black submarginal band running its full length and broadening in the rayed part of the fin; lappets yellow. Caudal fin dark grey-blue with light blue inter-ray membranes. Anal fin pale blue posteriorly, black submarginally with a white leading edge and 2–3 yellow-orange egg-dummies.

Pelvic fins yellow posteriorly, black submarginally with white leading edges.

**Females:** Body greyish-brown with two longitudinal rows of black blotches on the flanks. Head grey. Dorsal fin grey with distinct black submarginal band. Caudal, anal and pelvic fins grey.

**Habitat.** This species occurs mainly among small rocks of sheltered sediment-rich areas, but also occurs in the intermediate zones of sheltered areas. It was found from the surface waters down to a depth of 25 m, but is most numerous between 2 and 15 m.

**Feeding.** Members of this species feed from sediment-covered surfaces of rocky and sandy substrata.

#### 21. *Pseudotropheus tropheops* 'yellow chin' (Plate 4i)

**Synopsis.** A wide-mouthed species endemic to Likoma and Chisumulu Islands where it occupies the intermediate habitats in shallow water. Males are distinguished from other species at these islands by their lime-yellow chest, chin, gular and shoulder regions.

**Distribution.** Likoma I. (C), Chisumulu I. (C).

**Coloration. Likoma Island (Maingano) males:** Body lilac-blue with yellow chest, belly and shoulder. Head yellow except for blue-grey occipital region and snout. Dorsal fin pale blue with a thin black submarginal band, yellow lappets and a predominantly black trailing portion. Caudal fin light blue with black inter-ray membranes and black upper and lower borders. Anal fin black anteriorly, pale blue posteriorly with 1–4 yellow egg-dummies. Pelvic fins mainly yellow with narrow black submarginal bands and white leading edges.

**Likoma Island (Maingano) females:** Body grey with a dorso-lateral and a mid-lateral row of black blotches. Head light grey, but darker on snout and occipital region. Fins grey.

**Geographical variation.** At Khuyu, White Rock and Yofu Bay of Likoma Island (Figure 55) sexually active males may be almost entirely yellow. This yellow extends onto the fins and very little black is evident. At Chisumulu Island, females are more purple than lilac and the yellow is darker, tending to gold. The fins are lime-yellow with virtually no trace of black. Females of all populations are similar, though those of Chisumulu Island are not as grey, being more brown.

**Habitat.** This species is common in intermediate zones and along the rock-sand interface of shallow water. It occupies both sheltered and wave-washed areas. At Likoma Island it is most numerous from 1 to 5 m and was not found below 11 m depth. At Chisumulu, however, it is most common in the shallows, but has been recorded to 23 m.

**Territoriality.** Males normally hold territories at the base of rocks where they dig spawning-sites (nests), 2–4 cm deep and about 1–10 cm diameter, in the sand close to the rocks. Some individuals live in purely rocky habitats where they cannot excavate nests. They are particularly aggressive towards conspecific males and intolerant of most other intruders. Females are not territorial and occur singly or in small groups.

**Feeding.** *P. tropheops* 'yellow chin' feeds from rocks, sand and plants and quite often on plankton in the water column.

Stomachs of 35 individuals caught at Likoma Island contained mostly loose Aufwuchs (64%), C1 and C2 (both 14%) and the remaining 8% comprised benthic Invertebrata. Sand grains are common in the stomachs of these fishes.

### 22. *Pseudotropheus tropheops* 'membe' (Plate 4j)

**Synopsis.** A heavily barred, elongate species of sediment-covered, medium-sized rocks in the middle depths.

**Distribution.** Likoma I. (C).

**Coloration. Males:** Body dark blue with 8–10 dark brown bars; dorso-medial band golden-brown; belly black; chest bronzed gold. Head blue dorsally, golden-brown ventrally; single light blue interorbital bar; a broad, dark brown occipital bar. Dorsal fin golden-brown with black submarginal band, white lappets and yellow trailing edge. Caudal fin brown. Anal and pelvic fins dark brown; 1–4 yellow egg-dummies.

**Females:** Body beige-yellow with grey barring. Head yellowish. Dorsal fin off-white with yellow tinge posteriorly. Caudal fin grey with yellow-orange borders and trailing edge. Anal fin bright orange. Pelvic fins yellow with a dark submarginal band and white leading edges.

**Habitat.** Occurs principally among medium-sized rocks, but is also common among small rocks and at the rock-sand interface. Since it lives in deeper water, being most common between 10 to 30 m, the area it occupies is usually rich in sediment. Its total depth range is from 3 to at least 40 m.

**Territoriality.** Males are aggressively territorial, but most of their aggression is directed at conspecifics. Females are not territorial and occur in small groups of 5 to 10 individuals or singly.

**Feeding.** *P. tropheops* 'membe' feeds principally from sediment-covered rock surfaces. Stomachs of 5 specimens caught at Membe Point contained on average about 80% loose Aufwuchs, 15% C2 and 5% benthic Invertebrata.

### 23. *Pseudotropheus tropheops* 'dark' (Plate 5a)

**Synopsis.** A deep-bodied, dark brown species of rocky habitats. Pelvic fins are long, extending half-way along the anal fin when folded against the body.

**Distribution.** Likoma I. (C).

**Coloration. Males:** Upper half of head and body, and entire caudal peduncle and caudal fin dark brown. Ventral half of head as well as chest and belly ochre-yellow. Dorsal fin light brown with a dark brown, almost black, submarginal band running three quarters of the fin's length; lappets dull yellow. Anal fin black with 1–3 yellow egg-dummies. Pelvic fins golden-brown with black leading edges.

**Females:** Uniformly dull brown with black submarginal bands.

**Habitat.** This species is most common among medium-sized and medium-large rocks, but also ventures into intermediate zones and among small rocks. Its full depth range extends from the surface waters to at least 33 m but it is most numerous between 7 and 20 m.

**Territoriality.** Males are vigorous in the defence of their ter-

ritories, chasing away most intruders. Females are not territorial.

**Feeding.** Observations suggest that it feeds mainly from vertical surfaces of rocks from which it appears to pluck filamentous Aufwuchs.

### 24. *Pseudotropheus tropheops* 'gold' (Plate 5b)

**Synopsis.** A golden-yellow fish endemic to Chisumulu Island.

**Distribution.** Found only along the north and north-eastern shores of Chisumulu I. (C).

**Coloration. Males:** Uniform golden-yellow with a blue tinge on the trailing edge of dorsal and anal fins. Caudal fin yellow with pale blue inter-ray membranes.

**Females:** Uniformly brown.

**Habitat.** It is most numerous over medium-sized and small rocks in purely rocky environs, but it also occupies the intermediate zones of the rock-sand interface. It is common between 10 and 20 m, but occurs from 3 to 25 m depth.

**Territoriality.** Males are territorial, maintaining positions over the upper surfaces of prominent rocks. Most of their aggression appears directed at conspecifics. Females are not territorial.

**Feeding.** Observations of this species in the field indicate that it feeds upon Aufwuchs and plankton.

### 25. *Pseudotropheus tropheops* 'mauve' (Plate 5c)

**Synopsis.** A small lithophilous species in shallow water: males are predominantly mauve-blue, females are apricot-yellow.

**Distribution.** It is common at all rocky shores of the north-western coast from Chirombo Point to Chitande.

**Coloration. Nkhata Bay males:** Body pale mauve-blue with 7–8 faint purple bars that cross the flanks, but do not extend onto the belly; purple dorso-lateral and mid-lateral bands faintly visible in most specimens; chest pale blue with faint yellow tinge; belly pale blue, almost white ventrally. Head blue with a dark blue occipital bar, 2 dark blue interorbital bars and a pale iridescent blue band between the interorbital bars; chin blue with hint of yellow. Dorsal fin pale violet with a faint, thin, black submarginal band and yellow lappets. Inter-ray membranes of trailing edge black. Caudal fin blue with dark blue, almost black, inter-ray membranes. In some individuals the caudal fin has a yellow trailing edge and yellowish rays. Anal fin pale blue posteriorly, grey-black anteriorly with a very pale blue, almost white, leading edge; 1–3 yellow egg-dummies. Pelvic fins light brownish-yellow posteriorly, black submarginally with white leading edges.

**Nkhata Bay females:** Body apricot-yellow with two bands of brown blotches running longitudinally. Head apricot-yellow with mauve interorbital bars. Dorsal, caudal, anal and pelvic fins yellow with faint black markings on the anal and pelvic fins.

**Geographical variation.** At Lion's Cove and Chilumba sexually active males are similar in coloration to the Nkhata Bay form, but at Usisya and Mara Rocks all have a well-defined yellow-gold patch which covers the chin, gular

region and chest and may extend onto the belly. Females appear similar in colour throughout their distribution.

**Habitat.** *P. tropheops* 'mauve' lives among medium-sized rocks and is most common in purely rocky habitats of sediment-free zones, occasionally seen over sand patches among rocks. It is most numerous in water less than 5 m deep, but is found to at least 10 m depth.

**Territoriality.** Males hold territories over the upper surfaces of medium-sized rocks, frequently choosing prominent rocks from which to display. Females are not territorial, are solitary and tend to be aggressive towards one another.

**Feeding.** Members of this species appear to nip filamentous algae from the rocks, apparently favouring the upper surfaces. Males feed from within their defended areas while females feed from untenanted rocks in the preferred habitat.

#### 26. *Pseudotropheus tropheops* 'olive' (Plates 5d & 5e)

**Synopsis.** A lithophilous species in shallow water: males are predominantly olive-yellow; females are silvery-grey with black barring and banding.

**Distribution.** Common on all rocky shores of the north-western coast from Chirombo Point to Chitande.

**Coloration.** *Nkhata Bay males:* Body olive-yellow with 9–10 purple-blue vertical bars which are intense in some individuals but indiscernible in others. Head olive-yellow with a black patch behind the orbit, a black opercular spot, a dark purple-blue interorbital bar and an eye bar; a violet band running from the mouth, ventrally along the pre-operculum. Dorsal fin yellowish-green with lilac-blue spots. Caudal fin grey with olive-yellow inter-ray membranes. Anal fin orange-yellow posteriorly, black anteriorly, usually only one large yellow egg-dummy. Pelvic fins gold posteriorly, black anteriorly.

*Nkhata Bay females:* Body silvery-grey, sometimes with golden cast; 9–10 grey-brown vertical bars, which may have lilac or violet iridescence. Mid-lateral and dorso-lateral bands broken into a series of black blotches, being pitch-black where they cross the vertical bars; chest pale blue. Lower half of head violet-blue, upper half silvery-grey with a black patch posterior to orbit and a black bar running from the occipital, across the suboccipital and midway down the posterior margin of the operculum. Dorsal fin silvery-grey with a series of black blotches along its base and numerous small yellow, white or lilac spots which dot the fin. Caudal fin grey with purple rays. Anal fin hyaline with a blue patch anterodorsally and a single yellow egg-dummy. Pelvic fins hyaline, with a yellow cast posteriorly and a black submarginal band.

**Geographical variation.** At Chilumba and Ruarwe males are more yellow than those of Nkhata Bay, some tending to bright gold. All the fins are predominantly yellow, though the inter-ray membranes of the dorsal fin are lilac in some specimens at Mpanga Rocks. It was noted that the population within the bay at Chilumba and also the population at Mpanga Rocks, are a deeper golden-yellow than that at Chitande. Females at Chilumba and Ruarwe have the same markings as the Nkhata Bay form, but the ground colour is olive-yellow and not silvery-grey.

**Habitat.** The preferred habitat of *P. tropheops* 'olive' ap-

pears to be among medium-sized and medium-large rocks of sediment-free shores, but it may also occur over boulders and slabs (e.g. at Mpanga Rocks where other rock types are rare). It is rare in intermediate areas. Most individuals occur in less than 2 m and very few occur below 5 m depth.

**Territoriality.** Males are aggressive in the defence of their territories which occasionally contain algal gardens. Females are not territorial and usually occur in groups of 3–6 individuals.

**Feeding.** Both sexes feed from upper and vertical rock surfaces, apparently cropping filamentous algae. They have also been seen taking plankton.

#### 27. *Pseudotropheus tropheops* 'black' (Plate 5f)

**Synopsis.** A large, common species of the rocky zones of the north-western part of the lake. Males are purple-blue with a golden chest and gular region and virtually no trace of barring. Females and juveniles are black.

**Distribution.** Found at every diving station along the north-western coast (Figure 68).

**Coloration.** *Nkhata Bay males:* Body purple-blue, tending to black dorsally and light blue ventrally, usually unbarred, though 6–8 dark purple bars apparent in some individuals; chest and belly golden, sometimes ochre. Head dark purple, tending to black dorsally, but blue below the level of the eye with a violet base to the pre-operculum; chin, gular region and branchiostegal membranes golden tending to ochre; 2 light blue interorbital bars; opercular spot black with lilac iridescence. Dorsal fin golden-yellow, though portion below the prominent black submarginal band with a blue cast; lappets yellow with bright yellow tips; submarginal band broadening posteriorly to fill much of rayed portion of fin. Caudal fin dark purple-blue with faint yellowish trailing edge. Anal fin dark purple with light blue leading edge, an ochre tinge at its base and a single large orange-yellow egg-dummy, but occasionally 1–2 smaller egg-dummies present. Pelvic fins yellow with white leading edges and narrow faint black submarginal bands.

*Nkhata Bay females:* Usually entirely black, or dark grey with a prominent pitch-black submarginal band in the dorsal fin. *P. tropheops* 'black' may exhibit polychromatism, but until a successful mating with an OB female is observed this remains unconfirmed.

**Geographical variation.** Throughout its wide geographical distribution the basic colours and markings of this species remain virtually unchanged. At Ruarwe and Chilumba, however, the black submarginal band of males is reduced to a thin line except in the rayed portion of the fin where it expands to form a large fin-spot. Females of these northern populations are dark brown rather than black.

**Habitat.** *P. tropheops* 'black' is most numerous among medium-sized and large rocks. It also occurs over boulders and slabs, particularly at Mpanga Rocks and Mara Rocks where these rock types predominate. Members of this species occur from surface waters to at least 24 m depth, but are most numerous between 3 and 15 m.

**Territoriality.** Males are aggressively territorial holding territories of 2–3 m diameter. Females have been seen to chase conspecifics, but it is not certain whether they practise

territoriality.

**Feeding.** Both sexes feed from the upper and vertical surfaces of rocks, apparently taking filamentous algae.

### 28. *Pseudotropheus tropheops* 'rust'

**Synopsis.** Males are heavily barred with a prominent rusty-yellow patch on the head, shoulder and chest. Females are grey-brown with two rows of black blotches.

**Distribution.** Chirombo Point (C), Nkhata Bay (C), Lion's Cove (C).

**Coloration.** *Nkhata Bay males:* Body purple-blue with 10–12 dark purple bars, and, in some individuals, faint purple-grey mid-lateral and dorso-lateral longitudinal bands; chest and shoulder rusty-yellow; belly light blue. Head rusty-yellow with a black patch on the operculum, one on the snout and another in the position of an eye-band; single black interorbital bar; a large black patch situated mid-dorsally on the head a prominent feature. Dorsal fin pale blue, suffused with yellow; submarginal band comprising a few unconnected, narrow, black streaks. Caudal fin dark purple with lighter purple inter-ray membranes and a yellow trailing edge. Anal fin black anteriorly, hyaline posteriorly with 1–3 yellow egg-dummies. Pelvic fins yellow with thin black submarginal bands and white leading edges.

*Nkhata Bay females:* Body light grey-brown with a dorso-lateral and a mid-lateral row of black patches running the length of the body. Head grey with darker grey markings similar to those of males. Fins grey, suffused with yellow.

**Habitat.** *P. tropheops* 'rust' frequents small-medium and medium-sized rocks, occasionally occurring in the intermediate habitats and over large rocks and boulders. It appears most common in sediment-rich areas between 6 and 15 m, but also inhabits the extreme shallows and penetrates to depths of at least 23 m.

**Territoriality.** Only males are territorial. They appear relatively tolerant of heterospecific intruders, but highly aggressive towards conspecific males. Females are non-territorial, occurring singly or in small groups of up to 8 individuals.

**Feeding.** *P. tropheops* 'rust' feeds from the Aufwuchs mat and will also take plankton.

### 29. *Pseudotropheus tropheops* 'deep'

**Synopsis.** A small species which frequents deep water at Nkhata Bay.

**Distribution.** Nkhata Bay (C).

**Coloration.** *Males:* Body purple dorsally, lilac ventrally with a bright golden-orange patch covering the shoulder, pectoral region, chest and anterior belly; 5–6 faint grey bars. Head dark purple, almost black dorsally, lighter purple around the eye; cheek, chin, gular region and branchiostegal membranes golden-orange; opercular spot black; a single light blue interorbital bar. Dorsal fin golden-yellow with a narrow dark blue submarginal band and yellow lappets with white tips; trailing edge golden. Caudal fin black, suffused with yellow; trailing edge orange-yellow. Anal fin hyaline posteriorly, black submarginally and white anteriorly; a single orange egg-

dummy. Pelvic fins orange posteriorly, black submarginally and white anteriorly.

**Females:** Body reddish-brown tending to khaki-brown dorsally and yellow ventrally; 5–6 faint, grey bars. Head khaki-brown dorsally tending to lilac ventrally. Dorsal fin dull orange with numerous small white flecks and a narrow black submarginal band; lappets yellowish-white. Caudal fin khaki with blue cast and yellow trailing edge. Anal and pelvic fins orange-yellow, with black submarginal bands and white leading edges.

**Habitat.** *P. tropheops* 'deep' frequents small and medium-sized rocks in the sediment-rich deeper areas. It is most numerous between 15 and 20 m, but rare in water shallower than 10 m. Depth distribution extends to at least 30 m.

**Territoriality.** Males are aggressively territorial; females are not territorial.

**Feeding.** Members of this species feed from sediment-covered surfaces, but it is not known which components of the Aufwuchs it collects.

### 30. *Pseudotropheus tropheops* 'band'

**Synopsis.** A shallow-water species of the intermediate habitat where males nest on sand among or near rocks. Males are predominantly yellow with a conspicuous black submarginal band running half-way along the dorsal fin. Females are grey.

**Distribution.** Nkhata Bay (C).

**Coloration.** *Males:* Body yellow with bluish cast on flanks and caudal peduncle; belly and shoulder bright golden-yellow; 6–7 grey bars usually very faint, sometimes absent. Head golden-yellow with grey-blue patch running from between the eyes over the occipital region to the dorsal fin; snout light grey with 2 violet-blue interorbital bars; opercular spot greenish-black; chin, gular region and branchiostegal membranes gold. Dorsal fin yellow with violet tinge, a prominent solid black submarginal bar runs about half-way along the fin, but comprises broken black dashes posteriorly; lappets violet with gold edges. Caudal fin yellow with golden trailing edge and violet rays. Anal fin bluish with a yellow cast, black submarginally with a white leading edge and usually a single golden egg-dummy. Pelvic fins orange with black submarginal bands and white leading edges.

**Females:** Body grey with dark grey blotches. Head grey with bluish interorbital bars. Dorsal fin grey with a yellowish tinge in some individuals and a faint black submarginal band. Caudal fin grey. Anal and pelvic fins yellowish-grey with black submarginal bands.

**Habitat.** *P. tropheops* 'band' lives mainly over sand either among rocks or near to rocks. It is fairly common in both wave-washed and sheltered zones along the Nkhata Bay peninsula. It is most numerous in 1–3 m depth and is absent below 6 m.

**Territoriality.** Males are territorial and defend areas of about 2 m diameter. They dig saucer-shaped nests in sand alongside rocks or underneath rocky overhangs. Females are not territorial.

**Feeding.** Males feed mainly from rocks within their territorial boundaries, though they do occasionally venture further afield and may feed from sand also. Females feed from

both rock and sand.

### 31. *Pseudotropheus tropheops* 'no band'

**Synopsis.** A shallow-water species of the intermediate habitat where males nest on sand among or near rocks. Very similar in coloration to *P. tropheops* 'band', but males are more brightly coloured and do not have a submarginal band.

**Distribution.** Nkhata Bay (U).

**Coloration. Males:** Body bright golden-yellow, tending to lilac-blue posteriorly. Head golden with prominent grey patch on the occipital region of the head, 2 lilac-blue interorbital bars. Dorsal fin golden-yellow with faint lilac-blue hue posteriorly. The black submarginal band absent. Caudal fin golden-yellow with violet rays. Anal fin bluish-yellow with a black submarginal band and white leading edge, 1–2 orange egg-dummies. Pelvic fins orange with black submarginal bands and white leading edges.

**Females:** Very similar to those of *P. tropheops* 'band'.

**Habitat.** The habitat preferences are currently indistinguishable from those of *P. tropheops* 'band'.

**Feeding.** Feeding behaviour is also indistinguishable from that of *P. tropheops* 'band'.

**Note:** *P. tropheops* 'band' and *P. tropheops* 'no band' are very similar anatomically, in basic coloration, in behaviour and apparently in habitat preference. It is possible that they are conspecifics, but we regard them as distinct species because colour differences do exist, particularly the presence or absence of the submarginal band of the dorsal fin. In addition, the 10 largest territorial males of *P. tropheops* 'band' are larger (95–102 mm SL) than the 10 largest *P. tropheops* 'no band' (87–94 mm SL). As the differences between these fishes were not recognized until after the transect were completed, both populations are treated together as *P. tropheops* 'band' (Figures 69 & 70).

### 32. *Pseudotropheus tropheops* 'red fin' (Plate 5g)

**Synopsis.** This species occupies a variety of rocky and intermediate habitats. Males are dark blue with red markings in the dorsal fin. Females are yellowish with a prominent black submarginal band in the dorsal fin.

**Distribution.** Ruarwe (C), Chitande (C), Mpanga Rocks (U). Possibly Mara Rocks (unconfirmed observation).

**Coloration. Ruarwe males:** Body dark blue with silver-blue sheen and 4–7 black bars. Head dark blue with a light blue interorbital bar and a violet sheen along lower region of pre-operculum; opercular patch black with greenish cast. Dorsal fin bluish with orange-red interspine membranes and a well-defined black submarginal band; lappets white with orange-red tips; rayed portion of dorsal fin blue-grey with orange trailing edge and a variable number of orange ocelli. Caudal fin inter-ray membranes mauve, rays dark grey with orange tinge; trailing edge orange. Anal fin dark grey, almost black, but blue at base with a white leading edge and an orange egg-dummy. Pelvic fins dusky grey with narrow black submarginal bands and white leading edges.

**Ruarwe females:** Body brownish dorsally, beige ventrally with faint brown bars. Head beige, but grey-brown dor-

sally. Dorsal fin beige, with prominent black submarginal band which is flanked by white bands to form a well-defined and distinctive feature; lappets white with orange-yellow tips. Caudal fin brownish-yellow with white spots. Anal fin light brown with orange trailing portion, black submarginal band and a white leading edge. Pelvic fins ochre with black submarginal bands and white leading edges.

**Geographical variation.** Males at Chitande and Mpanga Rocks are darker blue than those of Ruarwe and usually have only 5 broad, black vertical bars. The dorsal fin has an overall darker appearance, being deep red rather than orange-red. The submarginal band, however, is narrower. Pelvic fins are orange-red and not dusky grey. Females are orange-grey with more distinct barring and faint grey mid-lateral and dorso-lateral bands. The submarginal band which is a distinctive feature of Ruarwe females is relatively narrow in the Chitande and Mpanga Rock forms, and fades posteriorly.

**Habitat.** *P. tropheops* 'red-fin' is most common among small and medium-sized rocks though it does occur in the intermediate zones. In areas such as Mpanga Rocks where boulders and slabs predominate, it occurs over large, open rock-faces. The depth distribution of this species is from 2 to at least 25 m depth though most individuals occur between 7 and 15 m.

**Territoriality.** Territorial males normally defend areas among small and medium-sized rocks though other areas are also used. When territories are over sand, nests are excavated. Males are highly aggressive and at Mpanga Rocks gardens were evident in some territories. Females are usually solitary and are not territorial.

**Feeding.** Members of this species feed by nipping and jerking at the Aufwuchs in a manner which suggests that filamentous algae are harvested.

### 33. *Pseudotropheus tropheops* 'weed'

**Synopsis.** A fish of shallow intermediate, often vegetated, habitats.

**Distribution.** Dankanya Bay (U), Usisya (U) and Chitande (U). It was not found at Ruarwe where we studied the rocky environment only.

**Coloration. Chitande males:** Body violet-blue with 8 grey bars traversing flanks, but usually not extending all the way to base of dorsal fin or to the ventral part of the belly. The 5 anterior bars broad and dark grey, but 3 posterior bars dull grey; shoulder and chest rusty-yellow. Head dark grey dorsally, black ventrally with two iridescent metallic-blue interorbital bars, the lower bar being particularly bright. Dorsal fin blue ventrally, yellow-orange dorsally. Caudal fin orange distally, dusky proximally with light blue inter-ray membranes. Anal fin dark grey anteriorly, fading to hyaline posteriorly with a single large yellow egg-dummy. Pelvic fins ochre-yellow with black submarginal bands and white leading edges.

**Chitande females:** Body grey-brown with 8 dark grey bars. Head dark grey with 2 light grey interorbital bars flanked by black interorbital bars. All fins grey.

**Habitat.** *P. tropheops* 'weed' lives among scattered rocks

in areas covered by macrophytes. This species was not found below 6 m depth.

**Territoriality.** Males are territorial, females are not. Male aggression is restricted mainly to conspecifics.

**Feeding.** Members of this species were seen to feed from rock and sand substrata and from plants, but it is not known which components of the Aufwuchs are taken.

**Note:** This species is superficially similar to *P. cf. novemfasciatus*, but has a steeper snout profile and heavier barring.

**34. *Pseudotropheus tropheops* 'chitande yellow' (Plate 5h)**

**Synopsis.** This species inhabits sediment-rich, sheltered zones and intermediate habitats in shallow water. Males are predominantly yellow; females are grey-brown.

**Distribution.** Chitande (C), harbour jetty at Chilumba (C).

**Coloration. Chitande males:** Body yellow, particularly bright on shoulder, pectoral region and chest, but with bluish cast on flanks; caudal peduncle mauve. Head yellow with grey-blue patch on forehead and snout; opercular spot black with green sheen. Dorsal fin inter-ray and inter-spine membranes blue-violet, spines and rays golden-yellow; lappets yellow. Caudal fin grey-mauve with yellow rays. Anal fin greyish-blue with a dark grey leading edge and violet-blue patch along its base; usually a single large egg-dummy. Pelvic fins golden-yellow with narrow black submarginal bands and white leading edges.

**Chitande females:** Body grey-brown though some individuals are khaki-brown; a narrow dorso-lateral band of grey blotches and a broad mid-lateral band of grey blotches running the length of the body; occasionally 7–9 faint grey bars visible. Head grey-brown or khaki-brown. Dorsal and caudal fins pale brown. Anal fin grey-brown with light brown leading edge. Pelvic fins khaki-yellow with black submarginal bands and white leading edges.

**Habitat.** *P. tropheops* 'chitande yellow' is most numerous in the intermediate zone. It lives along the rock-sand interface which it follows down to a depth of at least 12 m at Chitande. It also occurs in rocky zones where it favours sediment-covered areas in sheltered, shallow waters.

**Territoriality.** Males are territorial and where territories are over sand, nests are excavated. Females usually occur singly and do not hold territories.

**Feeding.** Members of this species were observed to feed from the Aufwuchs mat on rocky substrata, but it is not known which components of the Aufwuchs are harvested.

***Pseudotropheus williamsi* (Günther 1893) species-complex (Figures 8a–c)**

Members of this species-complex are anatomically similar; all species inhabit the shallows, usually less than 4 m; males of all populations are weakly territorial, and non-territorial individuals normally form schools. Most allopatric populations differ in coloration and markings and some differ in maximum adult size and in preferred habitat. By virtue of the way in which we apply the specific mate recognition hypothesis to the biological species concept, those populations which differ markedly from one another are regarded as distinct species. The distribution of the members of the *P. williamsi* species-complex is given in Table 5.

**1. *Pseudotropheus williamsi* 'nkudzi' (Plate 5i)**

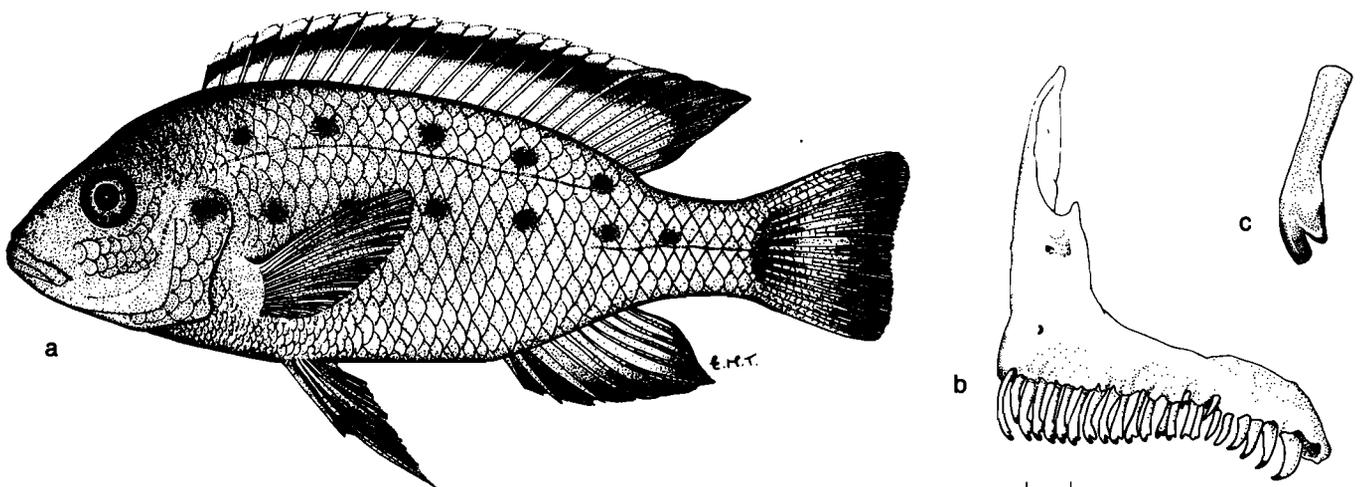
**Synopsis.** A large, cryptic and apparently uncommon lithophilous species of shallow water.

**Distribution.** Nkudzi (R–U), Boadzulu I. (U), Monkey Bay (R), Nkhata Bay (R).

**Coloration. Nkudzi males:** Body lilac-blue with yellow-orange chest and yellowish belly; 5 faint darker blue bars present. Head lilac-blue dorsally with golden-yellow snout, chin, cheek, gular region and branchiostegal membranes; 2 iridescent blue interorbital bars. Dorsal fin pale blue with a broad submarginal band that runs its entire length; lappets blue-white, rays black. Caudal fin inter-ray membranes violet-blue, rays black. Anal fin blue with black submarginal band and white leading edge; 3–5 yellow egg-dummies. Pelvic fins yellow with black submarginal bands and white leading edges.

**Nkudzi females:** Body grey with two rows of black spots running along its length (Figure 8a). Head grey. Fins grey with black submarginal bands on all but caudal fin which is light grey proximally and dark grey distally.

**Geographical variation.** Males at Boadzulu Island have almost identical colours and markings at those of Nkudzi,



**Figure 8** (a) *Pseudotropheus williamsi* 'nkudzi', Nkudzi Point, 121 mm SL. (b) Lateral aspect of left premaxilla of *P. williamsi* 'nkudzi' (Scale = 1 mm). (c) Anterior outer row tooth of *P. williamsi* 'nkudzi'.

**Table 5** The members of the *Pseudotropheus williamsi* species-complex. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-)

Species	Maximum size		Distribution													
	mm (SL)	Locality	1	Ila	IIb	IIc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Pseudotropheus williamsi</i> 'nkudzi'	114	Boadzulu I.	+	+	+	-	-	-	-	-	-	-	-	+	-	-
2. <i>P. williamsi</i> 'makanjila'	not	caught	-	-	-	+	-	-	-	-	-	-	-	-	-	-
3. <i>P. williamsi</i> 'maleri'	104	Maleri I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-
4. <i>P. williamsi</i> 'namalenje'	108	Namalenje I.	-	-	-	-	-	-	-	-	+	-	-	-	-	-
5. <i>P. williamsi</i> 'mbenji'	not	caught	-	-	-	-	-	-	-	-	-	+	-	-	-	-
6. <i>P. williamsi</i> 'maingano'	101	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
7. <i>P. williamsi</i> 'khuyu'	110	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
8. <i>P. williamsi</i> 'chisumulu'	106	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-

but differ in that the lower half of the head and the chest are a deep golden-orange and not yellow-orange. Furthermore, in the Boadzulu form the two interorbital bars are a more intense iridescent blue and the submarginal band in the dorsal fin, although conspicuous, is narrower. At Monkey Bay this species is rare and none was caught for detailed examination of male coloration, but observations in the lake indicate that males are very similar, perhaps identical, to those of Nkudzi. Females of all populations appeared to be identical.

**Habitat.** This species lives amongst medium-sized and medium-large rocks in the sediment-free zones within 3 m of the surface.

**Territoriality.** Males are weakly territorial and slowly patrol areas of 3–4 m diameter, occasionally chase intruders and frequently stop and hover 50–100 cm above the rocks. Although rare at most sites, on the south-western corner of Boadzulu Island territorial males are sufficiently close together to have abutting boundaries where occasional displays between neighbours were observed. In general, this species has cryptic behaviour and is not easily observed. Females, juveniles and non-territorial males occur in small groups which swim along the 0–3 m depth zone, but these groups are not often seen. At Monkey Bay, where this species appears to be rare, and where groups of non-territorial fishes had not been seen in about 800 h diving, a school of about 50 individuals was seen swimming in surface waters on the sheltered side of the Island of Thumbi East in April 1981. This sudden appearance, and subsequent disappearance, of numerous non-territorial individuals is unexplained.

**Feeding.** This species was seen to feed occasionally from Aufwuchs and also from the water column. Stomachs of five individuals caught at Boadzulu Island and one caught at Nkudzi were almost empty, but each contained remains of both adult and larval insects and smaller proportions of zooplankton, C2 and loose Aufwuchs.

**Note:** Two males which had similar coloration and markings to the Boadzulu Island population were found among medium-large rocks in 1 to 2 m of water at Nkhata Bay. As these fishes appeared superficially identical (none was caught and as both hid among the rocks no detailed comparison was possible) to the Boadzulu form they are considered as conspecifics for the time being.

### 2. *Pseudotropheus williamsi* 'makanjila'

**Synopsis.** A large fish of the rocky and intermediate habitats of shallow water.

**Distribution.** The reefs off Makanjila Point (R), Masinje Rocks (R).

**Coloration.** *Makanjila males:* Body pale blue with light yellow chest and yellowish-white belly. Head pale blue with 2 lilac-blue interorbital bars; snout, chin, lower half of each operculum and branchiostegal membranes pale yellow. Dorsal fin blue with a broken, narrow, black submarginal band; lappets white; rays black and a conspicuous black dorsal fin-spot in rayed portion. Caudal fin pale blue with black rays. Anal fin blue with a black submarginal band and white leading edge; 2–6 yellow egg-dummies. Pelvic fins pale yellow with black submarginal bands and white leading edges.

*Makanjila females:* Identical to those of *P. williamsi* 'nkudzi', but without the prominent submarginal band of the dorsal fin.

**Geographical variation.** Although slight differences in the intensity of coloration were noted between populations, they all appeared essentially the same. However, D.S.C. Lewis (pers. comm.) found a population on one of the reefs off Makanjila which had a red dorsal fin and an unbroken submarginal band.

**Habitat.** This species frequents rocky reefs from just below the surface to 4 m depth. It was seen over the rocks forming the reef and at the rock-sand interface. This area is usually wave-washed.

**Territoriality.** Males hold territories among the rocks or at the sand-rock interface. These are weakly defended, perhaps because heterospecifics are largely ignored and conspecifics are widely separated and therefore intraspecific encounters are rare.

**Feeding.** On the rare occasions when this species was seen feeding it appeared to take detritic material which had accumulated among the rocks.

### 3. *Pseudotropheus williamsi* 'maleri' (Plate 5j)

**Synopsis.** A cryptic medium-large lithophilous species of shallow, sediment-free zones. Males have orange-red dorsal fins.

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**Distribution.** Maleri I. (U), Nankoma I. (R–U), Nakantenga I. (U).

**Coloration. Maleri Island males:** Body blue with a golden-yellow patch that covers the chest, lower shoulder (pectoral region) and anterior part of the belly. Head and face golden-yellow with a single light blue interorbital bar and lilac-blue occipital region. Dorsal fin orange-red; submarginal band faint except posteriorly where it contributes to the dorsal fin-spot; rays black. Caudal fin grey-blue with black rays fanning out distally; trailing edge orange. Anal fin pale blue with a black submarginal band and a white leading edge; 2–4 yellow egg-dummies. Pelvic fins orange with black submarginal bands and white leading edges.

**Maleri Island females:** Body grey with two longitudinal rows of dark grey spots. Fins grey with a black submarginal band in the anal and pelvic fins, but not in the dorsal fin.

**Geographical variation.** The colour pattern of males is the same at all three Maleri islands, but the population at Nakantenga has a brighter red dorsal fin, a deeper blue body and a more golden head and chest than the populations at Maleri and Nankoma Islands.

**Habitat.** This species lives among medium-sized and medium-large rocks. Most individuals were found at less than 3 m depth, but one territorial male was found at 5 m.

**Territoriality.** Males are territorial and usually hover motionless in the water column, but are stimulated into a frenzy of activity when conspecifics intrude, either courting females or chasing males. Usually the males ignore heterospecific intruders, but at times of courtship or active patrolling of the territories all intruders are chased.

**Feeding.** This species was occasionally observed feeding from the rocks or from the water column, but relative to other Mbuna it appears to feed very seldom. Stomachs of five territorial males caught at Nakantenga were all empty.

#### 4. *Pseudotropheus williamsi* 'namalenje' (Plate 6a)

**Synopsis.** A darkly barred species of medium-large rocks in shallow waters.

**Distribution.** Namalenje I. (U).

**Coloration. Males:** Body iridescent, silvery-blue with 7–9 black bars and a tarnished gold chest and gular region. Head grey-blue along occipital region and snout with 2 silvery-blue interorbital bars; cheeks, chin and branchiostegal membranes tarnished gold. Dorsal fin pale blue with a prominent black submarginal band and black patches where each body bar enters the fin; orange patches immediately below the submarginal band increasing in size posteriorly; lappets light blue with orange-yellow tips; rays black and trailing edge orange-red. Caudal fin blue-grey with black rays that fan outwards posteriorly; trailing edge red. Anal fin pale blue with yellow cast, black submarginal band and white leading edge; 2–4 yellow egg-dummies. Pelvic fins golden-brown with black submarginal bands and white leading edges.

**Females:** Grey with dark grey barring and black submarginal bands in fins.

**Habitat.** This species lives among medium-large and large rocks in the upper 3 m of water.

**Territoriality.** The cryptic behaviour of this species made it difficult to observe territoriality. Limited observations, however, suggest that males are territorial. Females, juveniles and non-territorial males were seen once in a school numbering about 40 individuals.

**Feeding.** These fishes were not seen to feed and none were caught for analysis of stomach contents.

#### 5. *Pseudotropheus williamsi* 'mbenji'

**Synopsis.** A large species which inhabits the shallows among small and medium-sized rocks close to sandy, sedimented areas.

**Distribution.** Mbenji I. (R–U).

**Coloration. Males:** Body slate-blue with a yellow cast on the chest and belly. Head slate-blue with a light blue interorbital bar and a yellowish cast to the cheeks and chin. Dorsal fin slate-blue with a wide, black submarginal band running entire length of fin; lappets red. Caudal fin inter-ray membranes blue, rays black fanning out posteriorly; trailing edge red. Anal fin pale blue with a thin black submarginal band and white leading edge; 2–4 large yellow egg-dummies. Pelvic fins yellowish with black submarginal bands and white leading edges. **Females:** Body blue-grey with two rows of dark grey spots running along the length of the body. Head blue-grey. Dorsal fin light grey with black submarginal band. Caudal fin dark grey distally, grey at base. Anal fin and pelvic fins blue-grey with darker leading edges.

**Habitat.** Most individuals at Mbenji Island were found in less than 2 m of water over small and medium-sized rocks, close to areas of sand. Some were found at the rock-sand interface and a few were found over medium-sized rocks in purely rocky environs.

**Territoriality.** Males are weakly territorial. Non-territorial individuals occur in small groups of 5–15 members.

**Feeding.** Non-territorial fish were seen to feed occasionally upon detritic material, but territorial males were not observed feeding.

#### 6. *Pseudotropheus williamsi* 'maingano'

**Synopsis.** A large lithophilous species of the shallows of the north-eastern shore of Likoma Island.

**Distribution.** Maingano (U) and Membe Point (R) at Likoma Island.

**Coloration. Males:** Body uniform slate-blue. Head slate-blue with a pale blue interorbital bar. Dorsal fin slate-blue with a prominent black submarginal band and light blue lappets. Caudal fin slate-blue with black upper and lower borders and black rays. Anal fin slate-blue with black submarginal band and white leading edge; 2–4 yellow egg-dummies. Pelvic fins hyaline with faint yellow cast, black submarginal bands and white leading edges. **Females:** Body blue-grey with a row of black spots running mid-laterally and another running dorso-laterally. Head blue-grey. Fins greyish with black submarginal bands.

**Habitat.** This species was found among medium-sized and medium-large rocks in sediment-free areas. Most individuals live within 1.5 m of the surface, but some were found to

a depth of at least 3 m.

**Territoriality.** Males hold territories about 3 m in diameter which they patrol slowly. Quite frequently they spend many minutes hovering motionlessly above the rocks. Females and other non-territorial individuals were seen most often in small groups.

**Feeding.** This species was seen to feed from the Aufwuchs and also from the water column. Stomachs of two individuals contained mostly zooplankton, which was abundant at that time (August 1980), some insect remains and small proportions of loose Aufwuchs and C1.

#### 7. *Pseudotropheus williamsi* 'khuyu'

**Synopsis.** A large species which lives among small rocks in the intermediate zones of shallow water.

**Distribution.** Khuyu Bay (R–U), Likoma I.

**Coloration. Males:** Body pale blue, with two longitudinal rows of black spots, usually characteristic of females, clearly visible; most of the flank with a pale yellow cast; chest, pectoral region and much of the belly yellowish-white. Head pale blue, but opercula, cheek, chin and branchiostegal membranes pale yellow. Dorsal fin blue with a narrow, broken, black submarginal band; lappets white with yellow tips; rays black with yellow inter-ray membranes. Caudal fin blue with yellow cast, orange trailing edge and black upper and lower borders. Anal fin pale blue with black submarginal band and white leading edge; 1–4 yellow egg-dummies. Pelvic fins pale blue with black submarginal bands and white leading edges.

**Females:** Body grey with two longitudinal rows of black spots; faint yellowish cast on chest and belly. Head grey, but faintly yellow ventrally. Fins grey with black markings which are similar to those of males.

**Habitat.** This species was found among small rocks in the intermediate zone, most individuals occurring in less than 2 m of water. This area is rich in sediment.

**Territoriality.** Males were seen defending territories, but little is known of their territorial behaviour as they are extremely wary fish which hide when approached by divers. Females and other non-territorial fishes were seen in groups of up to 15 individuals.

**Feeding.** Stomach contents of four individuals were examined: two were empty and the other two were less than half-full and contained remains of larval and adult insects

and small proportions of loose Aufwuchs and C1.

#### 8. *Pseudotropheus williamsi* 'chisumulu'

**Synopsis.** A large, shallow-water species which inhabits areas of small and medium-sized rocks.

**Distribution.** Chisumulu I., at Same Bay (U) and Liwelo Bay (R).

**Coloration. Males:** Body uniform slate-blue with golden-yellow gular region and chest. Head slate-blue with a light blue interorbital bar and golden-yellow cheeks, chest and branchiostegal membranes. Dorsal fin slate-blue with prominent black submarginal band and light blue lappets. Caudal fin slate-blue with black upper and lower borders, black rays and an orange trailing edge. Anal fin blue with a black submarginal band and white leading edge; 1–4 yellow egg-dummies. Pelvic fins golden-yellow with black submarginal bands and white leading edges.

**Females:** Grey with the two rows of black spots running longitudinally across the flanks. Fins grey with black submarginal bands.

**Habitat.** This species lives among small and medium-sized rocks, usually in water less than 2 m deep.

**Territoriality.** Males are territorial. Non-territorial fishes were seen in schools.

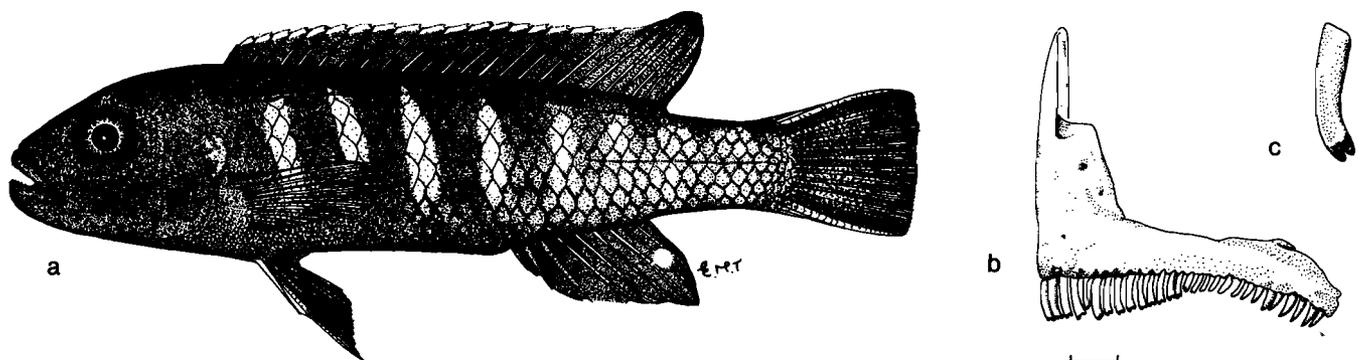
**Feeding.** The stomach contents of three individuals were examined: two contained remains of larval and adult insects, loose Aufwuchs and C1; the other stomach was empty.

**Note:** This species shares colour patterns with both of the Likoma Island populations and it inhabits an environment which is intermediate between that of the Khuyu form and that of the Maingano form.

#### *Pseudotropheus elongatus* species-group (Figures 9a–c)

The principal criterion for considering the fishes listed in Table 6 together is that they are elongate, resembling *Pseudotropheus elongatus* Fryer, 1956. This group is undoubtedly polyphyletic as it includes species which show differences in head shape and dentition. Furthermore, while some species are extremely long and slender, such as that illustrated by Figure 9a, others are deeper bodied and may eventually prove to have tenuous claims to membership of this group.

Members of this group inhabit a variety of habitats and



**Figure 9** (a) *Pseudotropheus elongatus*, Nkhata Bay, 80 mm SL. (b) Lateral aspect of left premaxilla of *P. elongatus* 'black' of Chinyankwazi I. (Scale = 1 mm). (c) Anterior outer row tooth of *P. elongatus* 'black' of Chinyankwazi I.

**Table 6** The members of the *Pseudotropheus elongatus* species-group. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-)

Species	Maximum size		Distribution														
	mm (SL)	Locality	I	IIa	IIb	IIc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc	
1. <i>Pseudotropheus elongatus</i> 'aggressive'	111	Zimbabwe I.	+	+	-	-	-	+	+	-	-	-	-	-	-	-	
2. <i>P. elongatus</i> 'yellow tail'	98	Zimbabwe I.	+	+	-	-	-	+	+	-	-	-	-	-	-	-	
3. <i>P. elongatus</i> 'boadzulu'	72	Boadzulu I.	-	-	+	-	-	-	-	-	-	-	-	-	-	-	
4. <i>P. elongatus</i> 'reef'	79	Eccles Reef	-	-	-	+	-	-	-	-	-	-	-	-	-	-	
5. <i>P. elongatus</i> 'brown'	96	West Reef	-	-	-	+	-	-	-	-	-	-	-	-	-	-	
6. <i>P. elongatus</i> 'dinghani'	70	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	
7. <i>P. elongatus</i> 'chinyamwezi'	76	Chinyamwezi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	
8. <i>P. elongatus</i> 'black'	94	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	
9. <i>P. elongatus</i> 'slab'	84	Mumbo I.	-	-	-	-	-	+	+	+	-	-	-	-	-	-	
10. <i>P. elongatus</i> 'bar'	66	Nakantenga I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-	
11. <i>P. elongatus</i> 'namalenje'	97	Namalenje I.	-	-	-	-	-	-	-	-	+	-	-	-	-	-	
12. <i>P. elongatus</i> 'mbenji blue'	83	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-	
13. <i>P. elongatus</i> 'mbenji brown'	92	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-	
14. <i>P. elongatus</i> 'mbako'	69	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-	
15. <i>P. elongatus</i> 'ndumbi'	111	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-	
16. <i>P. elongatus</i> 'ornatus'	93	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-	
17. <i>P. elongatus</i> 'gold bar'	86	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-	
18. <i>P. elongatus</i> 'chisumulu'	84	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-	
19. <i>P. elongatus</i>	76	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-	
20. <i>P. elongatus</i> 'nkhata brown'	81	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-	
21. <i>P. elongatus</i> 'mara'	57	Mara Rocks	-	-	-	-	-	-	-	-	-	-	-	-	+	-	
22. <i>P. elongatus</i> 'bee'	86	Chitande	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
23. <i>P. elongatus</i> 'mpanga'	72	Mpanga Rocks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
24. <i>P. elongatus</i> 'ruarwe'	66	Ruarwe	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+

the behaviour of the species varies from strongly territorial to non-territorial. Territories of some members of this species-group are so aggressively defended that only the resident feeds there, thus the filamentous algae grows to a larger size than in surrounding areas, clearly marking the territories. These areas of apparently rich growth are referred to as algal gardens.

Of the 24 species recorded in Table 6 only *P. elongatus* has already been described.

### 1. *Pseudotropheus elongatus* 'aggressive' (Plate 6b)

**Synopsis.** A darkly coloured highly aggressive species which lives among small and medium-sized rocks.

**Distribution.** Nkudzi (C), Kanchedza I. (U), Monkey Bay (C-N), Nankumba Peninsula (C), Domwe I. (C), Zimbabwe I. (C), Thumbi West I. (C), Mumbo I. (U).

**Coloration.** *Monkey Bay males:* Body black with 5-6 blue bars. Head black. Dorsal fin black with light blue lap-pets. Caudal fin black with light blue edges and longitudinal blue streaks. Anal fin black with a light blue leading edge and 1-3 egg-dummies. Pelvic fins black with light blue leading edges.

*Monkey Bay females:* Coloration similar to that of males except that the body bars tend to be brownish rather than blue and the blue edges to the fins are not as intense.

**Geographical variation.** The populations at Nkudzi, Kanchedza Island, Thumbi West Island and Mumbo Island appear deeper bodied and are not as intensely coloured as those of Monkey Bay, Nankumba and Domwe Island.

At Zimbabwe the individuals are larger than those of Monkey Bay, deeper bodied and almost jet-black with hardly any indication of barring, and the dorsal, caudal and anal fins have orange trailing edges.

**Habitat.** The preferred habitat is among small and medium-sized rocks though some individuals take up residence in gaps between large rocks and boulders. This species is most numerous in the shallows, but occurs to at least 25 m depth.

**Territoriality.** Males, females and juveniles larger than 60 mm hold territories which they defend fiercely against all intruders. These territories are usually in gaps between rocks or in rocky fissures. Territories are so fiercely defended that once they become established they invariably have gardens of long green Aufwuchs which are in marked contrast with the heavily cropped regions that surround them.

**Feeding.** Territorial fishes feed from within their 'gardens' and on plankton in the water column. The stomach contents of 97 territorial individuals caught in 1-3 m depth at Monkey Bay contained on average 50% loose Aufwuchs, 20% benthic Invertebrata, 18% C1, 6% C2 and 6% plankton. The stomach contents of 28 non-territorial individuals contained on average 58% loose Aufwuchs, 19% plankton, 10% benthic Invertebrata, 8% C1, and 5% C2.

### 2. *Pseudotropheus elongatus* 'yellow tail'

**Synopsis.** An elongate species which lives in holes and caves among the rocks, usually beyond 10 m depth. It is frequently seen on the roofs of caves swimming upside down.

**Distribution.** Nkudzi (C), Mpandi I. (U), Kanchedza I. (R), Monkey Bay (U – C), Nankumba Peninsula (U – C), Domwe I. (C), Zimbabwe I. (C), Thumbi West I. (U), Mumbo I. (C).

**Coloration. Monkey Bay males:** Body sky-blue with 4 – 5 pitch-black bars anterior to the vent and 3 – 4 faint bars posterior to the vent; barring so faint on caudal peduncle that it appears unbarred in many individuals; belly yellowish. Head black with two bright blue interorbital bars. Dorsal fin light blue suffused with yellow; prominent black submarginal band running most of the fin's length; vertical black bars of the body penetrating the fin in some individuals to merge with the submarginal band; lappets bright blue tending to white with yellow flecks and yellow tips; trailing edge orange-yellow. Caudal fin blue with yellow cast, black upper and lower borders and light blue outer edges. Anal fin black with hyaline trailing edge, light blue leading edge; 2 – 5 orange-yellow egg-dummies. Pelvic fins black with light blue leading edges.

**Monkey Bay females:** Body blue-grey with dark grey barring. Head dark grey with blue-grey interorbital bars. Dorsal fin blue-grey with black submarginal band. Caudal fin blue-grey with black upper and lower borders. Anal and pelvic fins black.

**Geographical variation.** A clinal gradation with regard to adult male coloration was found: the tail and caudal peduncle become progressively more yellow as the distance from Monkey Bay increases northwards along the Nankumba Peninsula, Domwe Island and eventually to Zimbabwe Island. At the islands of Thumbi West and Mumbo, males resemble closely the yellow-tailed form which occurs at Zimbabwe. To the south of Monkey Bay, at Nkudzi, Mpandi Island and Kanchedza Island males have, in addition to the yellow tail and caudal peduncle, a brighter yellow belly and dorsal fin than has the Monkey Bay form. Females appear alike in all areas, but south of Monkey Bay have a yellow cast on the belly, caudal peduncle and tail.

**Habitat.** This species is most common among large rocks and boulders but also occurs among smaller rocks. It is usually associated with holes and caves which are provided by rounded or broken rocks. *P. elongatus* 'yellow tail' appears to be most common at depths greater than 10 m and occurs to at least 40 m depth at the islands of Thumbi West, Domwe and Zimbabwe. It also lives in shallow water, and at Kanchedza Island and Mpandi Island it is restricted to the shallows as these islands are in water which goes to sand in less than 10 m.

**Territoriality.** Aggression of territorial males is directed at conspecifics only, but as individuals of this species are fairly widely spaced, encounters are uncommon.

**Feeding.** This species always orientates with its belly towards the rock surface, thus it is typically found upside down beneath rocky overhangs where it crops Aufwuchs from the underside of rocks; it also feeds from vertical and horizontal surfaces. It has also been seen feeding on plankton. Analysis of the stomach contents of 13 individuals caught between 5 and 15 m depth in Monkey Bay revealed that they had ingested on average 65% loose Aufwuchs, 28% phytoplankton, 3% zooplankton, 2% benthic Invertebrata and about 1% C1 and C2.

### 3. *Pseudotropheus elongatus* 'boadzulu'

**Synopsis.** A blue and black barred, lithophilous species endemic to Boadzulu Island.

**Distribution.** Boadzulu I. (C).

**Coloration.** This species is similar in coloration and markings to *P. elongatus* 'slab' except that in males the belly is black and the rayed portions of the dorsal and caudal fin are blue and not yellow. However, these fins do have yellow spots on the trailing portions. Female coloration is similar to that of males, but slightly darker.

**Habitat.** The preferred habitat of *P. elongatus* 'boadzulu' is among small and medium-sized rocks. The depth distribution of *P. elongatus* 'boadzulu' is from 3 to at least 40 m.

**Territoriality.** Males of this species were found to be weakly territorial and females are apparently not territorial. Non-territorial individuals are solitary.

**Feeding.** It was seen to feed by nipping at the Aufwuchs mat and catching plankton in the water column.

### 4. *Pseudotropheus elongatus* 'reef' (Plate 6c)

**Synopsis.** A heavily barred species found at rocky reefs.

**Distribution.** Eccles Reef (C), West Reef (C).

**Coloration. Eccles Reef males:** Body royal blue with 10 prominent, black bars which all merge dorsally to form a black dorsomedial band; belly black. Head black with a blue occipital bar and blue interorbital bar. Dorsal fin blue, but dominated by a broad, pitch-black submarginal band; lappets blue-white; rays pale blue. Caudal fin blue with black rays and black upper and lower borders; edges white. Anal fin black with 1 – 4 yellow egg-dummies. Pelvic fins black with blue-white leading edges.

**Eccles Reef females:** Markings identical to males, but ground colour grey-blue and the barring and banding dark brown.

**Habitat.** The preferred habitat is over medium-sized and large rocks from 3 to 15 m depth.

**Territoriality.** No definite territorial defence was seen. Members of this species normally occur singly.

**Feeding.** Seen to feed from the Aufwuchs mat and upon plankton.

### 5. *Pseudotropheus elongatus* 'brown' (Plate 6d)

**Synopsis.** A brown species which inhabits rocky reefs.

**Distribution.** Eccles Reef (C), West Reef (C).

**Coloration. Eccles Reef males and females:** Body and head uniform chocolate-brown with a faint blue-grey interorbital bar. Dorsal fin grey-brown with a black submarginal band running its full length; lappets white with orange tips. Caudal fin brown at base, black distally with light blue inter-ray membranes; upper and lower borders pitch-black with white edges. Anal fin black with a single orange-yellow egg-dummy. Pelvic fins black with white leading edges.

**Habitat.** The preferred habitat appears to be over the upper surfaces of large rocks, boulders and slabs in water 3 – 12 m deep. The total depth range extends from the surface to 18 m.

**Territoriality.** Males defend territories in gaps between rocks or in cracks or fissures within rocks or alongside protuberances on slabs or boulders. Both conspecific and heterospecific aggression is fierce and algal gardens occur in most territories. Females and other non-territorial individuals are normally solitary, occasionally forming small groups.

**Feeding.** This species feeds by nipping at the Aufwuchs and employing an upward or sideways jerk of the head to wrest filamentous algae from the rocks. It remains close to the rock surface, but will nevertheless feed upon plankton in the water immediately above the rocks.

#### 6. *Pseudotropheus elongatus* 'dinghani' (Plate 6e)

**Synopsis.** A common yellow-and-black species of the rocky shores of Chinyankwazi Island.

**Distribution.** Chinyankwazi I. (C – N).

**Coloration. Males:** Body olive-yellow with 7–8 black vertical bars, but the 3–4 posterior bars are faint; chest and belly black. Head grey-brown tending to black with 2 olive-yellow interorbital bars and 1 occipital bar; chin and gular region black. Dorsal fin olive-yellow with a prominent black submarginal band and yellow lappets. Caudal fin yellowish with black upper and lower borders and black rays. Anal fin black with a whitish-blue leading edge, a hyaline trailing portion and usually only 1 yellow egg-dummy. Pelvic fins black with whitish-blue leading edges.

**Females:** Similar to males except that ground coloration is beige-brown rather than olive-yellow and black markings are dull.

**Habitat.** The preferred habitat is among small and medium-sized rocks at 8–15 m depth, but it also occurs over large rocks, boulders and slabs and has a depth range from the surface to at least 35 m.

**Territoriality.** Males hold territories in crevices and gaps between rocks. All intruders are chased aggressively. None of the territories had clearly defined gardens at the time of the survey (Jan./Feb. 1980). Non-territorial individuals may occur in large schools of several hundred individuals, most of which stay in the water column a metre or more above the substratum. The remaining individuals are solitary and occur among the rocks.

**Feeding.** Territorial males feed from Aufwuchs within their territories and also upon plankton. Non-territorial individuals feed almost exclusively in the water column. The stomach contents of 14 individuals caught at 6–8 m depth contained on average 90% phytoplankton (*Anabaena* spp.), 7% loose Aufwuchs and small quantities of C1 and C2. Three specimens had ingested a few Copepoda and one had eaten two insect larvae. This result was biased by a phytoplankton bloom at the time of sampling (Jan./Feb. 1980).

The stomach contents of a sample of 6 specimens caught in Dec. 1980 were dominated by zooplankton (50%) and also contained C1 (22%), phytoplankton (10%) and the remainder comprised C2, loose Aufwuchs, benthic crustaceans and insects. Possibly in the absence of plankton *P. elongatus* 'dinghani' would feed mainly on Aufwuchs.

#### 7. *Pseudotropheus elongatus* 'chinyamwezi' (Plate 6f)

**Synopsis.** A blue and yellowish-brown, lithophilous species

common at Chinyamwezi.

**Distribution.** Chinyamwezi I. (C – N).

**Coloration. Males:** Body sky-blue with 8 grey-brown bars; belly, gular region and the ventral part of the chest tan coloured tending to orange in some individuals. Head tan on cheeks, chin and opercula; occipital region and snout dark grey-brown with a light blue occipital bar and 2 interorbital bars. Dorsal fin golden-brown with a narrow black submarginal band and light blue lappets; dorsal fin-spot black and elongate. Caudal fin violet-blue with orange trailing edge and black upper and lower borders. Anal fin black with bluish-grey trailing portion and 2–4 yellow egg-dummies. Pelvic fins orange-brown with black submarginal bands and white leading edges. **Females:** Coloration and markings similar to males, but relatively drab.

**Habitat.** The preferred habitat is among small and medium-sized rocks between 3 and 17 m though individuals are present from the surface to at least 43 m.

**Territoriality.** Males aggressively defend areas around caves, crevices and gaps among the rocks. Many territories contained algal gardens. Territorial males were common to about 20 m depth and though males in breeding dress were found from 20 to 43 m it was not ascertained whether they were defending territories. Females, juveniles and non-territorial adult males usually occur in groups of about 30 individuals, but sometimes as many as 70 individuals shoaled together.

**Feeding.** Stomachs of 8 specimens caught in Jan./Feb. 1980, when a phytoplankton bloom was present contained on average 70% *Anabaena* spp., 12% loose Aufwuchs, 6% zooplankton and small proportions of C1, C2 and benthic Invertebrata. Six specimens caught in December 1980 had eaten zooplankton (65%), phytoplankton (15%), loose Aufwuchs (10%) and filamentous algae (10%).

#### 8. *Pseudotropheus elongatus* 'black' (Plate 6g)

**Synopsis.** An uncommon black, lithophilous species occurring over large rocks.

**Distribution.** Chinyankwazi I. (U – N), Chinyamwezi I. (C).

**Coloration. Males and females:** Uniformly black except for a blue interorbital bar, bluish-white dorsal fin lappets and yellow egg-dummies.

**Habitat.** This species was found over the upper surfaces of medium-sized and large rocks, and boulders. At Chinyankwazi it was found between 6 and 12 m only, but at Chinyamwezi it occurs between 3 and 15 m.

**Territoriality.** Territoriality ranges from extremely fierce defence of crevices in which algal gardens develop, to no indication of territoriality at all. Males were found defending territories most often, but territorial females were also found.

**Feeding.** *P. elongatus* 'black' was seen to nip and jerk at the Aufwuchs and to feed upon plankton.

#### 9. *Pseudotropheus elongatus* 'slab' (Plate 6h)

**Synopsis.** This elongate, barred species is common over upper surfaces of slabs, boulders and large rocks.

**Distribution.** Thumbi West I. (C), Mumbo I. (C) and

**Nakantenga I. (U).**

**Coloration. Thumbi West males:** Body blue with 4 distinct black bars anteriorly and 4–5 faint bars posteriorly. Head pitch-black with bright blue interorbital and occipital bars. Dorsal fin blue with the 4 anterior bars of the body extending into the fin where they merge with the prominent, black submarginal bar; lappets white; rayed portion yellowish with an orange-yellow trailing edge. Caudal fin pale blue with orange-yellow trailing edge and black upper and lower borders. Anal fin blue with black submarginal band and white leading edge; 1–3 yellow egg-dummies. Pelvic fins black with white leading edges.

**Thumbi West females:** Body light yellowish-brown with a blue cast and grey barring. Head grey-brown with blue interorbital and occipital bars. Fin colours and markings similar to those of males, but fainter.

**Geographical variation.** The population at Mumbo Island appears identical with that at Thumbi West, but that at Nakantenga has a black belly and 6 distinct bars on the anterior part of the body which extend into the dorsal fin to merge with the submarginal band. The rayed part of the dorsal fin is blue having less yellow than the Thumbi West form.

**Habitat.** The preferred habitat appears to be over the upper surfaces of large rocks, boulders and slabs. This species is found from the surface waters down to a depth of at least 35 m, but is most abundant between 3 and 15 m.

**Territoriality.** Males hold territories along cracks or crevices in slabs or in clefts between adjacent rocks. They defend these territories so aggressively against all intruders that algal gardens develop. Preliminary observations suggest that most males are not territorial from April to July. Females, juveniles and non-territorial adult males usually form schools of up to 150 individuals which remain close to the surfaces of large rocks and slabs. Solitary individuals may be found among small and medium-sized rocks.

**Feeding.** This species feeds by nipping at the Aufwuchs with rapid upward and sideways jerks of the head. It also feeds on plankton, but remains close to the rock surface when doing so.

**10. *Pseudotropheus elongatus* 'bar' (Plate 6i)**

**Synopsis.** A heavily barred, aggressive species of large rocks, boulders and slabs.

**Distribution.** Maleri I. (C), Nakantenga I. (C), Nankoma I. (U).

**Coloration. Maleri Island males:** Body pale blue with a tan cast and 8–9 grey-brown bars. Head pale brown with a grey-brown occipital region and snout; 2 pale blue interorbital bars and 2 pale blue occipital bars. Dorsal fin pale blue with a conspicuous black submarginal band running its full length; lappets blue-white with yellow-orange tips. Caudal fin blue-grey with black upper and lower borders and white edges. Anal fin black with white leading edge and bluish trailing portion; 2–4 yellow egg-dummies. Pelvic fins grey-brown with black submarginal bands and white leading edges.

**Maleri Island females:** Markings similar to males, but the ground colour dull grey and the barring brown.

**Habitat.** It is most common over large rocks, boulders and slabs in 5 to 15 m depth. Its full depth range is from the surface to at least 28 m.

**Territoriality.** Males and occasionally females are highly aggressive in territorial defence, frequently chasing intruding conspecifics 3–4 m. They also exclude heterospecifics. Territories are usually held in crevices and although well defended against all intruders, few had conspicuous algal gardens when studied (March/April 1980).

**Feeding.** It feeds by nipping at the Aufwuchs and also collects plankton from the water immediately above the rock surfaces, but seldom ventures more than 30–40 cm from the rocks to feed.

**11. *Pseudotropheus elongatus* 'namalenje'**

**Synopsis.** A deep-bodied member of the *P. elongatus* species-group which inhabits the upper surfaces of large rocks, boulders and slabs.

**Distribution.** Namalenje I. (C–N).

**Coloration. Males:** Body pale blue with 8–9 dark grey-brown bars, the posterior 3 normally being faint. Head dark grey-brown with a light blue occipital bar and an interorbital bar; chin, cheeks, opercular and gular regions ochre-brown. Dorsal fin pale blue with black bars from the body crossing its base to merge with the prominent black submarginal band; lappets white with yellowish-orange tips. Caudal fin blue with a yellow tinge and black upper and lower borders. Anal fin yellowish-blue posteriorly, black submarginally with a white leading edge; 1–3 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Markings similar to those of males but dull grey-brown against a yellowish-blue ground colour.

**Habitat.** This species is common over the upper surfaces of large rocks, boulders and slabs which are characteristic of Namalenje Island. It occurs from the surface waters down to the rock-sand interface at 10 m depth.

**Territoriality.** Males vigorously defend territories which are centred around crevices, fissures or gaps in the rocks. Females form schools with non-territorial conspecifics.

**Feeding.** This species feeds from the rock surface and although it takes plankton also, it does not venture more than 10–20 cm into the water column.

**12. *Pseudotropheus elongatus* 'mbenji blue' (Plate 6j)**

**Synopsis.** A blue and black barred species which lives over the upper surfaces of large rocks and boulders in sediment-free zones.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Body royal blue with 7–8 black bars, caudal peduncle tarnished yellow; belly black in most individuals, ochre-yellow in some individuals; dorso-medial ridge black. Head black dorsally with a blue occipital bar and 2 blue interorbital bars; chin and cheeks brownish-yellow. Dorsal fin penetrated by black bars from body that merge with a broad, black submarginal band that runs the full length of the fin; windows of blue occur between the bars; lappets whitish with yellow tips. Caudal fin tarnished yellow with black upper and

lower edges. Anal fin black with 3–7 yellow egg-dummies. Pelvic fins black with light blue leading edges.

**Females:** Markings as those of males, but the bars are grey-brown and the ground colour blue-grey.

**Habitat.** This species is most numerous over the upper surfaces of large rocks, boulders and slabs and occurs from 2 to 16 m depth.

**Territoriality.** Males are territorial, defending areas between rocks, or in cracks in rocks. Females and other non-territorial individuals are usually solitary.

**Feeding.** It feeds from the upper surface of rocks and upon plankton.

### 13. *Pseudotropheus elongatus* 'mbenji brown' (Plate 7a)

**Synopsis.** A dark brown fish occurring on vertical faces of large rocks.

**Distribution.** Mbenji I. (U).

**Coloration. Males:** Body dark brown with darker brown barring. Head dark brown with 2 light blue interorbital bars and an incomplete light blue occipital bar. Dorsal fin brown with a black submarginal band, white lappets with orange tips and orange-tinged trailing edge. Caudal fin brownish-yellow with black upper and lower borders. Anal fin black with 1–3 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Darker in colour than males, tending to be uniformly black with white dorsal fin lappets.

**Habitat.** This species is usually found on the vertical surfaces of large rocks, particularly where vertical pillars of rock are close to one another. Its depth range is from 5 to 18 m.

**Territoriality.** Males are weakly territorial and females are not territorial. This species is normally solitary, but occasionally it is found in small groups, though the members of such groups usually behave independently of one another.

**Feeding.** It crops the Aufwuchs growing on vertical surfaces of rocks and in this respect differs from *P. elongatus* 'mbenji blue' which feeds mainly from upper surfaces.

### 14. *Pseudotropheus elongatus* 'mbako' (Plate 7b)

**Synopsis.** A small, relatively deep-bodied member of the *P. elongatus* species-group occurring among small and medium-sized rocks and in intermediate habitats.

**Distribution.** Found along the north-eastern shores of Likoma Island at Maingano (U), Mbako Point (C) and Makulawe Point (C).

**Coloration. Males:** Body bright royal blue with 8–9 broad black bars. Head black except for 2 light blue interorbital bars and a light blue occipital bar which may be fragmented to form blue patches. Dorsal fin blue, but crossed by extensions of the vertical bars of the flanks which merge with the prominent, broad, black submarginal band; lappets light blue. Caudal fin royal blue with black rays, and black upper and lower borders with white edges. Anal fin black with 1–4 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Almost identical to males, but blue duller and egg-dummies smaller and less intensely coloured.

**Habitat.** It is most common over the upper surfaces of small

and medium-sized rocks, but it also lives over large rocks and in the intermediate zones of the rock-sand interface. It occurs from the surface waters, where it lives in a sediment-free environment, down to depths of at least 40 m where it encounters sediment-covered rocks, but nowhere is it really numerous and so its preferred habitat is not known.

**Territoriality.** Most individuals are not territorial, though some are weakly territorial, defending areas among small and medium-sized rocks.

**Feeding.** This fish feeds by nipping at the Aufwuchs and has been seen to take zooplankton.

### 15. *Pseudotropheus elongatus* 'ndumbi'

**Synopsis.** A truly elongate species from large rocks, where both sexes defend territories containing algal gardens.

**Distribution.** Likoma Island at Ndumbi Rocks (U), Makulawe Point (C), Masimbwe Islet (C).

**Coloration. Makulawe males and females:** Uniformly dark blue-grey with traces of darker barring. A light blue interorbital bar provides the only break in the uniformity of colour.

**Habitat.** Its preferred habitat is among large rocks and boulders in exposed, sediment-free zones. It is most common from 4 to 15 m depth, but its range is from the surface to about 23 m.

**Territoriality.** Territories are held within cracks or gaps among the rocks and are so aggressively defended that algal gardens are apparent. Both sexes are territorial. Territories at Makulawe Point are on average 112 cm long (range 86–147 cm), 21 cm wide (range 8–43 cm) ( $N=8$ ) and all were in rocky fissures that were at least 40 cm deep. The distance between neighbours depends upon the distance between suitable refuges and although the fishes are highly aggressive they tolerate neighbours as close as 38 cm.

**Feeding.** Members of this species feed from within their territories and the stomach contents of 11 individuals caught at Makulawe Point in 6–8 m depth contained on average 84% loose Aufwuchs, 11% zooplankton and the remaining 5% comprised benthic crustaceans and filamentous algae.

### 16. *Pseudotropheus elongatus* 'ornatus' (Plate 7c)

**Synopsis.** Black and blue barred males, yellowish females, restricted to Ndumbi Rocks and Makulawe Point.

**Distribution.** Likoma Island at Ndumbi Rocks (C) and Makulawe Point (U).

**Coloration. Ndumbi males:** Body royal blue with 8 black bars; chest and belly black. Head black with a royal blue occipital bar and 2 royal blue interorbital bars. Dorsal fin black with white lappets and pale blue inter-ray membranes. Caudal fin black at base, but with blue inter-ray membranes distally and black upper and lower borders. Anal fin black anteriorly, hyaline posteriorly with 2–7 yellow egg-dummies. Pelvic fins blue-grey with black submarginal bands and white leading edges.

**Ndumbi females:** Body pale yellow with a light blue cast and faint grey barring. Head grey with blue-yellow interorbital and occipital bars. Dorsal fin blue-yellow with a conspicuous broad, black submarginal band; lappets bluish-white. Anal and pelvic fins yellow with narrow

black submarginal bands and white leading edges.

**Habitat.** This species occurs over the upper surfaces of large rocks, boulders and slabs. Although it occurs down to at least 40 m depth, most adults live in the shallows.

**Territoriality.** Males apparently defending territories were found occasionally, but this is not usually a territorial species. Mixed groups containing adults and juveniles of both sexes congregate over the upper surfaces of rocks. These groups may contain more than 100 members, but they usually comprise less than 30 individuals.

**Feeding.** Members of this species pluck Aufwuchs from rocks and feed on plankton.

#### 17. *Pseudotropheus elongatus* 'gold bar' (Plate 7d)

**Synopsis.** A gold and brown barred species which frequents intermediate habitats of sediment-rich areas in shallow water.

**Distribution.** Likoma I. at Khuyu Bay (C), Chisumulu I. at Liwelo Bay (C).

**Coloration. Likoma males:** Body golden with 7–8 dark brown bars and a black belly. Head black with 2 bluish-yellow interorbital bars and an occipital bar. Dorsal fin black with yellow lappets and a yellow-orange trailing edge. Caudal fin yellow at base, but black distally with black upper and lower borders and yellowish-white edges. Anal fin tarnished yellow posteriorly, black submarginally and with white leading edges; 1–3 yellow egg-dummies. Pelvic fins gold posteriorly with black submarginal bands and white leading edges.

**Likoma females:** Identical to males in markings, but ground colour relatively dull yellow with dark grey-black barring.

**Geographical variation.** The population at Chisumulu Island is slightly deeper bodied, has broader black bars and more black on the belly. Furthermore, the fins are almost totally black with traces of yellow in the trailing portions. Females are also darker than the Likoma Island population.

**Habitat.** This species lives in water which is less than 6 m deep. It occupies intermediate habitats or lives among rocks close to intermediate habitats. Both Khuyu Bay and Liwelo Bay are areas which are rich in sediment.

**Territoriality.** Males are aggressively territorial defending areas among small and medium-sized rocks, sometimes excavating sand-scrape nests. Females are not territorial and are normally solitary.

**Feeding.** This species feeds from the Aufwuchs and forages in the sand.

#### 18. *Pseudotropheus elongatus* 'chisumulu' (Plate 7e)

**Synopsis.** A darkly barred, weakly territorial species.

**Distribution.** Chisumulu I. (C).

**Coloration. Males:** Body pale blue with yellowish tinge and 8–9 broad, black bars and black belly. Head black with pale blue occipital bar and 2 pale blue interorbital bars. Dorsal fin black with pale blue lappets. Caudal fin black with pale blue inter-ray membranes and yellowish trailing edge. Anal fin black with light blue leading edge and 2–3 golden-yellow egg-dummies. Pelvic fins black with

light blue leading edges.

**Females:** Markings identical to those of males, but ground colour is beige-yellow.

**Habitat.** Its preferred habitat is among large rocks, but it occurs in a variety of rocky habitats and sometimes in the intermediate zone. Its full depth range is from the surface to at least 30 m, but it is most numerous between 5 and 15 m.

**Territoriality.** Males are weakly territorial and females are not territorial. This species normally occurs singly or in small groups.

**Feeding.** It feeds from all rock surfaces, but appears to favour vertical surfaces.

#### 19. *Pseudotropheus elongatus* Fryer, 1956

**Synopsis.** A darkly coloured, aggressive fish of medium-sized rocks in shallow water.

**Distribution.** Nkhata Bay (U), and probably also on the rocky shores to the north and to the south.

**Coloration. Males:** Body black with 8 royal blue wedges of colour extending from the base of the dorsal fin to half-way across the flanks. Head black with violet sheen on the posterior and ventral edges of opercula, 2 blue interorbital bars. Dorsal fin black with turquoise lappets and an orange trailing edge to the rayed portion. Caudal fin black with turquoise upper and lower edges. Anal fin dark grey with 2–6 yellow egg-dummies. Pelvic fins black with blue leading edges.

**Females:** Black but usually without the half-barring and turquoise edges to the fins; the yellow egg-dummies inconspicuous.

**Habitat.** It occurs mainly over medium-sized rocks in shallow water.

**Territoriality.** Males are strongly territorial, defending areas within crevices between rocks. Algal gardens occur in many territories. Some individuals in female coloration were also seen defending territories, but none were caught to establish their sex.

**Feeding.** Fryer (1959a) noted that it collects loose Aufwuchs from the rock surfaces.

#### 20. *Pseudotropheus elongatus* 'nkhata brown'

**Synopsis.** An uncommon reddish-brown lithophilous species in deepish water.

**Distribution.** Nkhata Bay (U), but probably also on the rocky shores to the north and south.

**Coloration. Males:** Body and head brown with a reddish tinge. Dorsal fin brown with a narrow, but prominent, black submarginal band running the full length of the fin; lappets yellow; trailing edge of rayed portion reddish-orange. Caudal fin dark brown, but orange-red distally and on the upper and lower borders. Anal fin black with a reddish-brown trailing portion and white leading edge; egg-dummy yellow, usually only one present, but absent in some individuals. Pelvic fins orange-red posteriorly with black submarginal bands and white leading edges.

**Females:** Dark chocolate-brown tending to black, with orange-brown trailing edges to the fins.

**Habitat.** This species lives among medium-sized and large rocks in sediment-rich zones from 8 to 30 m.

**Territoriality.** Males are weakly territorial. In general the individuals of this species are solitary.

**Feeding.** This species feeds from all rock surfaces, though preliminary observations suggest that it favours vertical surfaces.

### 21. *Pseudotropheus elongatus* 'mara' (Plate 7f)

**Synopsis.** A small species of the rock-sand interface.

**Distribution.** Mara Rocks (C).

**Coloration. Males:** Body pale blue with 6–7 faint grey bars. Head pale blue with a grey occipital region and snout. Dorsal fin orange with a light blue rayed portion and yellow lappets. Caudal fin blue with black rays. Anal fin black with 2–4 yellow egg-dummies. Pelvic fins pale blue with white leading edges.

**Females:** Not known.

**Habitat.** This species lives over sand at the rock-sand interface in 7–10 m depth.

**Territoriality.** Males are territorial, usually excavating nests beneath rocks.

**Feeding.** No information.

### 22. *Pseudotropheus elongatus* 'bee' (Plate 7g)

**Synopsis.** An elongate yellow and black barred species which inhabits intermediate zones.

**Distribution.** Chitande (C), Mara Rocks (C).

**Coloration. Chitande males:** Body yellow with 7–8 black bars and a black belly. Head black with 2 yellowish-blue interorbital bars. Dorsal fin yellowish with a prominent, broad, black, submarginal band and yellow lappets. Caudal fin blue with a yellow cast and prominent black upper and lower borders with white edges. Anal fin black with white leading edges and 2–5 yellow egg-dummies. Pelvic fins black with white leading edges.

**Chitande females:** With a similar but duller pattern of yellowish-brown and black markings.

**Geographical variation.** Males of the Mara Rocks population are bluish-yellow and relatively faintly barred. The head has a distinct blue cast. Each fin has a greater area of yellow than the Chitande form. The Mara Rocks females are similar to the Chitande form.

**Habitat.** This species occupies the intermediate zones and is most numerous along the rock-sand interface. At Chitande it follows this habitat from 3 to at least 40 m depth and at Mara Rocks it occurred from 6 to 15 m depth.

**Territoriality.** Territorial males dig sand-scrape nests alongside or beneath rocks. Females are not territorial and are normally seen in small groups with other non-territorial individuals.

**Feeding.** Members of this species feed from rocky and sandy substrata.

### 23. *Pseudotropheus elongatus* 'mpanga'

A fish which appears similar in colour and markings to *P. elongatus* 'slab' of Thumbi West Island was seen at Mpanga

Rocks in 3–5 m of water. This species is uncommon and no details of coloration and markings were obtained. As it was seen over the upper surfaces of boulders it may be inferred that this is its usual habitat.

### 24. *Pseudotropheus elongatus* 'ruarwe'

**Synopsis.** A small vividly marked blue and black barred lithophilous species of shallow waters.

**Distribution.** Ruarwe (C).

**Coloration. Males:** Body bright royal blue with 9–10 pitch-black bars. Head black with 2 bright royal blue interorbital bars and one occipital bar. Dorsal fin pitch-black with whitish-blue lappets; trailing edge pale blue. Caudal fin blue with black rays and black upper and lower borders; edges of fin white. Anal fin black with hyaline trailing portion and white leading edges; 1–3 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Similar to males but with duller markings.

**Habitat.** This species lives among small and medium-sized rocks in the sediment-free zones from the surface to 15 m, but is most common between 3 and 8 m.

**Territoriality.** Males defend territories which are usually situated between the rocks, but sometimes their territories are over the upper surfaces of rocks. Most aggression is directed towards conspecifics, though they also chase heterospecific intruders. Females, juveniles and non-territorial adult males are usually solitary, but sometimes form small groups over the upper surfaces of rocks.

**Feeding.** This species was seen to feed from the upper surfaces of sediment-free rocks.

### *Pseudotropheus* 'aggressive' species-group

It is unlikely that the morphologically diverse species listed in Table 7 represent a natural group as they possess no apparent uniting morphological characteristic. The group emerged from the results of this study as a convenient categorization of strongly territorial fishes which live among small and medium-sized rocks in shallow water. The territories of these fishes are so aggressively defended that they develop algal gardens. The possession of algal gardens by at least some individuals within each species is a characteristic of the members of this species-group. A further characteristic is that it is usual for both sexes to practise territoriality.

Several members of the *P. elongatus* species-group also show strong territoriality and possess algal gardens, but these fishes are slender-bodied whereas those of the *P.* 'aggressive' species-group are relatively deep-bodied.

Of the 12 species listed in Table 7, four are described. *Pseudotropheus* cf. *Melanochromis perspicax* has been placed in this group as we believe that it has closer ties with the strongly territorial *Pseudotropheus* species than with the weakly territorial *Melanochromis* species (p.207–209).

#### 1. *Pseudotropheus* 'aggressive blue' (Plate 7h)

**Synopsis.** A small, highly aggressive species which lives among small rocks in shallow water.

**Distribution.** Monkey Bay (C), Tsano Rock (C), Thumbi West I. (C), Nankoma I. (C) and Maleri I. (C).

**Coloration. Monkey Bay males:** Body sky-blue with golden-

**Table 7** The members of the *Pseudotropheus* 'aggressive' species-group. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	Ila	Ilb	Ilc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Pseudotropheus</i> 'aggressive blue'	74	Monkey Bay	+	-	-	-	-	+	-	+	-	-	-	-	-	-
2. <i>P.</i> 'aggressive brown'	93	Thumbi West	-	-	-	-	-	+	-	-	-	-	-	-	-	-
3. <i>P.</i> 'aggressive yellow head'	84	Maleri I.	-	-	-	-	-	-	+	-	-	-	-	-	-	-
4. <i>P.</i> 'aggressive grey head'	76	Maleri I.	-	-	-	-	-	-	+	-	-	-	-	-	-	-
5. <i>P.</i> 'aggressive zebra'	101	Mbenji I.	-	-	-	-	-	-	+	-	+	+	-	-	-	-
6. <i>P. tursiops</i> 'mbenji'	102	Mbenji I.	-	-	-	-	-	-	-	-	+	-	-	-	-	-
7. <i>P. tursiops</i>	94	Chisumulu I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
8. <i>P.</i> 'aggressive grey'	103	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
9. <i>P.</i> 'aggressive yellow fin'	94	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
10. <i>P. fuscus</i>	77	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
11. <i>P. fuscooides</i>	86	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
12. <i>P. cf. M. perspicax</i>	66	Chilumba	-	-	-	-	-	-	-	-	-	-	-	-	-	+

yellow gular region, chest, shoulder and belly; 6–7 faint grey-blue bars. Head pale blue dorsally, but snout, cheek, opercular region, chin and branchiostegal membranes golden-yellow; a dark grey interorbital bar and black opercular spot. Dorsal fin pale blue with black rays that fan outwards to produce a blackish trailing edge. Caudal fin pale blue with black rays, black upper and lower borders and yellowish-white edges. Anal fin yellowish-blue with a black patch at its base; 1–3 yellow egg-dummies. Pelvic fins golden-yellow with black submarginal bands and white leading edges.

**Monkey Bay females:** Body khaki-brown with 6–7 dark brown bars and a dark brown mid-lateral band. Head khaki-brown with a grey interorbital bar and black opercular spots. Dorsal and caudal fins pale brown with black rays. Anal and pelvic fins pale brown with black submarginal bands.

**Habitat.** This species lives among small rocks, and at Nankoma Island it also lives among pebble-sized rocks. It is most numerous between 3 and 6 m, but occurs from the surface to 9 m depth.

**Territoriality.** Adults and subadults of both sexes hold territories, about 80 cm in diameter, which are aggressively defended against all intruders. Although algal gardens were apparent in territories among small rocks, they were not readily discernible in territories held among pebbles at Nankoma Island. Territories are centred on gaps between the rocks. Where the rocks or pebbles lie on a sandy substratum, small mounds of sand mark the entrance to each excavated burrow. Gravid females leave their territories to spawn. Four females were found brooding eggs while also defending territories which suggests that at least some return to territories after spawning.

**Feeding.** Territorial members of this species feed from within their territories. The stomach contents of 25 individuals caught at Monkey Bay contained on average 60% loose Aufwuchs, 28% benthic Invertebrata, 5% phytoplankton, 5% C2 and 2% C1.

## 2. *Pseudotropheus* 'aggressive brown'

**Synopsis.** A brown fish which inhabits small and medium-

sized rocks in shallow water where both sexes aggressively defend territories.

**Distribution.** Thumbi West I. (C).

**Coloration. Males:** Body and head chocolate-brown. Dorsal fin brown with a black submarginal band. Caudal fin pale brown with black rays that fan outwards posteriorly. Anal fin black anteriorly, brown posteriorly with 2–3 yellow egg-dummies. Pelvic fins black anteriorly, orange-brown posteriorly.

**Females:** With similar coloration but lighter, the submarginal band in the dorsal fin not as conspicuous and the egg-dummies not as bright as those of males.

**Habitat.** It lives among small and medium-sized rocks in water which is less than 6 m deep.

**Territoriality.** Adults of both sexes are highly aggressive in the defence of their territories. Many territories develop algal gardens.

**Feeding.** This species probably harvests loose Aufwuchs, as it feeds by combing its teeth through the filamentous algae.

## 3. *Pseudotropheus* 'aggressive yellow head' (Plate 7i)

**Synopsis.** A small blue and yellow fish of small rock and intermediate habitats in shallow water.

**Distribution.** Nakantenga I. (C), Maleri I. (C), Nankoma I. (C).

**Coloration. Nakantenga males:** Body sky-blue with 6–7 grey-blue bars; chest and gular region golden-brown. Head blue-grey dorsally on occipital region and snout; cheeks, chin, opercular regions and branchiostegal membranes golden-brown; opercular spot black. Dorsal fin light blue with white lappets. Caudal fin light blue with black upper and lower borders and white edges. Anal fin blue with a black submarginal band and white leading edge. Pelvic fins ochre with black submarginal bands and white leading edges.

**Nakantenga females:** Similar to males in coloration, but not as bright.

**Habitat.** It is common among small rocks and where small

rocks are surrounded by mud or sand. Its greatest numbers occur between 5 and 10 m, but its full depth distribution is from 2 to 18 m.

**Territoriality.** Both sexes are aggressively territorial and will chase most intruders. Algal gardens were found in about 20% of the territories. Nests are occasionally excavated alongside rocks, but usually the fishes tunnel beneath rocks. Two mouth-brooding females were seen defending territories which suggests that they leave their territories to spawn, and resume territoriality thereafter.

**Feeding.** This species was seen to feed upon plankton and from rock surfaces. It nips at the Aufwuchs, apparently combing its teeth through the filamentous strands. Stomach contents of seven individuals caught in 6–8 m at Nakantenga contained on average 55% zooplankton, 30% loose Aufwuchs, 10% filamentous algae (C1 and C2) and 5% phytoplankton.

#### 4. *Pseudotropheus* 'aggressive grey head' (Plate 7j)

**Synopsis.** A small, grey-headed aggressive Mbuna found among small rocks in the shallows of the Maleri Islands.

**Distribution.** Nakantenga I. (C), Maleri I. (U).

**Coloration.** *Nakantenga males:* Body deep blue with 6–7 grey-brown bars; chest and gular region tan coloured. Head grey-brown, tending to rusty-brown in some individuals. Dorsal fin blue with white lappets and a prominent black dorsal fin-spot. Caudal fin blue with black rays; upper and lower borders black with white edges. Anal fin black with white leading edge; 1–2 small yellow egg-dummies. Pelvic fins ochre with black submarginal bands and white leading edges.

*Nakantenga females:* Ground colour of females brown, otherwise with similar markings and colours as males.

**Habitat.** It lives among small rocks in 1–12 m of water, but is most numerous between 3 and 8 m.

**Territoriality.** Males are aggressively territorial and about 60% of territories contained algal gardens. Females keep conspecifics out of their territories and chase away some heterospecific intruders, but no algal gardens were found in areas defended by them.

**Feeding.** This species feeds in a *P. zebra*-like manner and also on plankton. Stomach contents of 6 individuals caught at 6–8 m depth contained on average 45% zooplankton, 18% phytoplankton, 36% loose Aufwuchs and 1% filamentous algae.

#### 5. *Pseudotropheus* 'aggressive zebra' (Plate 8a)

**Synopsis.** A sombre fish which resembles *P. zebra* superficially but is highly aggressive in the defence of its territories. It occurs in shallow water among small and small to medium-sized rocks and has stouter teeth than *P. zebra*.

**Distribution.** Nakantenga I. (U), Maleri I. (C), Nankoma I. (C), Mbenji I. (C), Likoma I. (C–N).

**Coloration.** *Maleri Island males:* Body dark blue with 6–7 black bars and an ochre-yellow chest and gular region. Head dark grey-blue on occipital region and snout with 2 light blue interorbital bars; cheeks, chin and lower parts of opercular regions ochre-yellow. Dorsal fin dark blue, almost black, with a narrow red-orange sub-

marginal band and white lappets; rayed portion orange. Caudal fin rays black with light blue inter-ray membranes, edges of fin orange-red. Anal fin dusky with a black submarginal band and white leading edge; 2–5 yellow egg-dummies. Pelvic fins golden-brown with black submarginal bands and white leading edges.

*Maleri Island females:* Similar to males but darker in colour.

**Geographical variation.** No differences were apparent between the populations of the three Maleri Islands. The population at Mbenji Island is also very similar to the Maleri populations, but does not have as much red on the dorsal and caudal fins and is generally lighter coloured. The Likoma Island population differs from the other populations in that it is darker in colour, has less gold on the head and chest, and does not have any red on the fins.

**Habitat.** This species lives among small and medium-sized rocks in less than 10 m of water and is most numerous between 2 and 7 m.

**Territoriality.** Both sexes are territorial, but males are highly aggressive and almost all of their territories contain algal gardens. In areas where this species is numerous intraspecific interactions are frequent. Territories centre around a refuge in the rocks.

**Feeding.** This species feeds with its mouth pressed against the rock surface and with its body at right angles to the rock. Although it remains very close to the substratum it does also take plankton. Stomach contents of 8 specimens, caught at Nakantenga Island at 4–6 m depth, contained on average 80% loose Aufwuchs, 10% benthic Invertebrata particularly insect larvae, and 10% plankton. Stomach contents of 11 specimens caught at Maingano, Likoma Island, at about 4 m depth, contained on average 85% loose Aufwuchs, 10% zooplankton and 5% benthic Invertebrata.

#### 6. *Pseudotropheus tursiops* 'mbenji' (Plate 8b)

**Synopsis.** A darkly barred species with an elongate rounded snout living among medium-sized rocks of the shallows.

**Distribution.** Mbenji I. (C).

**Coloration.** *Males:* Body deep metallic-blue with 9–10 black bars; belly black. Head black with 2 narrow, blue interorbital bars. Dorsal fin black with whitish-blue lappets that are orange tipped; inter-ray membranes light blue. Caudal fin black with light blue streaks and light blue edges. Anal and pelvic fins black with white leading edges; 1–4 yellow egg-dummies on anal fin.

*Females:* Khaki-brown with dark brown bars and dark brown fins.

**Habitat.** This species lives among medium-sized rocks in sediment-free zones. Most individuals live between 1 and 3 m, but some occur to 6 m depth.

**Territoriality.** Territorial males are aggressive towards all intruders. Some females are territorial and those which are not territorial occur singly. Algal gardens were found in about 15% of territories in May 1980 and in 30% of territories in September 1980.

**Feeding.** This species feeds with the terminal part of its mouth, but it and *P. tursiops* are unusual among the Mbuna in that they can also use the side of their elongate jaws. This

enables them to utilize food in cracks that would be inaccessible to fishes of similar size which feed at right angles to the rock face.

#### 7. *Pseudotropheus tursiops* Burgess & Axelrod, 1975

**Synopsis.** An aggressive lithophilous species which lives among small and medium-small rocks in shallow water.

**Distribution.** Chisumulu I. (C).

**Coloration. Males:** Body bluish-purple with a faint mid-lateral band broken into 10–12 black patches and a dorso-lateral band comprising 7–9 small black patches. Head bluish-purple with a single bright blue interorbital bar and an iridescent light blue band along lower jaw and bases of opercula; prominent black opercular spot. Dorsal fin slate-blue with black rays and an orange-brown trailing edge. Caudal fin blue at base with black rays and hyaline inter-ray membranes distally; trailing as well as upper and lower edges reddish-brown. Anal fin grey-brown with a black submarginal band and whitish leading edge; 3–6 golden egg-dummies. Pelvic fins grey-brown with black submarginal bands and white leading edges.

**Females:** Body brown with 2 faint, black mid-lateral and dorso-lateral bands. Head brown with prominent black opercular spot. Fins yellowish-brown with black dorsal and caudal fin rays, and black submarginal bands in anal and pelvic fins.

**Habitat.** It occurs among small and medium-sized rocks from the extreme shallows to 8 m depth.

**Territoriality.** Both males and females are territorial and males are particularly aggressive in the defence of their territories. In August 1980 about 70% of male territories contained algal gardens. Territories are normally centred around a gap or crevice among the rocks in which the fish might take refuge or spawn. The algal growth around the entrances to those holes was particularly dense. Not all adult females are territorial and those which did not defend territories occurred singly.

**Feeding.** This species fed from the Aufwuchs mat by using both the terminal and lateral parts of the jaw.

#### 8. *Pseudotropheus 'aggressive grey'* (Plate 8c)

**Synopsis.** A highly aggressive greyish fish from small and medium-sized rocks in shallow water.

**Distribution.** Common all around Likoma Island.

**Coloration. Males:** Body blue-grey with 7 dark grey bars, a grey chest and a grey caudal peduncle. Head dark grey-brown with two blue-grey interorbital bars. Dorsal fin pale blue with a yellowish tinge, white lappets and a large black dorsal fin-spot. Caudal fin dark grey, with black upper and lower borders, black rays distally and pale blue inter-ray membranes. Anal fin black with a white leading edge and 2–3 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Similar in colour and markings to males, but grey-brown rather than blue-grey and with inconspicuous egg-dummies.

**Habitat.** It inhabits areas of small and medium-sized rocks, usually in water between 4 and 10 m deep, but its depth distribution may extend from the surface to at least 13 m.

**Territoriality.** Both sexes aggressively defend territories, and algal gardens were found in more than 50% of territories in August 1980.

**Feeding.** Members of this species feed mainly from within their territories, but they also take plankton. Stomach contents of 9 individuals caught at Maingano at about 6 m depth contained on average 80% loose Aufwuchs, 10% insects, 4% filamentous algae with plankton and benthic crustaceans comprising the remaining 6%.

#### 9. *Pseudotropheus 'aggressive yellow fin'* (Plate 8d)

**Synopsis.** A deep-bodied yellow-finned, aggressive species of the rocky zones in shallow water.

**Distribution.** Chisumulu I. (C).

**Coloration. Males:** Body dark blue with darker blue barring. Head dark blue. Dorsal fin pale blue anteriorly, but yellow posteriorly. Caudal fin blue, but yellow distally. Anal fin yellow with a blue-grey base; 2–4 bright yellow egg-dummies. Pelvic fins bright yellow with whitish-blue leading edges.

**Females:** Dark, almost black, with dull yellow fin markings.

**Habitat.** This species lives among small and medium-sized rocks in water less than 6 m deep.

**Territoriality.** Males are highly aggressive and most have algal gardens in their territories. Females do not appear to hold territories. Non-territorial individuals are solitary.

**Feeding.** Males feed from the rock surfaces within their territories and also take plankton from the water column, but remain close to the rocks at all times. Non-territorial fishes also stay close to the rocks even when feeding on plankton.

#### 10. *Pseudotropheus fuscus* Trewavas, 1935

**Synopsis.** A small sombre species which lives in the shallows among small and medium-sized rocks.

**Distribution.** Nkhata Bay (A) and Lion's Cove (U).

**Coloration. Nkhata Bay males:** Body dark metallic, royal blue with 7–8 black bars, a black belly, chest and caudal peduncle. Head black with dark greenish-black opercular spot. Dorsal fin dark blue with a broken black submarginal band and large dorsal fin-spot; trailing edge with 2–6 bright orange ocelli. Caudal fin black with royal blue inter-ray membranes, and an orange trailing edge. Anal fin black with blue leading edge and 2 or 3 large yellow-orange egg-dummies. Pelvic fins black with blue leading edges.

**Nkhata Bay females:** Body and head dark brown. Dorsal fin light brown with orange trailing edge and dark brown fin-spot. Caudal fin light brown with black rays and an orange trailing edge. Anal and pelvic fins black with blue-white leading edges and orange trailing edges.

**Habitat.** This species lives among small and medium-sized rocks, usually in a purely rocky environment, but also along the rock-sand interface. However, it always remains very close to the rocks. It is most numerous in less than 5 m of water and is rare beyond 6 m depth.

**Territoriality.** This is a highly aggressive species and adults of both sexes hold territories. Algal gardens were apparent in about 60% of male territories and about 15% of female

territories in October 1980. However, in winter (June 1981) very few gardens were discernible. Some of those males which hold territories among rocks which lie on a sandy substratum excavate burrows under the rocks.

**Feeding.** Food is nipped, nibbled and wrenched from the rocks but in spite of these feeding methods filamentous algae are not removed and stomach contents are comprised almost entirely of loose Aufwuchs (Fryer 1959a).

### 11. *Pseudotropheus fuscoides* Fryer, 1956

**Synopsis.** A sombre, lithophilous species, the members of which aggressively defend territories among small and medium-sized rocks in shallow water.

**Distribution.** Nkhata Bay (C) and Lion's Cove (C).

**Coloration.** The coloration and markings of *P. fuscoides* are almost identical with those of *P. fuscus* and we experienced considerable difficulty in distinguishing between the two species within the lake. This is especially so since the habitat requirements and depth distributions overlap. In general, *P. fuscoides* males are a lighter blue than those of *P. fuscus*, though they do turn dark when disturbed. Females could not be told apart in terms of coloration and markings.

**Habitat.** *P. fuscoides* lives among small and medium-sized rocks and is most numerous between 3 and 8 m depth, but it does occur to 12 m depth.

**Territoriality.** Adults of both sexes are highly aggressive and algal gardens were present in about 20% of male and 10% of female territories (October 1980).

**Feeding.** This species was seen to feed from the Aufwuchs and Fryer (1959a) records that the stomachs he examined contained mainly insect larvae.

**Note:** The similarity of *P. fuscus* and *P. fuscoides* made it very difficult to distinguish between them when counting fishes within the transects and it is possible therefore that considerable error exists. In addition to noting that *P. fuscoides* is lighter blue, we noted that it is more elongate and slightly smaller. At no stage, however, were we absolutely confident that we were not dealing with a single species; the smaller, elongate paler members living in slightly deeper water than the large, deeper bodied members. The differences in dentition and relative eye size may possibly reflect differences in age and size. At Monkey Bay, *Pseudotropheus elongatus* 'aggressive' moves from deeper to shallower water as it grows (Sharp 1981). It is possible that a parallel situation exists at Nkhata Bay and further investigation may show that *P. fuscus* and *P. fuscoides* are the same species. For the time being we have endeavoured to separate the two taxa.

### 12. *Pseudotropheus* cf. *Melanochromis perspicax*

**Synopsis.** A small, aggressive, lithophilous species of the shallows of the north-western lake.

**Distribution.** Ruarwe (C) and Chilumba (U).

**Coloration.** *Chilumba* males: Body powder-blue with faint grey barring and yellow-gold chest. Head pale blue with yellow-gold cheeks, snout, chin, gular region and branchiostegal membranes. Dorsal fin pale blue with whitish lappets and orange spots in the rayed section. Caudal

fin blue with orange spots in the inter-ray membranes; rays black. Anal fin pale blue with a black submarginal band and white leading edge; one large yellow egg-dummy. Pelvic fins blue with black submarginal bands and white leading edges.

*Chilumba* females: Body and head khaki-brown with faintly yellow chest, cheeks, chin and gular region. Fins pale brown but caudal fin with black rays and anal and pelvic fins with black submarginal bands.

**Geographical variation.** Ruarwe males appear identical to those of the Chilumba population, except that the yellow on the ventral side of the head and chest is pale. Furthermore, this population lacks the black rays which are prominent in the caudal fin of the Chilumba form. Females of the two populations are identical except that the Ruarwe form does not have black rays in the caudal fin.

**Territoriality.** Males are particularly aggressive in the defence of their territories, expelling all intruders. Some territories contain well-defined algal gardens. About 50% of females are territorial and an estimated 20% of their territories contained algal gardens. Non-territorial individuals occur singly.

**Feeding.** This species feeds from the Aufwuchs mat on the rocks and territorial individuals appear to feed exclusively from within their defended areas. Stomach contents of 4 males and 1 female caught at 6 m depth at Chilumba contained on average 90% loose Aufwuchs, 8% benthic Invertebrata and 2% filamentous algae.

**Note:** Superficially this species resembles *Melanochromis perspicax*, and may prove to be conspecific. By virtue of its aggressive behaviour and its lack of longitudinal barring, it has been placed in the *Pseudotropheus* 'aggressive' species-group for the time being.

### *Pseudotropheus* 'miscellaneous' species-group

Those members of the genus which show no clear affinity with the other five groups (Tables 2 to 7) are listed in Table 8. The species listed here are morphologically and behaviourally diverse and the group is undoubtedly polyphyletic. Three species have been described. A further described species *Pseudotropheus purpuratus* Johnson, 1976, cannot be matched with any of the fishes found during this survey.

#### 1. *Pseudotropheus lucerna* 'brown'

**Synopsis.** This species inhabits shallow, intermediate zones in the south-eastern arm of Lake Malawi. Males are brown and mauve. Females are brown. The large black dorsal fin-spot is a prominent feature of this species.

**Distribution.** Kanchedza I. (U), Chigubi (C), Nkudzi (C), Mpandi I. (U), Nkopola (U).

**Coloration.** *Nkudzi* males: Body brownish ground colour with mauve, sometimes purple, back and a yellowish-brown chest and belly. Head brownish, but mauve dorsally with yellow chin and gular region. Dorsal fin mauve with conspicuous, large black fin-spot. Detailed notes on other fin colours are not available.

*Nkudzi* females: Body light brown with numerous black blotches on the flanks. Most readily recognized by the conspicuous black dorsal fin-spot.

**Table 8** The members of the *Pseudotropheus* 'miscellaneous' species-group. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-), introduced (i)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	IIa	IIb	IIc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Pseudotropheus lucerna</i> 'brown'	not	caught	-	+	-	-	+	-	-	-	-	-	-	-	-	-
2. <i>P.</i> 'chinyankwazi'	70	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
3. <i>P.</i> 'tiny'	62	Thumbi West I.	-	-	-	-	-	+	-	-	-	-	-	-	-	-
4. <i>P. socolofi</i>	67	Thumbi West I.	-	-	-	-	-	i	-	-	-	-	-	-	-	-
5. <i>P.</i> 'dumpy'	58	Maleri I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-
6. <i>P.</i> 'burrower'	60	Maleri I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-
7. <i>P.</i> 'red dorsal'	81	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
8. <i>P.</i> 'yellow tail'	90	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
9. <i>P.</i> 'ndumbi gold'	82	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
10. <i>P.</i> 'cobalt'	97	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
11. <i>P.</i> 'thin stripe'	not	caught	-	-	-	-	-	-	-	-	-	-	+	-	-	-
12. <i>P.</i> 'fin spot'	94	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
13. <i>P.</i> 'membe deep'	61	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
14. <i>P.</i> 'lime'	52	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
15. <i>P.</i> 'kingsizei'	76	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
16. <i>P.</i> 'jacksoni'	92	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
17. <i>P.</i> 'newsi'	72	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
18. <i>P. minutus</i>	66	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	+	+
19. <i>P. lucerna</i>	93	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
20. <i>P.</i> 'polit'	58	Lion's Cove	-	-	-	-	-	-	-	-	-	-	-	+	-	-

**Habitat.** This species frequents intermediate zones, favouring regions where small rocks occur over sand. *P. lucerna* 'brown' has not been found below 4 m depth and is most numerous in the upper 2 m.

**Territoriality.** Males are aggressively territorial, but females are not territorial, occurring singly or in small groups.

**Feeding.** Members of this species were observed feeding from the Aufwuchs mat.

## 2. *Pseudotropheus* 'chinyankwazi'

**Synopsis.** A lithophilous fish which looks like *Pseudotropheus zebra*, but is smaller and has stouter dentition.

**Distribution.** Chinyankwazi I. (N).

**Coloration. Males:** Body blue with 8–10 wide black bars. Head black with 2 pale blue interorbital bars. Dorsal fin blue, but dominated by a very broad, black submarginal band.

**Females:** Same markings as males, but grey and not blue.

**Habitat.** It lives among small and medium-sized rocks from 3 to at least 35 m depth, but is most common between 15 and 25 m.

**Territoriality.** Males defend territories of about 1 m diameter principally against conspecifics, but they also evict other intruders. Females, juveniles and non-territorial adult males remain about 1–2 m above the rocks in large schools.

**Feeding.** The feeding behaviour of this species resembles that of *Petrotilapia* spp. and *Pseudotropheus zebra* in that it adopts a position perpendicular to the rock face. At the time of the survey (Jan./Feb. 1980) plankton was abundant at Chinyankwazi and few fish fed from the rock surfaces.

The stomachs of 7 non-territorial individuals contained on average 85% phytoplankton (*Anabaena* spp.) and 15% zooplankton. Stomachs of 5 territorial individuals contained on average 48% phytoplankton, 25% zooplankton, 30% C2 and 7% C3.

## 3. *Pseudotropheus* 'tiny' (Plate 8e)

**Synopsis.** Individuals of this species are small. They inhabit intermediate zones, mainly pockets of sand among rocks and the rock-sand interface.

**Distribution.** Thumbi West I. (C).

**Coloration. Males:** Body deep blue with 5–7 broad, black bars. Head with a black occipital region, and snout with a light blue interorbital bar; cheeks, chin and opercular areas dark brown. Dorsal fin blue, but with the black bars from the body extending into it to merge with the prominent black submarginal band that runs the length of the fin; lappets whitish-blue. Caudal fin blue with black rays and light blue edges. Anal fin mainly black with a white leading edge and pale blue trailing edge; 2–4 yellow egg-dummies. Pelvic fins mainly black with white leading edges and blue-grey trailing edges.

**Females:** Same markings as males, but grey instead of blue and therefore with a darker overall appearance.

**Habitat.** This species occurs in intermediate habitats, particularly where small pockets of sand occur in a predominantly rocky area. It also occurs over rocky slabs and at the rock-sand interface. It is most common between 3 and 15 m, but at Mitande Rocks, off Thumbi West, it was found to 25 m.

**Territoriality.** Males hold territories over sand alongside rocks and some individuals dig sand-scrape nests beneath

rocks. Territorial aggression appears to be directed at conspecifics mainly, though heterospecifics may also be chased. Females and juveniles occur singly.

**Feeding.** Members of this species feed by nipping at the epilithic algae, picking items from the sand and snapping up plankton.

**Note:** Superficially this species resembles *Pseudotropheus minutus* Fryer, 1956a.

#### 4. *Pseudotropheus socolofi* Johnson, 1974 (Plate 8f)

**Synopsis.** This is a small species which inhabits the intermediate zones in shallow water. Both sexes are pale blue.

**Distribution.** Otter Point (U) and Thumbi West I. (R). These populations were probably introduced by exporters of aquarium fishes. Its provenance is believed to be along the Mozambique coast.

**Coloration. Males and females:** Body pale blue with 9–10 slightly darker blue bars. Head pale blue. Dorsal fin blue with a narrow black submarginal band and white lappets, dorsal fin rays black. Caudal fin pale blue with black rays. Anal fin black with a white leading edge and a blue antero-dorsal section; 1–2 yellow egg-dummies. Pelvic fins black with white leading edges.

**Habitat.** This species occurs over sand near to rocks at 4–10 m depth.

**Territoriality.** Males defend territories over sand near to rocks, but owing to the rarity of this species at Thumbi West and Otter Point little is known of its behaviour.

**Feeding.** No data are available.

#### 5. *Pseudotropheus 'dumpy'* (Plate 8g)

**Synopsis.** A dumpy, barred species of the mud-rock substrata in deepish water.

**Distribution.** Maleri I. (C), Nakantenga I. (C).

**Coloration. Maleri males:** Body pale blue with a yellowish cast and 6–7 dark grey bars; lower chest tan-yellow. Head pale blue dorsally with a dark grey occipital bar and 2 dark grey interorbital bars; snout grey; cheeks, chin, lower opercular regions and branchiostegal membranes tan-yellow. Dorsal fin pale blue with a black submarginal band; the black bars of the body extending across the base of the fin; lappets white with yellow tips. Anal fin hyaline with a black submarginal band and white leading edge; a single large yellow egg-dummy. Pelvic fins black with white leading edges.

**Maleri females:** A nondescript sandy colour with conspicuous barring.

**Habitat.** This species was found from 13 to 28 m where it inhabits areas of small rocks set in the muddy substratum which are characteristic of these depths at the Maleri Islands (p.269).

**Territoriality.** Males defend territories against conspecifics. Nests are excavated beneath the rocks by digging away the underlying mud and sand. Females are solitary and not territorial.

**Feeding.** This species was observed feeding from both rock and mud substrata, and upon plankton.

#### 6. *Pseudotropheus 'burrer'* (Plate 8h)

**Synopsis.** A small fish of the intermediate habitats. Males are sky-blue, but females are reddish-brown. Males dig burrows in which to spawn and find refuge.

**Distribution.** Maleri I. (C), Nankoma I. (U), Nakantenga I. (C).

**Coloration. Maleri males:** Body and head uniform sky-blue. Dorsal fin sky-blue with white lappets that have orange tips. Caudal fin blue with black rays, white upper and lower edges and an orange distal edge. Anal fin black with a white leading edge and a yellow egg-dummy. Pelvic fins blue with black submarginal bands and white leading edges.

**Maleri females:** Body and head reddish-brown. Dorsal fin orange-brown with blue tints. Caudal fin orange-brown with orange edges. Anal and pelvic fins orange-brown with black submarginal bands and white leading edges.

**Habitat.** This species inhabits the intermediate zone, from 3 to 24 m depth.

**Territoriality.** Males are territorial and direct most of their aggression towards conspecifics, but they will chase heterospecific intruders, some of which are much larger than themselves. Territories may be so close to one another that nests of different males are only 60–80 cm apart. To build nests this species burrows under rocks, carrying the sand to the entrance where it is deposited in a mound which marks the excavation. The entrances to these burrows may be so narrow that the residents need to turn on their sides to enter. Females are not territorial, but are solitary and remain close to the substratum.

**Feeding.** This species feeds by nipping at the Aufwuchs. It was also seen to take particulate matter from the sediment which is prevalent in its habitat.

#### 7. *Pseudotropheus 'red dorsal'* (Plate 8i)

**Synopsis.** This species has a rounded head, a subterminal mouth and conspicuous red markings on the dorsal fin. It is lithophilous and lives in the shallows.

**Distribution.** Mbenji I. (C–N).

**Coloration. Males:** Body deep metallic-blue with 7 black bars and a faint black mid-lateral band. Head dark blue with a light blue interorbital bar and a black opercular spot. Dorsal fin grey-blue with a black submarginal band, red lappets, black rays and a narrow orange trailing edge. Caudal fin dark blue with black rays. Anal fin black anteriorly, blue posteriorly with 2–3 yellow egg-dummies. Pelvic fins reddish-orange with black submarginal bands and white leading edges.

**Females:** Body khaki-brown with 7 black bars and with black mid-lateral and dorso-lateral bands. Head brown with a greyish interorbital bar and black opercular spot. Dorsal fin brown with a broken black submarginal band. Caudal fin brown with black rays. Anal fin black. Pelvic fins orange-brown with black submarginal bands and white leading edges.

**Habitat.** This species occurs mainly on exposed shores, particularly on the south-east side of Mbenji Island. It lives among medium-sized and large rocks in less than 10 m

depth.

**Territoriality.** Males are territorial and direct most of their aggression towards conspecifics. Females, juveniles and non-territorial adult males occur in large schools numbering several hundred individuals. These schools occur in less than 2 m depth among large rocks and between rocky pillars.

**Feeding:** Territorial males feed from the Aufwuchs in their territories and upon plankton in the water column above their territories. All non-territorial individuals feed on plankton in the water column.

### 8. *Pseudotropheus* 'yellow tail'

**Synopsis.** An elongate, essentially planktivorous, lithophilous species. Its yellow caudal peduncle and tail are distinguishing features.

**Distribution.** Likoma I., at Masimbwe Islet (N), Ndomo Point (C), Khuyu Bay (R) and Makulawe Point (R).

**Coloration.** *Mazimbwe Islet males:* Body turquoise-blue with 6 brown, wedge-shaped bars; chest, belly and caudal peduncle yellow. Head brown on occipital region and snout with 2 light blue interorbital bars and a light blue occipital bar; cheeks, lips and chin mauve. Dorsal fin completely black anteriorly, tapering to a submarginal bar posteriorly; lappets white; remainder of fin yellow. Caudal fin yellow with black upper and lower borders. Anal fin yellow with black submarginal band and white leading edge; 1–3 bright yellow egg-dummies. Pelvic fins ochre-yellow with black submarginal bands and white leading edges.

*Mazimbwe Islet females:* Similar to males but coloration is not as bright.

**Habitat.** This species occupies regions of medium-sized and large rocks. It is most numerous between 1 and 10 m, but its distribution extends to a depth of at least 30 m.

**Territoriality.** Males are weakly territorial, sometimes leaving their territories to feed elsewhere. Females, juveniles and non-territorial adult males form schools at Mazimbwe Islet and at Ndomo Point where this species is common, but at Khuyu Bay and Makulawe Point it is rare, and non-territorial fish are normally solitary.

**Feeding.** This species feeds almost entirely upon plankton, but occasionally from the rock surfaces.

### 9. *Pseudotropheus* 'ndumbi gold' (Plate 8j)

**Synopsis.** A golden lithophilous species of deepish water. It has a terminal mouth and heavy jaws.

**Distribution.** Likoma I. at Ndumbi Rocks (U).

**Coloration.** Both males and females golden with a greyish cast on the body and black submarginal bands on the pelvic fins.

**Habitat.** It occurs among medium-sized and large rocks and also over boulders. It is most common at 15–25 m, with a full depth range of 8 to at least 40 m.

**Territoriality.** This fish does not appear to be territorial, but occurs singly or in pairs.

**Feeding.** It appears to take detritic material from crevices

and cracks among the rocks and was seen to feed on plankton.

**Note:** In its behaviour and general appearance this species is not unlike *Iodotropheus sprengerae*, but it is relatively large and differently coloured.

### 10. *Pseudotropheus* 'cobalt' (Plate 9a)

**Synopsis.** A medium-large species with a rounded head and subterminal mouth. It inhabits areas of small and medium-sized rocks in shallow, often intermediate, zones. Males are cobalt-blue at Chisumulu Island.

**Distribution.** Likoma I. at Khuyu Bay (C), Ndomo Point (C); Chisumulu I. at Same Bay (C), Membe Islet (U), Mkanila Bay (R).

**Coloration.** *Khuyu males:* Body blue-grey, but light blue ventrally with faint grey barring and brown flecks on the flanks. Head blue-grey, but lighter blue on cheek, chin, gular region and branchiostegal membranes; opercular spot black. Dorsal fin pale blue with a yellow-orange tinge to the rayed portion and an orange trailing edge. Caudal fin blue with a red hue and a yellow distal portion. Anal fin pale blue with an orange-yellow tinge, a faint black submarginal band and a white leading edge; one large yellow egg-dummy. Pelvic fins yellowish-blue, with black submarginal bands and white leading edges. *Khuyu females:* Grey-blue with 8 grey bars. Fins light grey.

**Geographical variation.** Males at Chisumulu Island have a lighter cobalt-blue body and head than males of Likoma Island. The fins are also lighter blue and have the merest hint of yellow. Females of both populations appear identical.

**Habitat.** *P.* 'cobalt' inhabits the shallows, seldom occurring below 4 m depth. It is most numerous among small and medium-sized rocks in sediment-rich areas, usually in intermediate zones or close to such habitats.

**Territoriality.** Males defend territories against conspecifics vigorously, but are less aggressive towards heterospecifics. Territories are among rocks, but occasionally over sand between rocks. Nests may be excavated in sand at the base of a rock. Females are not territorial and usually occur in small groups of less than 10 individuals. They remain close to the rocks, seldom venturing more than 1 m onto sand or 50 cm into the water column.

**Feeding.** Although the oral teeth are stout and appear suitable for cutting filamentous algae, stomach contents of 5 individuals caught at Same Bay each comprised over 90% loose Aufwuchs. The remaining 10% comprised small insects, benthic crustaceans and filamentous algae.

**Note:** The Chisumulu population is sold as 'Chisumulu cobalt' in the aquarist trade.

### 11. *Pseudotropheus* 'thin stripe'

**Synopsis.** A medium-sized, deep-bodied species with a blunt head and terminal mouth. Males are dark blue with narrow light blue bars. Females are dark blue, almost black, with grey bars.

**Distribution.** Likoma I. at Membe Point (U–C), Maingano (R), Mbako (R).

**Coloration.** *Membe Point males:* Body dark blue with 6–7 narrow, light blue bars. Head dark blue, almost black, with light blue interorbital and occipital bars. Dorsal fin dark blue with whitish-blue lappets. Caudal fin dark blue, almost black. Anal fin black with a white leading edge and 2–4 yellow egg-dummies. Pelvic fins black with white leading edges.

*Membe Point females:* Body dark blue, almost black, with 6–7 narrow, grey bars. Fins black.

**Habitat.** This species inhabits areas of medium-sized rock between 10 and 25 m depth.

**Territoriality.** Males are territorial, but as they are cryptic in their behaviour and spend most of their time hidden, little is known of their behaviour. Females are solitary and are apparently not territorial.

**Feeding.** Not recorded.

**Note:** Little is known of this fish which is difficult to approach.

### 12. *Pseudotropheus* 'fin-spot'

**Synopsis.** A grey fish with a prominent black dorsal fin-spot. It lives among small rocks of the intermediate zones in shallow water.

**Distribution.** Likoma Island at Membe Point (C), Maingano (C), Mbako (C), Khuyu (C), Ndomo Point (U), Mbuzi (U) and on a submerged reef of small rocks on the shoreward side of White Rock (C).

**Coloration.** *Maingano males:* Body and head uniform blue-grey. Dorsal fin pale grey with a broken, black submarginal band and a large black dorsal fin-spot. Caudal fin pale grey-blue with black rays and black upper and lower borders. Anal fin black anteriorly, hyaline posteriorly with 1–3 yellow egg-dummies. Pelvic fins bright orange with black submarginal bands and white leading edges.

*Maingano females:* Grey with black fin markings similar to those of males, but without the orange of the pelvics which is a conspicuous feature of males.

**Habitat.** This species is usually associated with small and medium-sized rocks in intermediate zones close to sandy areas. It was not found in water deeper than 7 m and is most numerous between 1 and 4 m.

**Territoriality.** Males defend territories vigorously against conspecifics, but they are less aggressive towards heterospecifics. Females occur singly or in small groups and are not territorial.

**Feeding.** This species feeds from the Aufwuchs and on plankton. Stomach contents of 8 individuals contained on average 92% loose Aufwuchs, 6% C1 and the remaining 2% was insect and crustacean remains.

**Note:** The closest relationship of this species may lie with *Pseudotropheus lucerna* Trewavas, 1935.

### 13. *Pseudotropheus* 'membe deep'

**Synopsis.** A small species in intermediate zones in deepish water. Males are predominantly light blue and black; females are grey and black.

**Distribution.** Likoma Island at Membe Point (C), Maingano (U).

**Coloration.** *Males:* Body pale blue, almost white, with a black chest. Head black except for a light blue interorbital bar and a blue flare on the occipital region. Dorsal fin pale blue with a prominent black submarginal band and contrastingly white lappets. Caudal fin pale blue with black upper and lower borders. Anal fin pale blue with a black submarginal band and white leading edge; 1–2 yellow egg-dummies. Pelvic fins pale blue with black submarginal bands and white leading edges.

*Females:* Same markings as males, but body colour grey-brown and fins light grey.

**Habitat.** This species lives between 10 and 35 m depth in sediment-rich intermediate zones in areas where rocks are small.

**Territoriality.** Males hold territories among small rocks and sometimes alongside a single rock in the sand several metres from other rocks. In many territories sand-scrape nests are dug alongside or beneath the rocks. Females are not territorial and are usually solitary.

**Feeding.** This species was seen to feed from the rocks and in the water column, but its members usually did not venture more than about 40 cm above the substratum to catch plankton.

**Note:** This species resembles superficially *P. 'dumpy'* of Maleri Island in general appearance, behaviour and preferred habitat. However, it is not barred and has different coloration.

### 14. *Pseudotropheus* 'lime'

**Synopsis.** This is probably the smallest of the Mbuna species and appears to have one of the most limited distributions. It lives in intermediate habitats of deep water. It is predominantly a lime-yellow colour.

**Distribution.** Likoma I. at Membe Point (C).

**Coloration.** *Males:* Body and head lime-yellow with an intensification of the yellow on the chin, gular region, branchiostegal membranes and lower chest; opercular spot dark grey. Dorsal fin lime-yellow. Caudal fin lime-yellow with a black upper border distally and black lower border which runs the full length of the fin. Anal fin black anteriorly, hyaline posteriorly with a single, bright yellow egg-dummy. Pelvic fins pale yellow with black submarginal bands and narrow white leading edges.

*Females:* Brownish-yellow with the same black markings as males.

**Habitat.** It lives in sediment-rich, intermediate zones from 15 to 35 m depth and is most numerous at about 25 m. At Membe Point the intermediate zone at this depth is characterized by small rocks in a sand-mud substratum.

**Territoriality.** Males are territorial and appear to chase conspecifics only. Within almost every territory there are 1–3 excavated burrows in which males may seek refuge and, presumably, in which they spawn.

**Feeding.** Individuals of this species were seen to feed from rock, sand and mud substrata and from the water column. Observations of feeding were limited, however, as individuals of this cryptic species hid when divers approached.

### 15. *Pseudotropheus* 'kingsizei' (Plate 9b)

**Synopsis.** A small, barred species of the intermediate zone.

It has an extremely limited distribution.

**Distribution.** The distribution of the species is limited to about 1 000 m<sup>2</sup> in what appears to be an ancient river bed at Maingano, Likoma Island.

**Coloration. Males:** Body pale blue with 6 well-defined black bars anteriorly and 3 to 4 faint bars posteriorly, belly black in some individuals. Head pale blue dorsally, but dark grey, almost black, below the level of the orbit; 2 light blue interorbital bars. Dorsal fin pale blue, tending to white; black patches along the base of the fin where the body bars extend into it; rays black. Caudal fin pale blue with black rays. Anal fin black with white leading edge and a pale blue trailing portion; 2–4 yellow egg-dummies. Pelvic fins black with white leading edges. **Females:** Grey-brown with black markings similar to those of males.

**Habitat.** *P. 'kingsizei'* occurs among small rocks within an intermediate sand-rock habitat. It is most numerous between 10 and 20 m, but has a depth range from 4 to 30 m.

**Territoriality.** Males are territorial, defending areas which are centred around sand-scrape spawning sites which are excavated beneath or alongside rocks. Females, juveniles and non-territorial adult males are solitary or occur in small groups of up to 10 individuals.

**Feeding.** This species feeds upon Aufwuchs, but at the time specimens were caught (August 1980) plankton was abundant and so the stomachs of 11 individuals were crammed with zooplankton (90%) and phytoplankton (10%).

**Note:** The trade name for this species is *P. 'kingsizei'*.

#### 16. *Pseudotropheus 'jacksoni'*

**Synopsis.** A shallow-water, lithophilous fish with a pointed head and terminal mouth. Males are blue-grey with bright orange-red anal and pelvic fins; females are blue-grey with dull orange-red fins.

**Distribution.** Chisumulu I. at Same Bay (C).

**Coloration. Males:** Body blue-grey, darker dorsally than ventrally, with a mid-lateral and a dorso-lateral line each of 8 faint, grey-black blotches. Head blue-grey, darker dorsally than ventrally, with an inconspicuous pale blue interorbital bar and a prominent black opercular spot. Dorsal fin pale blue, with whitish-blue lappets, black rays and an orange trailing edge. Caudal fin blue-grey with black rays, blue-white upper and lower edges and an orange trailing edge. Anal fin red, tending to orange posteriorly, with a red-black submarginal bar and a blue-white leading edge; 2–4 yellow egg-dummies. Pelvic fins bright orange, tending to red in some individuals, with black submarginal bands and blue-white leading edges. **Females:** Greyish with prominent black patches in 2 rows on the flanks. Fins grey with a hint of orange on the anal and pelvic fins.

**Habitat.** It was found in less than 2 m depth among small and medium-sized rocks.

**Territoriality.** Males defend territories aggressively against conspecifics and are usually intolerant of heterospecific intruders. Females are not territorial, but occur singly or in small groups among the rocks.

**Feeding.** This species feeds on Aufwuchs, and stomach

analyses of 4 territorial individuals revealed that they had eaten mainly loose Aufwuchs (85%), benthic Invertebrata (10%) and small proportions of filamentous algae and plankton.

**Note:** This fish is known in the aquarium trade as *P. 'jacksoni'*.

#### 17. *Pseudotropheus 'newsi'* (Plate 9c)

**Synopsis.** A small species of the intermediate zones. Males are predominantly pale blue and females reddish-gold.

**Distribution.** Chisumulu I. at Same Bay (C), Membe Islet (C), Machili Islet (C), Mkanila Bay (C).

**Coloration. Males:** Body and head usually powder-blue, but sometimes with faint darker blue barring and a greyish-blue head. Dorsal fin pale blue with white lappets, black rays, and 2–3 yellow ocelli on the trailing edge. Caudal fin pale blue with black rays, black upper and lower borders and white edges. Anal fin pale blue with a broad, black submarginal band and white leading edge; 3–6 orange-yellow egg-dummies. Pelvic fins blue with black submarginal bands and white leading edges. **Females:** Reddish-gold body, head and fins. Faint darker red barring on flanks. Blackish markings on the fins similar to those of males.

**Habitat.** This species inhabits areas of small rocks on sandy substrata usually in 3 to 10 m of water. The full depth range of *P. 'newsi'* is from the extreme shallows to at least 25 m.

**Territoriality.** Males are aggressively territorial. The foci of territories are either holes or gaps in the rocks or burrows which are excavated beneath rocks. Females are not territorial, but occur with juveniles and non-territorial adult males in small groups which remain close to the substratum.

**Feeding.** This species was seen to feed on plankton and upon Aufwuchs which is removed in a sideways, jerking manner from the rocks.

**Note:** (i) This species is referred to as *P. 'newsi'* in the aquarist press (Staeck 1977). (ii) An orange-red fish resembling *P. 'newsi'* females, though differing in that it has broad black submarginal bands in the dorsal, anal and pelvic fins, was found at Chisumulu Island. We originally considered this species to be conspecific with *P. 'newsi'* but as it did not show any behaviour which might confirm conspecificity we now believe it to be a separate species about which we know very little.

#### 18. *Pseudotropheus minutus* Fryer, 1956

**Synopsis.** A small blue and black barred species which lives among small rocks.

**Distribution.** Nkhata Bay (C), Lion's Cove (U), Ruarwe (C), Chitande (C).

**Coloration. Nkhata Bay males:** Body bright royal blue with 7–9 black bars. Head black with 2 blue interorbital bars. Dorsal fin blue with a black submarginal band and white lappets. Caudal fin blue with black rays, black upper and lower borders and white edges. Anal fin black with a white leading edge and 2–5 yellow egg-dummies. Pelvic fins black with white leading edges. **Nkhata Bay females:** Similar to males, but with a grey ground colour.

**Geographical variation.** The population at Lion's Cove appears to have similar colours and markings to that of Nkhata Bay, but at Ruarwe and Chitande the ground colour of males is dull bluish-brown and that of females is grey-brown. These northern populations are drably coloured relative to those of Nkhata Bay and Lion's Cove.

**Habitat.** This species inhabits areas of small and medium-sized rocks and may also be found on patches of sand among rocks. It is most numerous between 4 and 15 m depth but its total depth range extends from the extreme shallows to at least 25 m.

**Territoriality.** At Nkhata Bay, where this species was studied for the greatest period of time, it is one of the most active fishes on the shore. Males aggressively defend their territories against many species, and they frequently indulge in boundary fights. Females are not territorial, but are numerous over the areas occupied by territorial males.

**Feeding.** Loose Aufwuchs is collected by nipping, nibbling and jerking at the algal mat (Fryer 1959a).

### 19. *Pseudotropheus lucerna* Trewavas, 1935

**Synopsis.** A fish of the intermediate zone in shallow waters. Males are brown and purple with a prominent dorsal fin-spot and orange pelvics; females are silvery grey.

**Distribution.** Nkhata Bay (C), Lion's Cove (C). Fryer (1959a) found this species at Ruarwe.

**Coloration.** *Nkhata Bay males:* Body yellowish-brown dorsally with golden-brown shoulders; grey-brown flanks, mauve belly and a blue ventral region to the chest; 7 grey bars. Head yellowish-brown with a golden-brown occipital region; a narrow black interorbital bar; purple edges to the opercula; a black opercular spot and blue chin. Dorsal fin light purple with a broken black submarginal band and yellowish-blue lappets; rayed portion of the fin yellow-orange with a large, black fin-spot. Caudal fin yellow with black rays, yellow-orange trailing portion and black upper and lower borders. Anal fin hyaline with a black submarginal band, orange-red leading edge and reddish trailing portion; a single large yellow egg-dummy. Pelvic fins bright orange-red with black leading edges.

*Nkhata Bay females:* Body silvery-grey with a faint blue sheen and white belly. Head greyish with conspicuous black opercular spot. Dorsal fin pale transparent grey with yellow hue, a narrow, broken, black submarginal band, a prominent large black dorsal fin-spot and small black patches on the rays. Caudal fin grey with black rays and black upper and lower borders. Anal fin hyaline with a black submarginal band and white leading edge. Pelvic fins grey with black submarginal bands and white leading edges.

**Habitat.** *P. lucerna* is a fish of the intermediate zones and also occurs among macrophytes. It was not found below 7 m depth.

**Territoriality.** Males defend their territories aggressively against conspecifics, but are more tolerant of heterospecifics. They dig nests alongside rocks and sometimes among the fronds of *Vallisneria aethiopica*. Females are not territorial and usually occur in small groups of not more than 10 individuals.

**Feeding.** *P. lucerna* was seen to feed from the rocks, sand and macrophytes. Stomach contents examined by Fryer (1959a) comprised mainly loose Aufwuchs and some filamentous algae.

### 20. *Pseudotropheus 'polit'* (Plate 9d)

**Synopsis.** A small lithophilous species; males are white and black and have the ability to change colour rapidly. Females are grey-brown.

**Distribution.** Lion's Cove (C).

**Coloration.** *Males:* Body white with a bluish hue and very faint blue bars. Head black with two blue-white inter-orbital bars. Dorsal fin white with blue cast. Caudal fin pale blue with white inter-ray membranes. Anal fin white with a black submarginal band and white leading edge; 2–4 yellow egg-dummies. Pelvic fins black with white leading edges.

*Females:* Body blue-grey with a broad, dark grey mid-lateral and a broad dorso-lateral band. These longitudinal bands are broken to form three parts, the posterior part of the mid-lateral band forming a dark patch on the base of the caudal fin. Head grey-brown. Dorsal fin whitish-blue with a yellow trailing edge. Caudal fin grey-blue with a yellow trailing edge and a dark grey patch which forms the posterior part of the mid-lateral band. Anal fin yellow with a black submarginal band and white leading edge. Pelvic fins whitish-blue with black submarginal bands and white leading edges.

**Habitat.** *P. 'polit'* lives among medium-sized rocks and occasionally in intermediate areas between 1 and 25 m depth. Most individuals occur between 5 and 12 m.

**Territoriality.** Territorial males aggressively chase intruders and display frequently to neighbouring conspecifics. Females are solitary and none was seen holding a territory.

**Feeding.** It feeds on Aufwuchs and upon particulate detritic material which accumulates between rocks.

**Note:** Males of this species have the ability to change colour almost instantaneously from the startling blue-white of sexually active individuals to the drab grey-brown of females. They frequently changed colour when approached by divers and always did so immediately when trapped in the net.

### Genus *Melanochromis* Trewavas, 1935

Trewavas (1935) distinguished this genus from *Pseudotropheus* on the basis of differences in pharyngeal teeth; the *Melanochromis* studied had fewer and larger teeth on the pharyngeal bone. While working on the Mbuna of Nkhata Bay Fryer (1956a, 1957, 1959a) found that the distinction between the two genera was unclear in some instances. Since then the problem has been complicated further by the discovery of numerous species of both genera.

In several articles of the aquarist literature (Johnson 1975; Burgess 1976; Staeck 1977; Loisel 1979) it was suggested that those *Pseudotropheus* species with longitudinal bands (*P. auratus* (Boulenger, 1897); *P. johanni* Eccles, 1973; *P. simulans* Eccles, 1973) have more in common with similarly marked species of *Melanochromis* than they do with vertically barred species of *Pseudotropheus*. Consequently, aquarists now refer to these species as if they were already

members of the genus *Melanochromis* although no sound taxonomic data have been given to support such a change. Nevertheless, we have found behavioural traits in the field which suggest that these species are more closely related to the genus *Melanochromis*, while D.S.C. Lewis, who is preparing a taxonomic review of the Mbuna, has morphological data which indicate that these three species would be better placed in the genus *Melanochromis*. Consequently, Lewis is formally proposing that all longitudinally banded species which show a reversal of pigmentation patterns in males and females (darkly pigmented bands in males are light in females and *vice-versa*; see also reference to *P. auratus* in Fryer (1959a)) should be assigned to the genus *Melanochromis*. We have anticipated the proposal in this report. The genus *Melanochromis* as it is defined at present, encompasses several lineages, but only one species-complex.

**Melanochromis melanopterus species-complex**

These are slender-bodied fishes with wide terminal mouths and lips that are slightly thickened (Figure 10a). They have longitudinal banding and are, in general, weakly or intermittently territorial. The *M. melanopterus* species-complex appears to represent a single lineage, though Loisel (1979) suggests that the complex may be divided into the short-snouted forms which he refers to as the '*auratus* group' and the long-snouted species of the '*melanopterus* group'. We found little behavioural justification for such a division and D.S.C. Lewis (in prep.) examined members of both groups and found no morphological justification for the taxonomic subdivision proposed by Loisel. We, therefore, do not divide this species-complex.

The *M. melanopterus* species-complex contains 15 species, six which have already been described (Table 9).

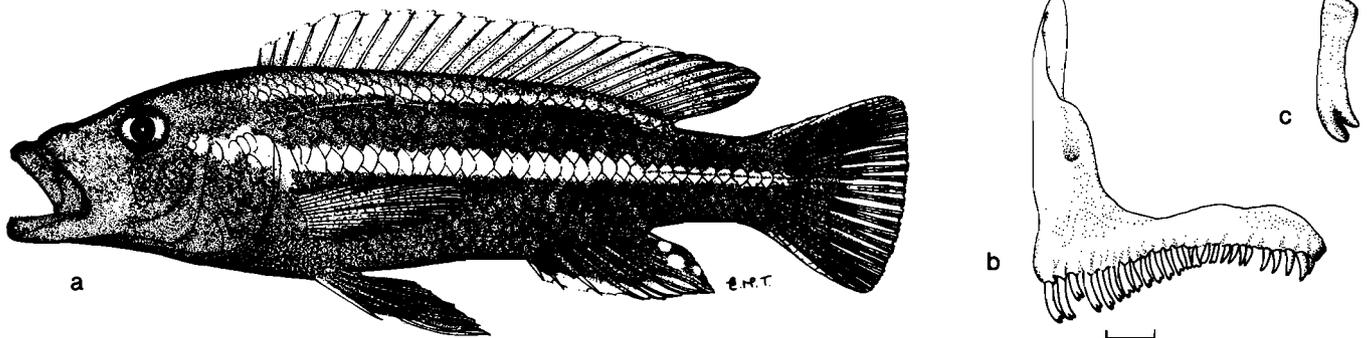


Figure 10 (a) *Melanochromis melanopterus*, Monkey Bay, 126 mm SL. (b) Lateral aspect of left premaxilla of *M. melanopterus* (Scale = 1 mm). (c) Anterior outer row tooth of *M. melanopterus*.

**Table 9** The members of the genus *Melanochromis*. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-), introduced (i)

A = *Melanochromis melanopterus* species-complex. B = *Melanochromis* 'heterogenous' species-group

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	IIa	IIb	IIc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
<b>A</b>																
1. <i>Melanochromis melanopterus</i>	114	Likoma I.	+	+	+	+	-	+	+	-	-	+	+	+	-	+
2. <i>M. auratus</i>	79	Monkey Bay	+	+	-	+	-	+	+	+	+	+	-	-	-	-
3. <i>M. vermivorus</i>	80	Zimbabwe I.	+	+	-	-	+	+	+	+	-	+	-	-	-	-
4. <i>M. simulans</i>	74	Masinje Rocks	-	-	-	+	-	-	-	-	-	-	-	-	-	-
5. <i>M. johanni</i>	67	Masinje Rocks	-	-	-	+	-	-	-	-	-	-	-	-	-	-
6. <i>M. 'blotch'</i>	98	Chisumulu I.	-	-	-	+	-	-	-	-	-	-	+	-	-	-
7. <i>M. 'lepidophage'</i>	103	Makanjila	-	-	-	+	-	-	-	-	-	-	-	-	-	-
8. <i>M. 'chinyamwezi'</i>	76	Chinyamwezi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
9. <i>M. cf. chipokae</i>	121	Thumbi West I.	-	-	-	-	-	+	+	-	-	-	-	-	-	-
10. <i>M. 'slab'</i>	92	Mbenji I.	-	-	-	-	-	-	-	+	?	+	-	-	-	-
11. <i>M. parallelus</i>	114	Likoma I.	-	-	-	-	-	i	-	-	-	-	+	+	+	+
12. <i>M. 'red'</i>	71	Chisumulu I.	-	-	-	-	-	i	-	-	-	-	+	-	-	-
13. <i>M. 'black-white johanni'</i>	84	Likoma I.	-	-	-	-	-	i	-	-	-	-	+	-	-	-
14. <i>M. 'maingano'</i>	70	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
15. <i>M. 'blue'</i>	101	Chitande	-	-	-	-	-	-	-	-	-	-	+	+	+	+
<b>B</b>																
1. <i>M. cf. brevis</i>	120	Boadzulu I.	+	+	+	-	+	-	-	+	-	-	-	-	-	-
2. <i>M. crabro</i>	94	Chinyankwazi I.	-	-	-	+	+	-	-	+	-	+	+	+	-	-
3. <i>M. labrosus</i>	101	Likoma I.	-	-	-	-	-	-	-	-	-	+	+	-	-	-
4. <i>M. 'brown'</i>	112	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
5. <i>M. joanjohnsonae</i>	74	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-

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Four additional species were described by Johnson (1975, 1976), but none of these species were found during the survey and consequently they are not included in the species list. *M. mellitus* Johnson, 1976 is purported to come from Mumbo Island, though we did not find a fish like it (other than female *M. vermicivorus*) at the island. *M. interruptus* Johnson, 1975 is supposed to come from Likoma Island, but we were unable to match fish of this island to the description. The putative type locality of *M. chipokae* Johnson, 1975 is Chipoka Rocks, an area which we did not visit. *M. loriae* Johnson, 1975 is very similar to *M. chipokae* but exhibits slight differences in coloration. *M. loriae* is also reputedly from Chipoka Rocks.

### 1. *Melanochromis melanopterus* Trewavas, 1935 (Figures 10a – c)

**Synopsis.** An elongate, lithophilous species with a large terminal mouth and longitudinal banding. It is most common among medium-sized and large rocks of deepish water.

**Distribution.** This species was found at all major areas visited except Chinyankwazi I., Chinyamwezi I., the Maleri Is. and Mbenji I. It is uncommon or rare at most diving stations.

**Coloration. Monkey Bay males:** Body dark brown, almost black with blue mid-lateral and dorso-lateral bands. Head black with a blue interorbital bar and a blue extension of the mid-lateral band which reaches the eye. Dorsal fin yellowish with blue cast; lappets white with orange tips; rays black, trailing edge orange-brown. Caudal fin black, but inter-ray membranes and the upper and lower borders blue; trailing portion of fin orange-brown. Anal fin dark brown, almost black, with blue edges and 1 – 2 yellow egg-dummies. Pelvic fins black with light blue leading edges.

**Monkey Bay females:** Body brown with dark brown mid-lateral and dorso-lateral bands. Head dark brown. Dorsal fin yellowish-brown, lappets and trailing portion yellow-orange. Caudal fin brown with orange trailing edge. Anal fin black with blue leading edge, orange trailing edge and yellow egg-dummy. Pelvic fins dark brown with blue leading edges and orange-yellow trailing edges.

**Geographical variation.** At Likoma Island, Chisumulu Island and the north-western coast of Lake Malawi, *M. melanopterus* of both sexes appear to have more yellow and orange on the body and fins than the Monkey Bay population. The populations at Thumbi West Island, Mumbo Island and the rocky shores of the south-eastern arm appear identical with those of Monkey Bay.

**Habitat.** *M. melanopterus* occurs over any type of rock and also occasionally in intermediate habitats, but we have seen it most often over medium-sized and large rocks. It is usually in water deeper than 10 m, but has a depth range from surface waters to at least 40 m.

**Territoriality.** This species appears to be non-territorial. Usually males and females are found hunting for food among the rocks. They usually occur singly or in groups of up to 9 individuals (except at Mumbo Island where as many as 15 – 20 individuals were in the groups). Occasionally males in breeding dress were seen defending an area, but since they vacated these sites almost immediately to approach the divers or join passing groups of conspecifics we

were unable to confirm whether they are territorial.

**Feeding.** *M. melanopterus* hunts among the rocks for fish fry, feeds from the Aufwuchs mat and catches plankton. Stomach contents of 15 individuals comprised a variety of food items: 2 stomachs were empty, but all the remaining stomachs contained some zooplankton, 4 of which were filled with zooplankton. Nine stomachs contained fish fry, 7 had insect larvae, 6 had benthic crustaceans, 8 contained loose Aufwuchs and 4 contained small amounts of filamentous algae. Fryer (1959a) found insect nymphs and larvae, crustaceans (ostracods and a small crab), fish fry and Aufwuchs in the stomachs of 5 specimens he examined.

### 2. *Melanochromis auratus* (Boulenger 1899) (Plates 9e & 9f)

**Synopsis.** A small attractive, lithophilous species with a wide depth range. Males are predominantly blue and black, and females are gold and black.

**Distribution.** Crocodile Rocks (R), Mpandi I. (U), Nkudzi (U), Mazinzi Reef (C), Chigubi (R), Kanchedza I. (U), Monkey Bay (C), Nankumba Peninsula (U), Domwe I. (U), Thumbi West I. (C), Otter Point (U), Mumbo I. (C), the Maleri Is. (C), Namalenje I. (C), Rifu (R), Mbenji I. (C), Masinje Rocks (U).

**Coloration. Monkey Bay males:** Body black with a broad, pale blue, mid-lateral band that has a golden band running along its centre; dorso-medial band pale blue with a broad golden-brown band running along its centre, both bands extend onto the head which is black with a yellowish-brown occipital region and a black occipital bar; snout yellowish-brown with 2 black interorbital bars. Dorsal fin golden-yellow. Caudal fin black with light blue edges. Anal fin black with pale blue outer edges; a single yellow egg-dummy. Pelvic fins black with blue-white leading edges.

**Monkey Bay females:** Body golden with a broad whitish mid-lateral band that has a black band running along its centre; dorso-medial band whitish with a black band that runs along its centre. Both bands extend onto the head which is golden-yellow with black interorbital bars. Dorsal fin golden-yellow with a black submarginal band and orange lappets. Caudal fin yellow with black patches of colour in the dorsal half. Anal fin bluish-yellow with a faint black submarginal band and an ill-defined yellow egg-dummy. Pelvic fins golden-yellow with bluish-white leading edges.

**Geographical variation.** The basic pattern of markings and colours of *M. auratus* remains the same throughout its distribution, but the intensity of colours varies. At Mumbo Island, Maleri Island and particularly Mbenji Island, males are a deeper black and the blue of the longitudinal bands is a bright royal blue that tends to mask the yellow inner bands. Females of these populations are a richer golden colour.

The Masinje Rocks population differs from those elsewhere in that the female has an off-white, rather than a yellow, belly. The longitudinal bands on the body are closer together than those of other populations and have irregular edges. Similarly, the submarginal band of the dorsal fin has poorly defined edges. The *M. auratus* of the western shores has the black markings of the caudal fin restricted to the dorsal sector, but in the Masinje Rock form these black

markings extend into the lower half of the fin and only the central margin is yellow. The anal and pelvic fins of the Masinje form lack black edges. The Masinje form is illustrated by Plate 9f and may be compared with colour illustrations of *M. auratus* of the western shores (Plate 9e).

**Habitat.** This species is most numerous among medium-sized rocks though it ventures onto all types of rocky habitat and into intermediate zones. It occurs from the surface to a depth of at least 40 m, but is slightly more numerous in the upper 10 m.

**Territoriality.** *M. auratus* males are weakly territorial and seldom stay to defend a particular site for more than a few hours. On occasion they will defend an area aggressively against all intruders, then for no apparent reason move elsewhere and defend another site, sometimes returning to the original site or to take up a different station near to it. Alternatively the male may become non-territorial. Females, non-territorial adult males and juveniles occur singly or in small groups of 8–10 individuals.

**Feeding.** *M. auratus* feeds from the Aufwuchs mat and frequently does so just within the territorial boundaries of highly aggressive species, apparently harvesting their algal gardens. Stomach contents varied considerably according to where and when specimens were caught. In general, however, stomach contents are dominated either by C2 or by loose Aufwuchs but this species also feeds upon plankton, benthic Invertebrata, C1, C3 and fish fry.

### 3. *Melanochromis vermicivorus* Trewavas, 1935

**Synopsis.** A relatively short, deep-bodied member of the *M. melanopterus* species-complex which lives among rocks. Males are dark blue with light blue banding; females are grey with black bands.

**Distribution.** Monkey Bay (C), Nankumba Peninsula (C), Domwe I. (C), Zimbabwe I. (N), Thumbi West I. (C–N), Mumbo I. (C), the Maleri Is. (C), Mbenji I. (C), Chinyankwazi I. (N–A), Eccles Reef (C), West Reef (C).

**Coloration.** *Monkey Bay males:* Body and head dark blue with contrasting light blue mid-lateral and dorso-lateral bands which continue on to the head; interorbital bar light blue. Dorsal fin pale blue with whitish lappets and black rays. Caudal fin dark blue at the base, but light blue distally; rays black. Anal fin black with a broad light blue periphery; 3–7 yellow egg-dummies. Pelvic fins black with whitish-blue leading edges.

*Monkey Bay females:* Body and head grey-white with black mid-lateral and dorso-lateral bands which continue onto the head; interorbital bar silvery-blue and bordered by black bars. Dorsal fin grey-white with blue cast, white lappets and black rays. Caudal fin dark grey with white upper and lower edges. Anal fin blue-grey with a black periphery; 2–5 yellow egg-dummies. Pelvic fins black with white leading edges.

**Geographical variation.** The population at Zimbabwe differs from that of Monkey Bay in that all males and most females have orange-red trailing edges to the dorsal and caudal fins. The males at Mumbo Island are a brilliant royal blue with longitudinal bands that are almost white. The populations at the Maleri Islands are relatively dull, males are grey-black with grey longitudinal bands while females are grey-brown with black bands. The Mbenji Island popu-

lation is the least colourful: males are a drab brownish-black ground colour with grey-blue bands while females are grey-brown with dull black banding. All other populations resemble closely the Monkey Bay populations.

**Habitat.** *M. vermicivorus* is most numerous among medium-sized rocks, on exposed sediment-free shores, in 3–12 m depth. However, it does venture onto both larger and smaller rocks, but is rare in intermediate habitats. Its depth range is from 0 to 30 m.

**Territoriality.** The territoriality of males of this species varies: at Monkey Bay, the Nankumba Peninsula, Domwe Island, the Maleri Islands and Mbenji Island it is not very aggressively territorial, but does not tolerate conspecific intruders. At Thumbi West Island it is more aggressive and at Zimbabwe and Chinyankwazi it is highly aggressive. At those sites where the level of aggression is low the population density of *M. vermicivorus* is low and intraspecific encounters are infrequent. However, at Thumbi West Island the population density is greater and at Zimbabwe and Chinyankwazi it is greater still with a commensurate increase in intraspecific encounters and aggressive activity. At Monkey Bay territorial males are 2–3 m apart in suitable habitats, but at Chinyankwazi they are about 70 cm apart. Not only are the territorial males more densely packed at Chinyankwazi, but there is also a greater number of non-territorial adults which intrude. Females are not territorial. At sites where this species occurs at low population densities females are found singly or in small groups, but at sites where their population density is high (Mitande Rocks, Zimbabwe I., and Chinyankwazi I.) they occur in large schools.

**Feeding.** *M. vermicivorus* feeds deep within gaps among the rocks and also in the water column. The stomachs of 23 individuals caught in 6–8 m of water at Monkey Bay contained on average 55% loose Aufwuchs, 30% C2, 8% C1, and 7% plankton.

Stomachs of 16 specimens caught at Thumbi West Island contained 70% benthic Invertebrata, 20% loose Aufwuchs, 5% C2 and the remainder was C1 and plankton. Twenty-two specimens were caught at Mitande Rocks (Thumbi West Island), when plankton was abundant; all had their stomachs filled with phytoplankton (80%) and zooplankton (20%). Fourteen non-territorial individuals caught during a plankton bloom at Chinyankwazi contained exclusively phytoplankton (75%) and zooplankton (25%), but stomachs of 4 territorial males contained, in addition to plankton (65% phytoplankton; 20% zooplankton), 10% C2 and 5% loose Aufwuchs. Apparently this species feeds on plankton when it is available, but on components of the Aufwuchs at other times.

### 4. *Melanochromis simulans* Eccles, 1973

**Synopsis.** This species resembles *M. auratus* closely in coloration, but has a more pointed head.

**Distribution.** Masinje Rocks (U). Eccles (1973) records its presence near Cape Ngombo, just south of Makanjila Point.

**Coloration.** This species resembles *M. auratus* in coloration. The principal difference between males is that *M. simulans* has a purple-blue ground colour (not black) and a darker blue dorsal fin, sometimes with a faint black submarginal band. Females are yellowish-white (not deep gold) and black markings cover the entire

caudal fin, not just the upper half as in *M. auratus* (see Axelrod & Burgess 1977: 50 for colour illustrations of females of both species).

**Habitat.** *M. simulans* was found in 0–6 m over rocky and rock-sand zones in a wave-washed area of Masinje Rocks.

**Territoriality.** This species appears to be non-territorial and its members are usually solitary, although small groups of 3–8 individuals of both sexes were found among the rocks.

**Feeding.** *M. simulans* was seen to feed from the rocks and to pick up particulate matter disturbed by the waves.

#### 5. *Melanochromis johanni* Eccles, 1973

**Synopsis.** A small, elongate fish of the intermediate zones in shallow water. Males are predominantly black; females are yellow-orange.

**Distribution.** Masinje Rocks (C). Eccles (1973) records its presence near Cape Ngombo, just south of Makanjila Point.

**Coloration. Males:** Body intense black with a royal blue band running from the base of the pectoral fin to the end of the caudal peduncle; a second band runs dorso-laterally from the upper cheek onto the upper, basal part of the caudal fin. Head black. Dorsal fin black with a row of pale blue streaks basally in the membranes; lappets whitish-blue. Anal fin black with whitish-blue leading and trailing edges; 2–3 yellow egg-dummies. Pelvic fins black with light blue leading edges.

**Females:** Head, body and fins yellow-orange with faint banding.

**Habitat.** This species was found syntopically with *M. simulans* in 0–6 m of water among rocks and in the rock-sand intermediate zones.

**Territoriality.** It is not known whether members of this species hold territories. Non-territorial adult males and females were found singly and in small groups.

**Feeding.** Individuals were seen to feed from both rocky and sandy substrata and on suspended matter in the water column.

#### 6. *Melanochromis* 'blotch' (Plate 9g)

**Synopsis.** A rare, dark brown and yellow blotched fish of shallow intermediate zones.

**Distribution.** Masinje Rocks (R), Chisumulu I. (R).

**Coloration. Males and females:** Body light yellow-brown with a broad, dark brown mid-lateral band running from the orbit onto the basal region of the caudal fin; a dark brown dorso-lateral band runs from the occipital region to the base of the rayed region of dorsal fin; 8–9 dark brown bars cross the bands to give a light and dark patched appearance; belly grey-brown; entire body with a slight bluish sheen. Head grey-brown with a blue inter-orbital bar and a blue iridescence. Dorsal fin yellow with blue rays and orange inter-ray membranes. Caudal fin dark brown at base, yellow distally with light blue inter-ray membranes. Anal fin bluish-yellow with a black leading edge and 2–4 yellow egg-dummies. Pelvic fins yellowish-blue with black submarginal bands and white leading edges.

**Habitat.** This species was found in the intermediate zones

between 3 and 10 m depth.

**Territoriality.** There is no evidence of territoriality. Only solitary individuals were found.

**Feeding.** This species swims close to the substratum and has been seen to feed upon matter stirred up from the bottom, to nip at Aufwuchs and to attack fishes caught in the net.

**Note:** It is not known whether males develop different coloration during periods of sexual activity.

#### 7. *Melanochromis* 'lepidophage' (Plate 9h)

**Synopsis.** A schooling, aquamarine-blue species which feeds upon scales of cichlid fishes. It inhabits intermediate zones in shallow water.

**Distribution.** At rocky reefs off Makanjila Point (C).

**Coloration. Males:** Body light aquamarine-blue with a silvery sheen; belly darker blue; a black mid-lateral band runs from the orbit to the base of the caudal fin; a black dorso-lateral band runs from the occipital region to the posterior basal edge of the dorsal fin. Head blue-grey with a conspicuous turquoise opercular spot. Dorsal fin blue-grey; lappets white with orange tips. Caudal fin dark grey at base, pale blue distally; upper and lower borders black with white edges; trailing edge white. Anal fin dusky blue with a dark grey submarginal band and white leading edge; 3–4 yellow egg-dummies. Pelvic fins dusky blue with dark grey submarginal bands and white leading edges.

**Females:** Similar to males, but a relatively dull grey-blue.

**Habitat.** This species inhabits the sand-rock interface of submerged rocky reefs at less than 8 m depth.

**Territoriality.** It occurs in schools numbering as many as 60 individuals. There is no evidence of territoriality.

**Feeding.** Eleven specimens were caught for analysis of stomach contents. One stomach was empty and all others contained cichlid scales only. Four stomachs were crammed to capacity with scales.

#### 8. *Melanochromis* 'chinyamwezi'

**Synopsis.** A brown, banded lithophilous species endemic to Chinyamwezi Island.

**Distribution.** Chinyamwezi I. (A).

**Coloration. Males:** Body light yellowish-brown with blue flecks and a dark brown mid-lateral line running from the orbit onto the caudal fin; a dorso-lateral line runs from the occipital region to the dorsal ridge of the caudal peduncle. Head yellowish-brown with blue flecks and a blue iridescence on the opercula; 2 dark brown inter-orbital bars. Dorsal fin pale yellowish-brown with a dark brown, almost black, submarginal band; lappets whitish with yellow-orange tips; trailing edge orange. Anal fin beige at base but remainder black; 2–4 bright yellow egg-dummies. Pelvic fins pale brown posteriorly and black anteriorly.

**Females:** Body beige with brown bands outlined by blue dots. Head beige with dark brown interorbital bars. Dorsal fin pale beige with brown submarginal band, yellow lappets and an orange trailing edge. Caudal fin brown. Anal fin yellow. Pelvic fins yellow with black leading edges.

**Habitat.** It was found everywhere at Chinyamwezi from the surface down to at least 43 m.

**Territoriality.** No territorial individuals were found. Large schools of this fish, comprising more than 100 individuals are common in the shallows. These schools follow divers and nip their exposed skin.

**Feeding.** Observations revealed that members of this species nipped Aufwuchs from the rocks, ate plankton and also tore pieces off small fishes which were caught in nets.

### 9. *Melanochromis cf. chipokae* (Plate 9i)

**Synopsis.** This species resembles *Melanochromis chipokae* Johnson, 1975 and is the largest of the *Melanochromis melanopterus* species-complex at the islands of Thumbi West and Mumbo. It lives in the intermediate zones.

**Distribution.** Thumbi West I. (C), Mumbo I. (R).

**Coloration. Males:** Body dark blue, almost black with a light blue mid-lateral band which runs from the orbit onto the caudal fin; a light blue dorso-lateral band runs from the occipital region to the anterior part of the rayed portion of the dorsal fin. Head dark blue, virtually black, with a light blue occipital bar and two light blue inter-orbital bars. Dorsal fin pale blue, almost white. Caudal fin black at the base, but light blue distally and along the upper and lower edges. Anal fin black with light blue leading and trailing edges; 2–4 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Brown with black mid-lateral and dorso-lateral bands occupying the position of the blue bands of males. Head dark brown. Fins pale brown and unpaired fins with orange trailing portions; anal and pelvic fins with black submarginal bands.

**Habitat.** It occupies all types of rocky shore, but territorial males were found most frequently over sand among rocks. This species is most numerous between 10 and 20 m, but it penetrates to at least 33 m and also occurs rarely in the extreme shallows.

**Territoriality.** Males defend territories against conspecifics, but they are not strongly territorial and occasionally leave territories to feed elsewhere. Territories held over sandy substrata usually contain an excavated nest and some individuals burrow beneath rocks.

**Feeding.** The stomach contents of 7 individuals examined showed that 5 had eaten cichlid fry and all contained C1, C2 and benthic Invertebrata. Three stomachs contained zooplankton.

**Note:** We have not been able to visit Chipoka Rocks to determine whether the Thumbi West population is conspecific with *M. chipokae* which it resembles closely.

### 10. *Melanochromis* 'slab'

**Synopsis.** A large, elongate, predatory Mbuna of rocky and intermediate habitats. The preferred sites for male territories appear to be over slabs and upper surfaces of large rocks.

**Distribution.** Nakantenga I. (C), Maleri I. (C), Nankoma I. (U), Mbenji I. (U).

**Coloration. Maleri Island males:** Body black with a light grey-blue mid-lateral band running from the eye to the base of the caudal fin; dorso-medial ridge pale blue-grey.

Head with blue-grey occipital region and snout with black interorbital bar; cheeks, chin and gular region brownish-grey. Dorsal fin grey with yellow flecks and broad orange trailing edge; lappets yellow-orange. Caudal fin black with an orange-yellow distal region. Anal fin black with a blue-grey leading edge and an orange trailing region; 2–4 yellow egg-dummies. Pelvic fins grey with pale blue leading edges. Pectoral fins orange.

**Maleri Island females:** Body brown with a black mid-lateral band and a black dorso-medial section (positioned as for blue-grey of males). Head brown with a dark brown interorbital bar and light yellow-brown cheeks, chin and gular region. Dorsal fin brown with orange-yellow lappets; distal section of the rayed region orange-yellow. Caudal fin brown at base; orange-yellow distally. Anal fin dark brown along its base; orange-yellow distal region; a white leading edge and 1–3 yellow egg-dummies. Pelvic fins yellowish-blue with white leading edges.

**Habitat.** This species was found mainly over slabs and large rocks, but sometimes over small and medium-sized rocks and in the intermediate zones. It occurs from 3 to 25 m depth.

**Territoriality.** Territorial males patrol about 1 m above the rocks. They intercept females from passing schools, court and lead them to spawning-sites. Territories are usually over rocks, but sometimes they are in intermediate zones where saucer-shaped nests may be dug. Conspecific males are not tolerated in the vicinity of a territory and are vigorously chased 3–6 m by the resident males. Non-territorial females, adult males and juveniles form schools numbering as many as 40 individuals at Nakantenga where this species is most numerous. Although males are aggressive in territorial defence relative to most other members of this genus, they have also been seen to vacate their territories to join schools of non-territorial individuals. This suggests that their ties to the territories are more tenuous than indicated by their aggression.

**Feeding.** This species was not seen feeding except when it attacked fishes caught in the nets. The stomachs of 11 specimens caught at Nakantenga Island were examined. Four were empty and the other 7 contained cichlid fry, C2, plankton and insects.

### 11. *Melanochromis parallelus* Burgess & Axelrod, 1976

**Synopsis.** A lithophilous species found along the north-western shores and at Likoma and Chisumulu Islands. Males are dark blue with light blue bands; females are whitish-yellow with black bands.

**Distribution.** Likoma I. (C), Chisumulu I. (C), Nkhata Bay (C), Lion's Cove (U), Mara Rocks (U), Ruarwe (U), Mpanga Rocks (R). An introduced population has become established at the island of Thumbi West where it is common at Mitande Rocks.

**Coloration. Likoma Island males:** Body dark blue, almost black, with a light blue mid-lateral band running from the orbit into the caudal fin; a light blue dorso-medial band running from the occipital region to the base of the posterior edge of the dorsal fin. Head very dark blue with 2 light blue interorbital bars. Dorsal fin black with

white lappets. Caudal fin dark blue with white upper and lower edges, and a white trailing portion. Anal fin black, but light blue postero-ventrally; 2–4 yellow egg-dummies. Pelvic fins black with white leading edges. *Likoma Island females*: Body and head whitish-yellow with black mid-lateral and dorso-medial bands, and also 2 black interorbital bars. Dorsal fin almost white with a prominent black submarginal band. Caudal fin whitish with black upper and lower borders and black streaks distally. Anal fin white posteriorly with black submarginal band and white leading edge. Pelvic fins white with narrow black submarginal bands.

*Habitat.* *M. parallelus* is found over a variety of rocky shores and infrequently in the intermediate zones. It occurs from the surface waters down to a depth of at least 40 m, but is most common between 5 and 20 m among large and medium-sized rocks.

*Territoriality.* Males defend territories against conspecifics only, but they frequently leave their territories to feed elsewhere and they will also do so to follow divers. This species is considered to be weakly territorial. Non-territorial males, females and juveniles usually occur singly or in small groups, but at Ndumbi Rocks, Likoma Island, schools of 30–100 individuals sometimes followed divers to feed upon the particulate matter disturbed by their fins.

*Feeding.* *M. parallelus* feeds from the Aufwuchs mat, from the water column, and attacks small fishes. The stomachs of 6 specimens caught at Makulawe Point, Likoma Island, were examined: all contained some loose Aufwuchs and benthic Invertebrata, 5 contained zooplankton, 4 contained cichlid fry, one contained mainly C2 and the contents of one were dominated by eggs of the catfish, *Bagrus meridionalis*.

*Note:* At Mitande Rocks, Thumbi West Island, an introduced population of *M. parallelus* has established territorial sites between 6 and 15 m among medium-sized and large rocks. This suggests that it has sought out its preferred habitat. Furthermore, the behaviour of the introduced individuals appears no different from that of conspecifics in their native regions.

### 12. *Melanochromis* 'red'

*Synopsis.* A small species which is endemic to Chisumulu Island where it frequents the upper surfaces of slabs, boulders and large rocks, usually in 4–12 m of water. Males are dark blue with lines of blue spots running along the flanks. Females are reddish-gold.

*Distribution.* This species is endemic to the rocky shores of south-western Chisumulu Island (C), but an introduced population occurs in the vicinity of the holding tanks of the exporters of aquarium fishes at Madimba Bay (U) at Likoma Island. Another introduced population is established at the island of Thumbi West (U).

*Coloration. Males:* Body dark blue, almost black, with a line of 9–10 light blue spots running mid-laterally along the body; a dorso-lateral line of blue spots is present in most individuals. Head dark blue with 2 light blue interorbital bars. Dorsal fin dark blue, almost black, with a narrow purple-blue band lying immediately below the black submarginal band; lappets whitish-blue; trailing edge whitish-blue with orange-red flecks. Caudal fin

dark blue, almost black, with pale blue inter-ray membranes and a pale blue trailing edge. Anal fin black with a yellowish-white leading edge and 2–4 yellow egg-dummies. Pelvic fins black with white leading edges. *Females:* Uniformly reddish-gold.

*Habitat.* This species occurs to a depth of at least 23 m, but is most numerous between 4 and 12 m. Although it may be found among rocks of virtually any description, most individuals congregate over slabs or over the upper surfaces of boulders and large rocks.

*Territoriality.* Males are weakly territorial and direct their aggression towards conspecifics only. Territories are held for short periods (1–2 hours) over the upper surfaces of rocks. Non-territorial individuals occur in groups of up to 60 individuals mainly over slabs and boulders.

*Feeding.* *M.* 'red' feeds by nipping and jerking at the filamentous algae.

### 13. *Melanochromis* 'black-white johanni' (Plate 9j)

*Synopsis.* A small species which inhabits the intermediate zones of the southern regions of Likoma Island. Males are predominantly black and females predominantly white.

*Distribution.* Endemic to the southern regions of Likoma Island (C), but it has been introduced to Thumbi West I. (R) and Otter Point (R).

*Coloration. Likoma Island (Mbuzi) males:* Body navy-blue with either 2 longitudinal light blue bands on the flanks or 2 rows of spots in the position of the longitudinal bands. Head black with 2 light blue interorbital bars. Dorsal fin black with white lappets. Caudal fin pale blue with black upper and lower borders and white edges; rays black distally. Anal fin black with a white leading edge and 1–4 yellow egg-dummies. Pelvic fins black with white leading edges.

*Females:* Body whitish-yellow with grey-black longitudinal bands. Head white-yellow with 2 black interorbital bars. Dorsal fin black with white lappets. Caudal fin beige with black upper and lower borders. Anal and pelvic fins black with white leading edges. Juveniles similar to females, but with an orange-yellow ground colour.

*Geographical variation.* The coloration of the populations at Mazimbwe Islet, Ndomo Point, White Rock and Madimba Bay is essentially similar to that of the Mbuzi form, but males of the Khuyu population have a pale blue wedge that extends forwards from the caudal fin.

*Habitat.* *M.* 'black-white johanni' is most common in intermediate zones, particularly at the rock-sand interface, but is also found in purely rocky habitats such as at Mazimbwe Islet. Its depth range is from the surface to at least 30 m, but most individuals occur in less than 10 m.

*Territoriality.* Males are weakly territorial. Non-territorial individuals of both sexes form groups of up to 60 individuals.

*Feeding.* This species feeds from both rock and sand substrata and upon plankton.

*Notes:* (i) This species is sold in the aquarium trade as 'black-white johanni'. (ii) This species occupies a similar rock-sand

habitat at Thumbi West and Otter Point to that at Likoma Island.

#### 14. *Melanochromis* 'maingano' (Plate 10a)

**Synopsis.** Both sexes of this small lithophilous species are the same colour. Its distribution is limited to Maingano and its adjacent rocky shores.

**Distribution.** Likoma I. at Membe Point (U), Maingano (C), Mbako Point (U).

**Coloration. Males and females:** Body dark navy-blue with contrasting light blue dorso-lateral band running from the interorbital bar to the base of the caudal fin; another light blue band running from the pectoral region to the caudal fin; a dorso-medial band usually absent but sometimes represented by a series of blue spots. Head dark navy-blue with a light blue interorbital bar across the snout and another across the forehead. Dorsal fin pale blue along its base with a broad, pitch-black submarginal band; lappets pale blue-white. Caudal fin pale blue-grey with black upper and lower borders and white edges. Anal fin black with a white leading edge and 2–5 yellow egg-dummies in a hyaline trailing portion. Pelvic fins black with white leading edges.

**Habitat.** This species is most numerous over small and medium-sized rocks, but it occasionally ventures into other habitats. It occurs from the surface down to at least 30 m, but is most common between 5 and 12 m.

**Territoriality.** Some individuals, presumed to be males, were weakly territorial, but they quite frequently vacated their defended areas to feed elsewhere, to court or to follow divers. Most individuals are solitary and show no sign of territoriality.

**Feeding.** This species was seen to feed from the upper surfaces of rocks and upon plankton. Stomach contents of 6 individuals caught at about 5 m depth at Maingano contained zooplankton (68%), benthic Invertebrata (25%), loose Aufwuchs (5%) and very small amounts of C1 and C2.

#### 15. *Melanochromis* 'blue' (Plate 10b)

**Synopsis.** A pale blue, large elongate species, with a terminal mouth and slightly hypertrophied lips.

**Distribution.** Likoma I. at Membe Point (R), Mbako (R),

White Rocks (R). Along the north-western shores at Nkhata Bay (R), Ruarwe (R), Mpanga (R), Chitande (R).

**Coloration. Nkhata Bay males:** Body blue-grey. Head blue-grey with black opercular patch. Dorsal fin blue-grey along the base, but with pale blue-white lappets and a prominent black fin-spot. Caudal fin blue with black upper and lower distal borders and white edges. Anal fin blue-grey at base, black submarginally with a white leading edge and hyaline trailing portion; 2–3 yellow egg-dummies. Pelvic fins blue-grey with black submarginal bands and white leading edges.

**Females:** Unknown.

**Geographical variation.** Too few specimens have been found for a comparison of live colours. Our records suggest, however, that the Likoma population and those of the north-western lake are probably identical.

**Habitat.** Most sightings of this fish were in water deeper than 20 m, but its total distribution is from 6 m to at least 40 m. It has been seen at the rock-sand interface, over sand and also in purely rocky habitats.

**Territoriality.** Only solitary individuals were found and none of these showed any signs of territoriality.

**Feeding.** On two occasions this species attacked fishes caught in our nets, but there are no other records of feeding behaviour.

#### *Melanochromis* heterogeneous species-group

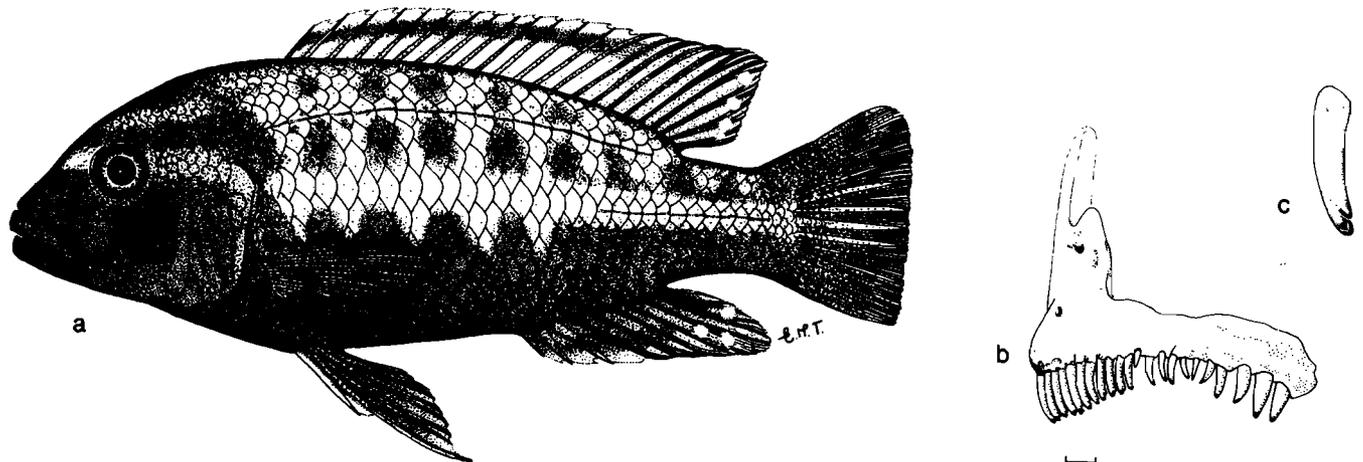
The members of this mixed species-group (Table 9) differ from the *M. melanopterus* species-complex in that they lack clear longitudinal banding and most species are deeper bodied. None of the five species appears to have close phyletic affinities with others in the group. The placement of at least three of the species in the genus may prove to be temporary.

##### 1. *Melanochromis* cf. *brevis* (Figures 11a–c)

**Synopsis.** A large, deep-bodied species which lives among medium-sized and large rocks in the upper 3 m of water.

**Distribution.** Boadzulu Island (U), Nkudzi (R), Monkey Bay (R), Chinyankwazi (U), Chinyamwezi (U), Mumbo Island (U).

**Coloration. Monkey Bay males:** Body dark blue with 2 pale



**Figure 11** (a) *Melanochromis* cf. *brevis*, Chinyankwazi Island, 118 mm SL. (b) Lateral aspect of left premaxilla of *M.* cf. *brevis* (Scale = 1 mm). (c) Anterior outer row tooth of *M.* cf. *brevis*.

blue longitudinal bands and 7–9 pale blue bars. Head black ventrally and dark blue dorsally with a pale blue interorbital bar. Dorsal fin light blue with a black submarginal band and orange lappets; 1–5 yellow ocelli on trailing edge. Caudal fin pale blue with black rays. Anal fin pale blue with a black submarginal band and a white leading edge; 2–7 yellow-orange egg-dummies. Pelvic fins pale blue with black submarginal bands and white leading edges.

*Monkey Bay females:* Markings the same as those of males but the bars and bands dark brown set against a khaki ground colour. Head brown with a turquoise interorbital bar. Fins pale brown. Anal and pelvic fins with black submarginal bands and all unpaired fins with orange trailing edges.

*Geographical variation.* With the exception of the Chinyankwazi and Chinyamwezi populations, which have yellow-orange chests, cheek, chin and gular regions, no geographical variation in colour was found. However, as this fish is uncommon or rare and difficult to catch we never had live individuals from different places at the same time for comparison.

*Habitat.* This species lives among medium-sized and large rocks in sediment-free zones which are exposed to wave action. It has never been found in water deeper than 4 m and most individuals are in water less than 2 m deep.

*Territoriality.* Males hold territories in gaps or crevices between rocks. Only conspecific males are excluded from these territories and as these are uncommon, aggression of *M. cf. brevis* is not often witnessed. One to four females are usually found in the vicinity of territorial males though the nature of the association is not clear. During calm weather, territorial males retreat into gaps or caves among the rocks, but during turbulent conditions they move to the entrances of their refuge sites.

*Feeding.* *M. cf. brevis* feeds upon plankton, loose Aufwuchs and small amounts of C1 and C2. Ants and flies have been found in the stomachs of these fishes which suggests that they also feed on insects which are washed or blown into the water from the shore.

*Note:* *M. cf. brevis* has elements of vertical barring and is deep bodied and in these respects it is unlike any of the members of the *M. melanopterus* species-complex. It is similar to the latter in that it has longitudinal banding (albeit interrupted banding) and it is weakly territorial. Loiselle (1979) suggests that *M. brevis* should be placed in the genus *Pseudotropheus*, but the illustration he gave is not of *M. brevis*. So for the time being *M. cf. brevis* should remain in the genus *Melanochromis*.

## 2. *Melanochromis crabro* Ribbink & Lewis, 1982

*Synopsis.* An uncommon to rare species with 5 broad bars. Males bluish-brown with buff-coloured bars. Females golden-yellow with dark brown bars.

*Distribution.* Eccles Reef (R), West Reef (R), Chinyankwazi I. (R–U), Chinyamwezi I. (R), Maleri I. (U), Mbenji I. (U), Likoma I. (R–U), Chisumulu I. (R–U), Nkhata Bay (R).

*Coloration. Maleri Island males:* Body greyish-brown with pronounced blue or turquoise iridescence; 5 short, broad

buff-coloured bars extend only part-way down flank. Head grey-brown with bluish iridescence and with a buff occipital bar and 2 buff interorbital bars. Dorsal fin dark brown except where buff bars enter its base; light blue lappets; tips of lappets yellow. Caudal fin dark brown at base; yellowish-brown distally with 1–2 ochre-yellow egg-dummies. Pelvic fins dark brown.

*Maleri Island females:* Body golden-yellow with 5 broad, dark brown bars; dark brown mid-lateral band present in some individuals. Head golden-yellow dorsally with dark brown occipital bar and 2 dark brown interorbital bars; snout pale brown; cheeks yellow; gular region and branchiostegal membranes yellowish-brown. Dorsal fin very dark brown to black with yellow patches at base continuous with body markings; lappets yellow with darker yellow tips; rayed portion yellow. Caudal fin brown at base, yellow distally. Anal fin yellow with greyish submarginal band and orange trailing edge. Pelvic fins yellow with grey submarginal bands and blue-white leading edges.

*Habitat.* Most *M. crabro* were found among large rocks but they have also been seen in other rocky habitats and in the intermediate zones. Its depth range extends from 3 to at least 40 m though it is most numerous between 10 and 25 m.

*Territoriality.* This species is apparently not territorial, but occurs singly, or occasionally in small groups of up to 4 individuals.

*Feeding.* *M. crabro* appears to be adapted to feed on *Argulus africanus*, a branchiuran parasite commonly found on the catfish, *Bagrus meridionalis*. It also robs *B. meridionalis* of its eggs which are laid on the substratum (Ribbink & Lewis 1982). In addition to these specialized food resources, *M. crabro* feeds upon zooplankton, phytoplankton, Aufwuchs and benthic Invertebrata (Ribbink & Lewis 1982).

*Note:* Ribbink & Lewis (1982) placed *M. crabro* in the genus *Melanochromis* because its pharyngeal dentition conforms to the diagnosis of the genus given by Trewavas (1935). Although *M. crabro* is similar to members of the *M. melanopterus* species-complex in that it is elongate, predatory and weakly territorial, it does not have longitudinal banding and so it is placed in the *M. 'heterogeneous'* species-group.

## 3. *Melanochromis labrosus* Trewavas, 1935

*Synopsis.* A bilaterally compressed fish with hypertrophied lips.

*Distribution.* Mbenji I. (R), Likoma I. (U), Chisumulu I. (R).

*Coloration. Males and females:* Brown, being lighter ventrally than dorsally. Sexually active males develop a purple-blue cast and have 3–6 yellow egg-dummies.

*Habitat.* This species was found among small and medium-sized rocks in water less than 8 m deep. It usually remains hidden among the rocks and appears to be rare. However, a rotenone sample at Maingano revealed that there are more *M. labrosus* among the rocks than indicated by transects and by observation.

*Territoriality.* *M. labrosus* appears to be a solitary fish and no territorial individuals were found.

**Feeding.** It moves from rock to rock placing its narrow mouth and large lips in cracks and grooves, which it seals, and then sucks the benthic Invertebrata and loose Aufwuchs from the sealed area.

**Note:** Although the aquarist literature suggests that *M. labrosus* would be better placed in the genus *Cyrtocara*, Loiselle (1979) believes this species to be an Mbuna. D.S.C. Lewis (in prep.) agrees with this diagnosis since *M. labrosus* has a small number of discrete egg-dummies which he considers to be an important characteristic of Mbuna. Loiselle (1978) argues that *M. labrosus* has closest affinities with the genus *Labidochromis*, but Lewis (in prep.) has found that it is so unlike any of the existing Mbuna genera that he is placing it in a separate, new genus.

#### 4. *Melanochromis* 'brown'

**Synopsis.** An elongate, reddish-brown species. Both sexes appear identical in coloration.

**Distribution.** Chinyankwazi I. (U), Chinyamwezi I. (U).

**Coloration. Males and females:** Body and head uniform reddish-brown. Fins orange-brown with 1–4 yellow egg-dummies on the anal fin of males.

**Habitat.** This species occurs among rocks of all sizes. Its full depth range extends from 5 to 40 m, but most individuals were seen between 12 and 30 m.

**Territoriality.** Only solitary non-territorial individuals were found.

**Feeding.** No data available.

#### 5. *Melanochromis joanjohnsonae* (Johnson, 1974)

**Synopsis.** A small species which is endemic to Likoma Island where it lives among small rocks usually in water less than 4 m deep. Males are blue with a prominent black submarginal band. Females are greenish-blue with scalloped orange bands.

**Distribution.** Likoma I. (C), but an introduced population is established at the island of Thumbi West (C).

**Coloration. Males:** Body iridescent-blue with very faint traces of 7–9 dark blue bars. Head bluish-green with 2 brownish interorbital bars; opercular spot greenish-black. Dorsal fin whitish with black submarginal band; lappets white with orange-brown tips; rayed portion has brown spots and orange-yellow ocelli on the trailing edge of some individuals. Caudal fin bluish-white with faint orange-brown flecks and an orange-brown trailing edge. Anal fin whitish-blue with a black submarginal band, a white leading edge and 1–5 yellow egg-dummies. Pelvic fins hyaline with black submarginal bands and white leading edges.

**Females:** Body greenish-blue with 5–6 irregular orange bands. Head iridescent blue-green with a criss-crossing network of orange-brown lines. Dorsal fin whitish-green with numerous orange-brown spots sometimes merging to form a dark orange-brown submarginal band. Caudal fin yellowish-blue with orange spots on the basal region, and with longitudinal orange dashes on the distal portion. Anal fin hyaline at base, remainder orange with 1–4 bright orange egg-dummies. Pelvic fins orange with white leading edges.

**Geographical variation.** The populations on the eastern and northern parts of Likoma Island are a deeper, brighter blue than those of the south-western region which have a greenish cast in both sexes.

**Habitat.** *M. joanjohnsonae* is most numerous among small rocks in water less than 2,5 m deep. However, it does occur over larger rocks and to a depth of 7 m, but it is very rare beyond 4,5 m depth. Normally it does not leave the rocks, but on hot, windless days in December 1979 we observed some specimens moving onto sand in 3–4 m of water in Madimba Bay, near to White Rock. They remained motionless over the sand in groups of up to 25 individuals. It is not known whether this behaviour was a response to the high surface temperature (31 °C) within the sheltered bay or was a response to some other factor. Such behaviour was not recorded elsewhere.

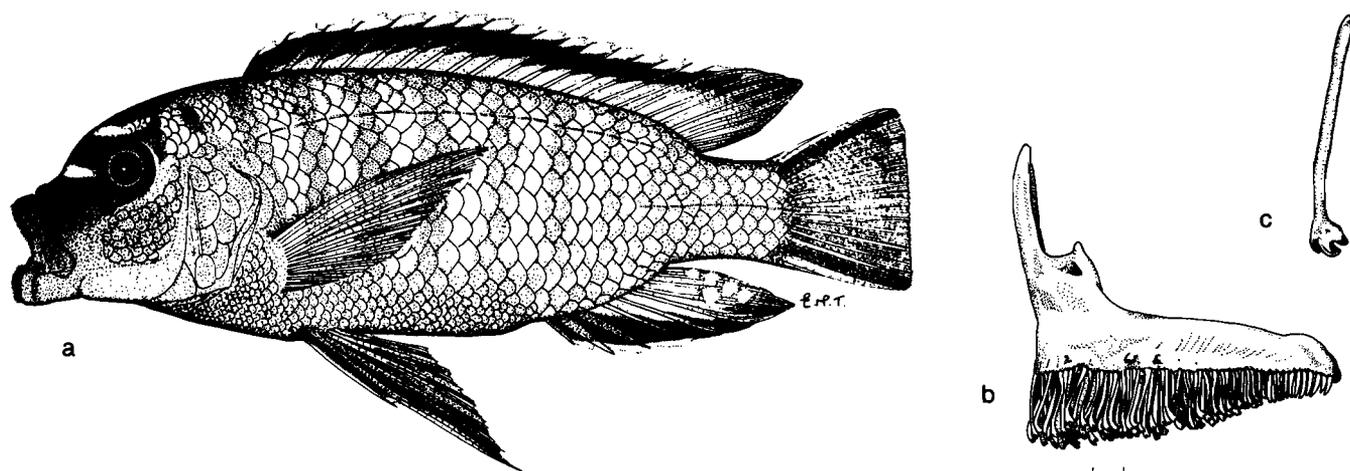
**Territoriality.** Males vigorously defend territories against conspecifics and sometimes protracted intraspecific bouts of fighting, particularly rapid circling of rivals, were seen. Females are usually solitary and occur most often over the upper surface of prominent rocks which they occasionally defend against conspecifics. However, this appears to be a temporary defence of a feeding area.

**Feeding.** This species nips at the Aufwuchs, frequently selecting its feeding site with apparent care. Stomach contents of 11 individuals caught at Membe Point, contained mainly insect nymphs and larvae, benthic crustaceans and small portions of C1 and loose Aufwuchs.

**Notes:** (i) At Thumbi West the introduced population of this species is found in less than 4 m of water, mainly among small rocks. Thus the preferred habitat at the introduced site corresponds with that occupied at Likoma Island. (ii) The taxonomic history of *M. joanjohnsonae* has been bedevilled by amateurish attempts to describe it. This led to unnecessary confusion which was partially resolved by Stock (1976) and finally resolved by Lewis (1980). At various times *M. joanjohnsonae* and other species confused with it, were described as *Labidochromis joanjohnsonae* by Johnson (1974), *Melanochromis exasperatus* by Burgess (1976) and *Labidochromis textilis* by Oliver (1975). In his redescription Lewis (1980) points out that *M. joanjohnsonae* lacks a number of the overt characteristics of the genus and so it is placed in the genus as a temporary measure until such time as the genus is redefined.

#### Genus *Petrotilapia* Trewavas, 1935 (Figure 12a – c)

Members of this genus are the largest of the Mbuna (Fryer 1959a). The mouth is terminal with a dense brush of long, slender tricuspid teeth on each jaw (Figure 12a – c). In adults the mouth is permanently in a partially open position with many of the teeth exposed to view. As the mouth is terminal, *Petrotilapia* species feed at right angles to the rock surface with their jaws pressed against the rocks. In feeding the teeth are combed through the filamentous Aufwuchs in a characteristic manner (Fryer 1959a; Marsh 1981) to collect loose Aufwuchs and its associated invertebrate fauna. Members of this genus also feed on plankton when it is plentiful (Marsh 1981). Originally this genus was considered to be monospecific (Trewavas 1935; Fryer 1959a), but it is now known to comprise 17 species (Table 10) of which three have already been described (Trewavas 1935; Marsh 1983) and descriptions of the remaining species are due shortly (A.C.



**Figure 12** (a) *Petrotilapia* 'mumbo blue', Mumbo Island, 128 mm SL. (b) Lateral aspect of left premaxilla of *Petrotilapia tridentiger* (Scale = 1 mm). (c) Anterior outer row tooth of *P. tridentiger*.

**Table 10** The members of the genus *Petrotilapia*. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	IIa	IIb	IIc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Petrotilapia tridentiger</i>	137	Monkey Bay	+	+	+	-	-	+	-	-	-	-	-	+	+	+
2. <i>P. genalutea</i>	126	Monkey Bay	+	+	+	+	-	+	+	+	+	+	-	+	+	+
3. <i>P. nigra</i>	122	Monkey Bay	+	-	-	-	-	+	-	-	-	-	-	-	-	-
4. <i>P. 'gold'</i>	130	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
5. <i>P. 'mumbo blue'</i>	135	Mumbo I.	-	-	-	-	-	+	+	-	-	+	-	-	-	-
6. <i>P. 'mumbo yellow'</i>	128	Mumbo I.	-	-	-	-	-	-	+	-	-	-	-	-	-	-
7. <i>P. 'yellow chin'</i>	135	Makanjila	-	-	-	+	-	-	-	+	+	+	-	-	-	-
8. <i>P. 'fuscous'</i>	118	Maleri I.	-	-	-	-	-	-	-	-	+	+	-	-	-	-
9. <i>P. 'likoma variable'</i>	145	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
10. <i>P. 'likoma barred'</i>	165	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
11. <i>P. 'orange pelvic'</i>	132	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
12. <i>P. 'retrognathous'</i>	125	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
13. <i>P. 'yellow ventral'</i>	125	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
14. <i>P. 'small blue'</i>	115	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
15. <i>P. 'ruarwe'</i>	no record		-	-	-	-	-	-	-	-	-	-	-	-	+	+
16. <i>P. 'black flank'</i>	no record		-	-	-	-	-	-	-	-	-	-	-	-	-	+
17. <i>P. 'chitande'</i>	no record		-	-	-	-	-	-	-	-	-	-	-	-	-	+

Marsh in prep.).

### 1. *Petrotilapia tridentiger* Trewavas, 1935

**Synopsis.** A widespread species which is common on most rocky shores in Lake Malawi where it occurs in shallow water. Males are predominantly pale blue.

**Distribution.** Chemwezi (R), Boadzulu I. (C), Mpandi I. (C), Kanchedza I. (C), Nkudzi (C), Monkey Bay (C), Domwe I. (C), Otter Point (U), Nkhata Bay (C), Lion's Cove (C), Cape Manulo (C), Mara Rocks (C), Ruarwe (C), Chilumba at Chitande I. (C), Mpanga Rocks (C).

**Coloration.** *Monkey Bay males:* Body pale blue with 7-9 darker blue bars on flanks, belly whitish-blue. Head pale blue with whitish-blue gular. Dorsal fin pale blue with dark blue to black posterior inter-ray membranes. Caudal fin with sky-blue inter-ray membranes, dark blue to black rays and pale orange-brown trailing edge. Anal

fin pale blue with dark blue to black posterior inter-ray membranes, 1-5 bright orange to yellow egg-dummies and whitish-blue leading edge and ventral edge. Pelvic fins pale blue with whitish-blue leading edges.

**Monkey Bay females:** Head and body grey-brown with 7-10 dark brown bars on flanks. Bars may be obscured on darker individuals. All fins semi-transparent and matching body coloration.

**Geographical variation.** Males at Chilumba have a brown-orange hue on the anal fin and have no black markings in the dorsal and pelvic fins.

**Habitat.** Occurs over all sizes of rock but appears to prefer large and medium-sized rocks. Usually confined to water less than 8 m deep but occurs down to 18 m at Boadzulu Island. At Monkey Bay males and females are most abundant at 1 m depth.

**Territoriality.** Males defend territories against conspecific

males. At Monkey Bay territories have a mean area of 22,16 m<sup>2</sup> (Marsh *et al.* 1981). Females and non-territorial males are usually solitary but occasionally a female was seen with a school of *Petrotilapia genalutea*.

**Feeding.** Adults and juveniles brush the surfaces of rocks in the manner typical of members of this genus and collect loose Aufwuchs and its associated invertebrate fauna. Plankton is utilized when it is abundant. Details of feeding habits are given in Marsh (1981) and McKaye & Marsh (1983).

## 2. *Petrotilapia genalutea* Marsh, 1983

**Synopsis.** A widespread species common in shallow water on most rocky shores south of Ruarwe on the western side of the lake and as far north as Makanjila on the eastern side. Males are predominantly bluish-grey with distinctive orange cheeks.

**Distribution.** Chemwezi (R), Boadzulu I. (C), Mpandi I. (C), Kanchedza I. (R), Nkudzi (C), Monkey Bay (C), Domwe I. (C), Otter Point (U), Thumbi East I. (C), Mumbo I. (C), the three Maleri Is. (C), Namalenje I. (C), Senga Point (R), Mbenji I. (C), Makanjila (C), Nkhata Bay (C), Lion's Cove (C), Cape Manulo (C), Mara Rocks (C), Ruarwe (C).

**Coloration. Monkey Bay males:** Body bluish-grey with 4–6 dark grey vertical bars on flanks, 4 anterior-most bars invariably distinct but remainder may be faded or absent. Anterior half of belly orange-brown, remainder dark bluish-grey. Head blue-grey with orange-brown cheeks and two dark grey interorbital bars. Dorsal fin hyaline grey with a broad, black submarginal band; all interspine and inter-ray membranes hyaline grey with orange-brown blotches except those of trailing edge which are black; lappets orange-yellow, but pale blue in some individuals. Caudal fin rays black, with pale blue inter-ray membranes and an orange trailing edge. Anal fin grey with a black leading section and 1–4 yellow egg-dummies. Pelvic fins orange-brown with black submarginal bands and blue-white leading edges.

**Monkey Bay females:** Body off-white to pale yellow-brown with white belly and a series of thick dark brown to black mid-lateral and dorso-lateral blotches on flanks. These blotches normally close together and often fused posteriorly to form a continuous band; 9–10 pale brown bars on flanks and caudal peduncle. Dorsal fin hyaline with a narrow dark grey or black submarginal band; rays orange-brown posteriorly; lappets orange-brown. Caudal fin hyaline grey. Anal fin hyaline grey with a dark grey submarginal band and small pale yellow egg-dummies. Pelvic fins hyaline grey with dark grey submarginal bands.

**Habitat.** *P. genalutea* occurs among rocks of all sizes, but is most numerous among medium-sized and large rocks. It inhabits the shallows and usually does not penetrate beyond 8 m, but at Boadzulu Island it occurs to 20 m. Females are usually most abundant in the extreme shallows and males are most abundant at about 3 m depth.

**Territoriality.** Males defend territories against conspecific males. At Monkey Bay territories have a mean area of 19,88 m<sup>2</sup> (Marsh *et al.* 1981). Females and non-territorial males may be solitary, hover in the water column in groups

of up to 200 individuals, or occur in schools numbering between 30 and 300 individuals. These schools often also contain a few members of *P. nigra* and occasionally some *P. tridentiger* females.

**Feeding.** Adult individuals feed by brushing rock surfaces to collect loose Aufwuchs and its associated invertebrate fauna; they also take plankton when it is abundant. Juveniles feed primarily on plankton. Details of feeding habits are given in Marsh (1981).

## 3. *Petrotilapia nigra* Marsh, 1983

**Synopsis.** A relatively small *Petrotilapia* species that occurs in the southern part of the lake. Males are predominantly black.

**Distribution.** Monkey Bay (C), Domwe I. (C), Otter Point (C), Thumbi West I. (C).

**Coloration. Monkey Bay males:** Body dark grey-blue with 7–10 broad black vertical bars on flanks; caudal peduncle black. Head black with a dark blue interorbital bar. Dorsal fin dark grey, with orange flecks in some specimens, submarginal band broad and black; lappets orange in most specimens, though some individuals have blue tinges particularly along the tips. Caudal fin rays black; inter-ray membranes sky-blue; trailing edge orange-brown. Anal fin black with pale blue leading edge and 1–4 bright yellow egg-dummies. Pelvic fins brown with black submarginal bands and whitish-blue leading edges.

**Monkey Bay females:** Head and body pale brown with dark brown to black mid-lateral and dorso-lateral blotches and 7–10 grey-brown bars on flanks. Dorsal fin hyaline with a narrow dark grey to black submarginal band and pale orange lappets. Caudal fin hyaline. Anal fin hyaline with pale blue distal border, a narrow brown to black submarginal band and a few yellow egg-dummies in some specimens. Pelvic fins hyaline with pale blue distal borders and narrow brown to black submarginal bands.

**Habitat.** Occurs over all sizes of rock but shows a preference for medium-sized rocks. Occupies a broad depth range from the extreme shallows down to 35 m at Thumbi West Island. Males are most common between 6 and 10 m whereas females are most numerous in the extreme shallows down to 2 m.

**Territoriality.** Males defend territories against conspecific males only. Territories have a mean area of 6,79 m<sup>2</sup> (Marsh *et al.* 1981). Females, non-territorial males and juveniles are usually solitary but occasionally form mixed feeding schools with *P. genalutea*.

**Feeding.** Adult individuals brush rock surfaces to collect loose Aufwuchs and Invertebrata. When plankton is plentiful members of this species (particularly females) may concentrate entirely on this resource. Juveniles feed predominantly on plankton. Details of feeding habits are given in Marsh (1981).

## 4. *Petrotilapia* 'gold'

**Synopsis.** A common fish at the islands of Chinyankwazi and Chinyamwezi. Males are predominantly black and females are predominantly golden.

**Distribution.** Chinyankwazi I. (C), Chinyamwezi I. (C).

**Coloration.** *Chinyankwazi males:* Body black with 7 narrow sky-blue bars on flanks. Head black. Dorsal fin black with sky-blue inter-ray membranes. Caudal fin black with sky-blue inter-ray membranes and a pale brown trailing edge. Anal fin black with 1–5 yellow-orange egg-dummies. Pelvic fins black with pale blue leading edges.

*Chinyankwazi females:* Usually intense gold but some individuals drab brown. Flanks with 2 parallel, horizontal rows of dark brown-black blotches.

**Habitat.** Occurs over all rock sizes, from the shallows to 35 m depth with the greatest numbers occurring in the shallows.

**Territoriality.** Males defend territories against conspecific males. Females, non-territorial males and juveniles occur singly or in groups of up to 30. Groups are particularly common on the exposed sides of the islands.

**Feeding.** Non-territorial individuals feed on plankton in the water column and on loose Aufwuchs on the rock surface. Territorial males feed predominantly on loose Aufwuchs.

### 5. *Petrotilapia* 'mumbo blue'

**Synopsis.** A large fish of the shallows. Males and females have a distinct black submarginal band in the dorsal fin. Males are predominantly blue whereas females are predominantly brown.

**Distribution.** Thumbi West I. (C), Mumbo I. (C), Mbenji I. (C).

**Coloration.** *Thumbi West Island males:* Body sky-blue with pale blue belly and 8–9 dark blue vertical bars on flanks. Head dark blue with broad dark grey interorbital bar. Dorsal fin pale blue with prominent black submarginal band; lappets blue with orange tips; rays black, inter-ray membranes blue with numerous orange ocelli along trailing edge. Caudal fin lilac-blue with black rays on orange trailing edge. Anal fin a semi-transparent blue-grey with a broad black submarginal band and a pale blue leading edge; 1–6 yellow egg-dummies. Pelvic fins orange with grey rays, black submarginal bands and blue leading edges.

*Thumbi West Island females:* Body and head uniform dark brown. Dorsal fin hyaline brown with pale orange lappets, a dark grey submarginal band and orange ocelli on posterior inter-ray membranes. Caudal fin hyaline brown with orange trailing edge. Anal fin dark grey anteriorly, hyaline brown posteriorly. Pelvic fins pale orange with dark grey submarginal bands and pale blue leading edges.

**Habitat.** Occurs over all rock sizes, but appears most numerous over medium-sized and large rocks, from the surface waters to 6 m depth.

**Territoriality.** Males defend territories against conspecific males. Females, non-territorial males and juveniles are usually solitary.

**Feeding.** Individuals feed in the manner typical of members of this genus.

### 6. *Petrotilapia* 'mumbo yellow'

**Synopsis.** A common fish at Mumbo Island particularly at about 10 m depth. Males have a distinctive yellow suffusion superimposed on their slate-grey ground colour.

**Distribution.** Mumbo I. (C).

**Coloration.** *Males:* Body slate-grey ground colour suffused with yellow, but chest, belly and shoulder bright yellow; 4–6 indistinct grey-green bars traverse flanks. Head grey along dorsal aspect of snout and occipital regions, remainder yellow with bright yellow cheeks, chin and gular regions; interorbital bar light blue; opercular patch black. Dorsal fin hyaline blue with patches of yellow; submarginal band broad and black; lappets blue with orange tips; rays black. Caudal fin blue with black rays and an orange trailing edge. Anal fin bluish-grey with a black submarginal band and light blue leading edge; 1–4 yellow egg-dummies. Pelvic fins yellow, tending to orange in some individuals.

*Females:* Body grey with 7–8 dark grey bars and a series of black blotches running mid-laterally along the flanks, another series of small black blotches running dorso-laterally. Dorsal fin hyaline grey with a narrow dark grey submarginal band and pale orange lappets. Caudal fin pale grey with dark grey rays. Anal fin light grey with dark grey borders. Pelvic fins pale grey.

**Habitat.** Members of this species occur over most rock types but are most common among medium-sized and large rocks. They occur in 3–22 m depth, in both sediment-free and sediment-rich zones, but most individuals were found at about 10 m.

**Territoriality.** Males defend territories against conspecific males, seldom chasing heterospecifics. Females, non-territorial males and juveniles are usually solitary.

**Feeding.** Individuals feed in the manner typical of members of this genus.

### 7. *Petrotilapia* 'yellow chin' (Plate 10c)

**Synopsis.** A large species in shallow waters. Males are sky-blue with a distinctive suffusion of yellow. Females are uniform brown.

**Distribution.** Makanjila (C), Maleri I. (C), Nankoma I. (C), Nakantenga I. (C), Namalenje I. (C), Mbenji I. (C).

**Coloration.** *Makanjila males:* Body blue with chest and anterior belly golden-yellow; 7–9 dark blue bars traversing the flanks. Head blue with golden-yellow snout, cheeks, chin, gular region and branchiostegal membranes. Dorsal fin usually blue with patches of yellow, but in some individuals the fin mainly yellow; lappets yellow; rays black; trailing edge orange frequently with orange ocelli. Caudal fin blue with a yellow hue, blue-white upper and lower edges and an orange trailing edge. Anal fin blue, suffused with yellow and with 3–7 bright yellow egg-dummies. Pelvic fins golden-yellow with light blue leading edges.

*Makanjila females:* Uniformly dull brown.

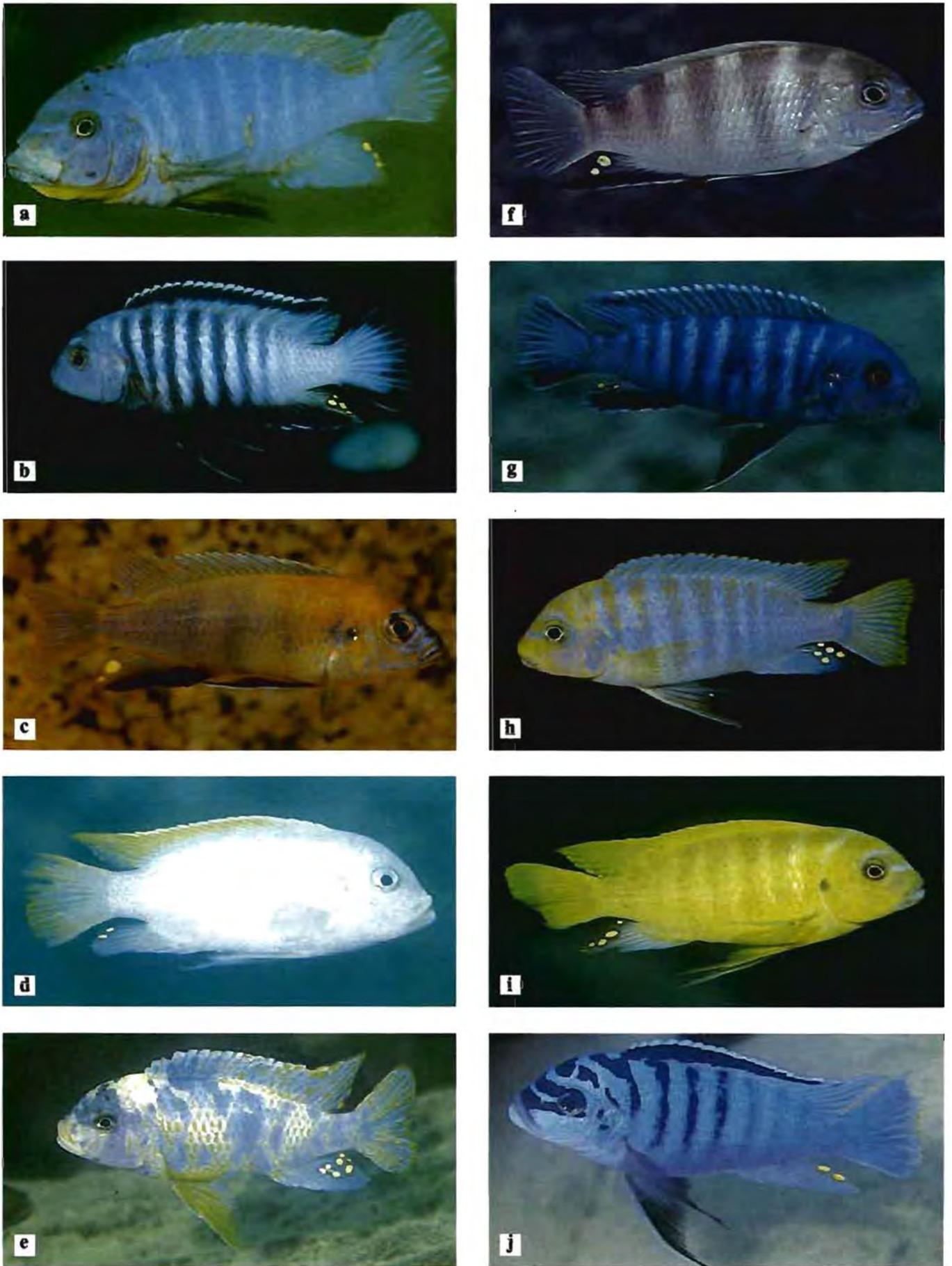
**Geographical variation.** Males at Mbenji Island vary slightly from the pattern mentioned above. Some specimens have a faint dusky submarginal band in the dorsal fin. The caudal fin rays are dark grey to black. In some individuals there is a dark grey stripe adjacent to the pelvic fin spines.

**Habitat.** Occurs over all rock types in the shallows and extreme shallows, but is most numerous among medium-sized and large rocks. It normally occurs down to a depth of 6 m



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**Plate 1** (a) *Pseudotropheus zebra*, Monkey Bay. (b) *Pseudotropheus zebra*, Zimbabwe Island. (c) *Pseudotropheus zebra*, Nkudzī. (d) *Pseudotropheus zebra*, West Reef. (e) *Pseudotropheus livingstonii*, Monkey Bay. (f) *Pseudotropheus zebra* 'fusco', Maleri Island. (g) *Pseudotropheus heteropictus*, Thumbi West Island. (h) *Pseudotropheus zebra* 'mumbo', Mumbo Island. (i) *Pseudotropheus zebra* 'blue', Maleri Island. (j) *Pseudotropheus zebra* 'red dorsal', Nakantenga Island. The caudal fin of this individual has been bitten three times by *Genyochromis mento*.



**Plate 2** (a) *Pseudotropheus zebra* 'yellow throat', Maleri Island. Photographed while adjusting its mouth. (b) *Pseudotropheus zebra* 'black dorsal', Maleri Island. (c) *Pseudotropheus zebra* 'patricki', Maleri Island. (d) *Pseudotropheus zebra* 'mbenji', Mbenji Island (normal male). (e) *Pseudotropheus zebra* 'mbenji', Mbenji Island (OB male). (f) *Pseudotropheus livingstonii* 'likoma', Likoma Island. (g) *Pseudotropheus zebra* 'bevous', Likoma Island. (h) *Pseudotropheus zebra* 'greberi', Chisumu Island. (i) *Pseudotropheus zebra* 'gold', Nkhata Bay. (j) *Pseudotropheus zebra* 'chilumba', Chitande.



**Plate 3** (a) *Pseudotropheus zebra* 'mpanga', Mpanga Rocks. (b) *Pseudotropheus zebra* 'pearly', Mpanga Rocks. (c) *Pseudotropheus zebra* 'ianth', Mpanga Rocks. (d) *Pseudotropheus* cf. *gracilior*, Monkey Bay. (e) *Pseudotropheus tropheops* 'orange chest', Monkey Bay. (f) *Pseudotropheus tropheops* 'broad mouth', Monkey Bay. (g) *Pseudotropheus* cf. *microstoma*, Monkey Bay. (h) *Pseudotropheus tropheops* 'red cheek', Likoma Island. (i) *Pseudotropheus tropheops* 'boadzulu', Boadzulu Island. (j) *Pseudotropheus tropheops* 'black dorsal', West Reef.



**Plate 4** (a) *Pseudotropheus tropheops* 'chinyamwezi', Chinyamwezi Island. (b) *Pseudotropheus tropheops* 'lilac', Thumbi West Island. (c) *Pseudotropheus tropheops* 'lilac mumbo', Mumbo Island. (d) *Pseudotropheus tropheops* 'intermediate' Thumbi West Island (male). (e) *Pseudotropheus tropheops* 'intermediate' Thumbi West Island (female). (f) *Pseudotropheus tropheops* 'maleri yellow', Maleri Island. (g) *Pseudotropheus tropheops* 'mbenji blue', Mbenji Island. (h) *Pseudotropheus tropheops* 'mbenji yellow', Mbenji Island. (i) *Pseudotropheus tropheops* 'yellow chin', Likoma Island. (j) *Pseudotropheus tropheops* 'membe', Likoma Island.



**Plate 5** (a) *Pseudotropheus tropheops* 'dark', Likoma Island. (b) *Pseudotropheus tropheops* 'gold', Chisumulu Island. (c) *Pseudotropheus tropheops* 'mauve', Nkhata Bay. (d) *Pseudotropheus tropheops* 'olive', Nkhata Bay (male). (e) *Pseudotropheus tropheops* 'olive', Nkhata Bay (female). (f) *Pseudotropheus tropheops* 'black', Nkhata Bay. (g) *Pseudotropheus tropheops* 'red fin', Ruarwe (female). (h) *Pseudotropheus tropheops* 'chitande yellow', Chitande. (i) *Pseudotropheus williamsi* 'nkudzi', Nkuḽzi. (j) *Pseudotropheus williamsi* 'roaleri', Maleri Island.



**Plate 6** (a) *Pseudotropheus williamsi* 'namalenje', Namalenje. (b) *Pseudotropheus elongatus* 'aggressive', Monkey Bay. (c) *Pseudotropheus elongatus* 'reef', West Reef. (d) *Pseudotropheus elongatus* 'brown', Eccles Reef. (e) *Pseudotropheus elongatus* 'dinghani', Chinyankwazi Island. (f) *Pseudotropheus elongatus* 'chinyamwezi', Chinyankwazi Island. (g) *Pseudotropheus elongatus* 'black', Chinyankwazi Island. (h) *Pseudotropheus elongatus* 'slab', Thumbi West Island. (i) *Pseudotropheus elongatus* 'bar', Maleri Island. (j) *Pseudotropheus elongatus* 'mbenji blue', Mbenji Island.



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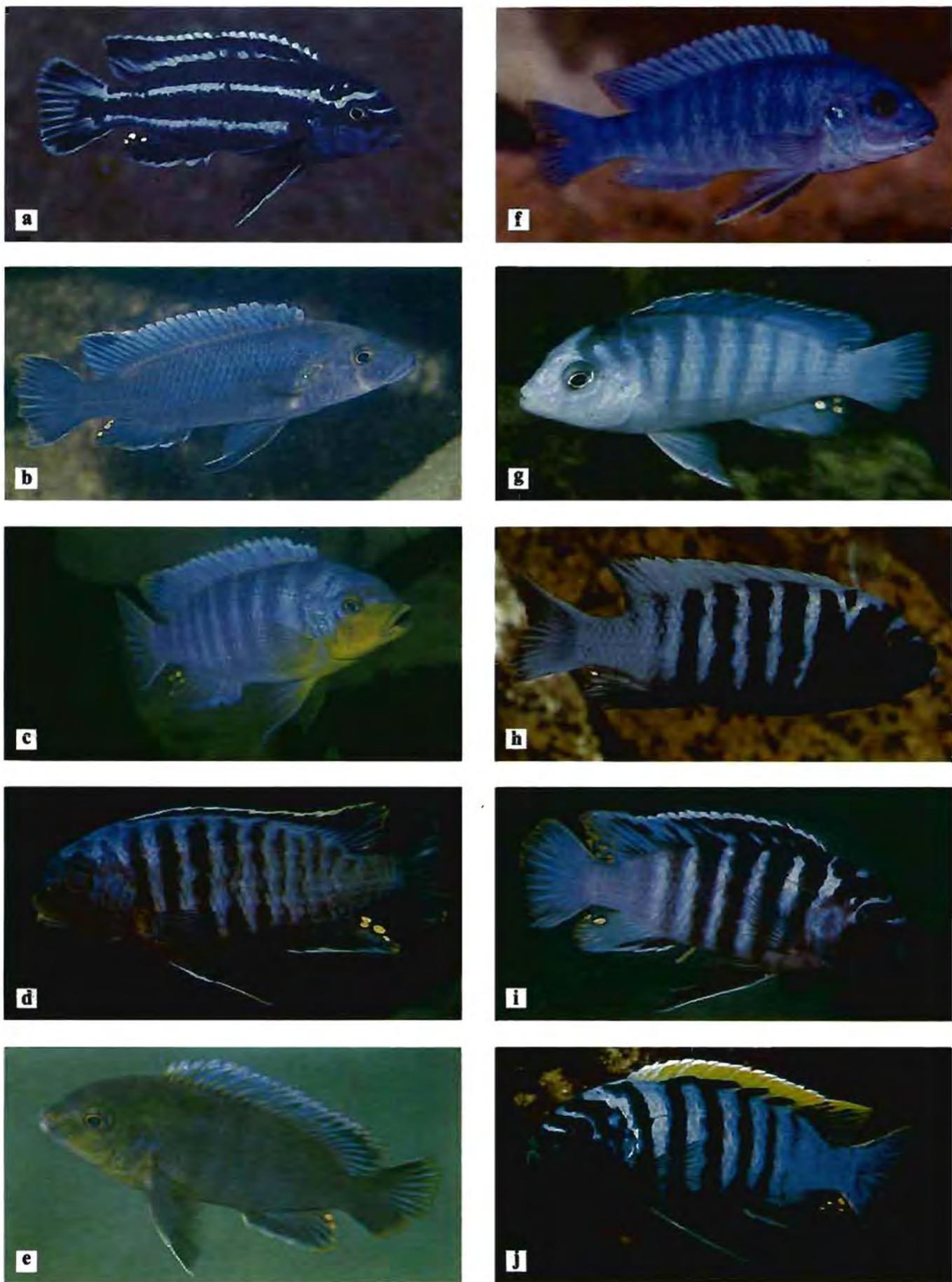
**Plate 7** (a) *Pseudotropheus elongatus* 'mbenji brown', Mbenji Island. (b) *Pseudotropheus elongatus* 'mbako', Likoma Island. (c) *Pseudotropheus elongatus* 'ornatus', Likoma Island. (d) *Pseudotropheus elongatus* 'gold bar', Chisumulu Island. (e) *Pseudotropheus elongatus* 'chisumulu', Chisumulu Island. (f) *Pseudotropheus elongatus* 'mara', Mara Rocks. (g) *Pseudotropheus elongatus* 'bee', Ruarwe. (h) *Pseudotropheus* 'aggressive blue', Monkey Bay. (i) *Pseudotropheus* 'aggressive yellow head', Maleri Island. (j) *Pseudotropheus* 'aggressive grey head', Maleri Island.



**Plate 8** (a) *Pseudotropheus* 'aggressive zebra', Likoma Island. (b) *Pseudotropheus tursiops* 'mbenji', Mbenji Island. (c) *Pseudotropheus* 'aggressive grey', Likoma Island. (d) *Pseudotropheus* 'aggressive yellow fin', Chisumulu Island. (e) *Pseudotropheus* 'tiny', Thumbi West Island. (f) *Pseudotropheus socolofi* (carrying eggs), Thumbi West Island. (g) *Pseudotropheus* 'dumpy', Maleri Island. (h) *Pseudotropheus* 'burrower', Maleri Island. (i) *Pseudotropheus* 'red dorsal', Mbenji Island. (j) *Pseudotropheus* 'ndumbi gold', Likoma Island.



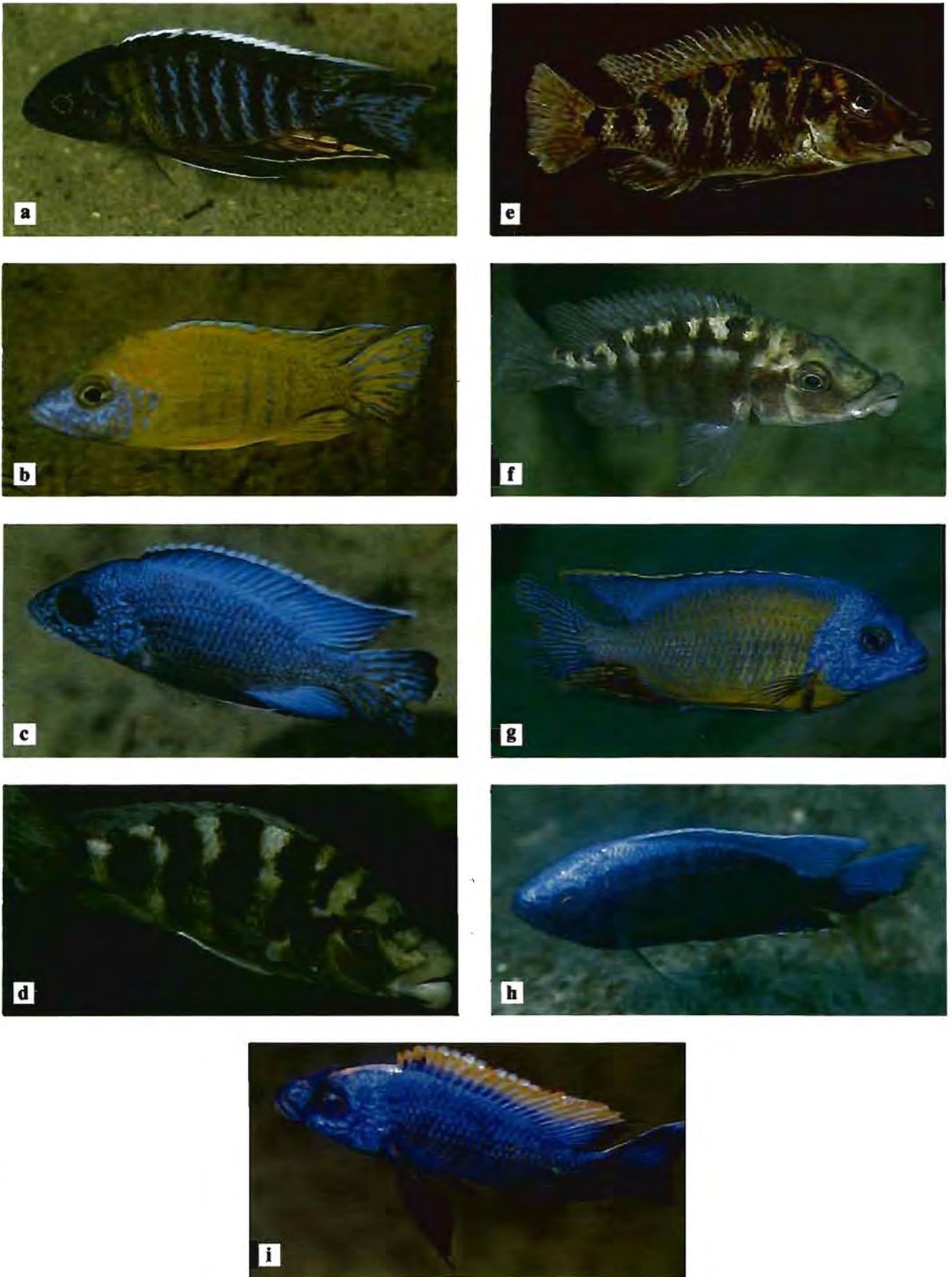
**Plate 9** (a) *Pseudotropheus* 'cobalt', Likoma Island. (b) *Pseudotropheus* 'kingsizei', Likoma Island. (c) *Pseudotropheus* 'newsi', Chisumulu Island. (d) *Pseudotropheus* 'polit', Lion's Cove. (e) *Melanochromis auratus*, Monkey Bay (female). (f) *Melanochromis auratus*, Masinje (Masinje form, female). (g) *Melanochromis* 'blotch', Makanjila. (h) *Melanochromis* 'lepidophage', Makanjila. (i) *Melanochromis* cf. *chipokae*, Thumbi West Island. (j) *Melanochromis* 'black-white johanni', Likoma Island.



**Plate 10** (a) *Melanochromis* 'maingano', Likoma Island. (b) *Melanochromis* 'blue', Chitande. (c) *Petrotilapia* 'yellow chin', Maleri Island. (d) *Petrotilapia* 'likoma barred', Likoma Island. (e) *Labidochromis vellicans*, Monkey Bay. (f) *Labidochromis* 'blue bar', Thumbi West Island. (g) *Labidochromis chisumulae*, Chisumulu Island. (h) *Cynotilapia* 'chinyankwazi', Chinyankwazi Island. (i) *Cynotilapia* 'black dorsal', Maleri Island. (j) *Cynotilapia afra* (with a yellow dorsal fin), Likoma Island.



**Plate 11** (a) *Cynotilapia afra* (with a white dorsal fin), Likoma Island. This individual is feeding on plankton. (b) *Cynotilapia* 'mbamba', Likoma Island. This individual is feeding on plankton. (c) *Cynotilapia* 'mbamba', Chitande. (d) *Cynotilapia* 'lion', Lion's Cove. (e) *Labeotropheus suelleborni*, Mara Rocks. (f) *Labeotropheus trewavasae*, Thumbi West Island. (g) *Iodotropheus sprengerae*, Chinyankwazi Island. (h) *Genyochromis mento*, Mpanga Rocks. (i) *Cyathochromis obliquidens*, Monkey Bay. (j) *Aulonocara* 'yellow collar', Thumbi West Island.



**Plate 12** (a) *Aulonocara* 'blue collar', Monkey Bay. (b) *Aulonocara* 'maleri gold', Maleri Island. (c) *Aulonocara* 'mbenji blue', Mbenji Island. (d) *Cyrtocara* 'labrosa', Monkey Bay. (e) *Cyrtocara* 'maleri thick lip', Maleri Island. (f) *Cyrtocara* 'mbenji thick lip', Mbenji Island. (g) *Cyrtocara* cf. *borleyi*, Monkey Bay. (h) *Cyrtocara* sp. (Utaka group), Monkey Bay. (i) *Cyrtocara* 'red dorsal', Monkey Bay.



**Plate 13** (a) *Cyrtocara laeniolata* female, Monkey Bay. (b) *Cyrtocara fenestrata* blowing into the substratum, Monkey Bay. (c) *Cyrtocara picta* sucking food from the substratum, Monkey Bay.

although at Namalenje Island it is restricted to the upper 3 m.

**Territoriality.** Males defend territories against conspecific males. Females, non-territorial males and juveniles are usually solitary.

**Feeding.** Individuals feed in the manner typical of members of this genus.

### 8. *Petrotilapia* 'fuscous'

**Synopsis.** Males are predominantly dark brown with a brown-orange cheek region.

**Distribution.** Maleri I. (C), Nankoma I. (C), Nakantenga I. (C), Mbenji I. (C).

**Coloration. Maleri Island males:** Body fuscous brown with orange-brown chest and belly. Head dark brown, almost black dorsally, but with orange-brown cheeks, chin, gular region and branchiostegal membranes, lips yellowish-brown. Dorsal fin blue-grey with a broad, black submarginal band; lappets blue with orange tips. Caudal fin fuscous brown with whitish upper and lower edges and an orange-yellow trailing edge. Anal fin blackish-brown with light brown edges and 1–5 bright yellow egg-dummies. Pelvic fins yellowish-brown with black submarginal bands and whitish leading edges.

**Maleri Island females:** Ground colour pale brown to khaki, some specimens dark brown. Flanks with prominent, narrow, black mid-lateral and dorso-lateral bands, which may be divided into blotches by 7–9 vertical black bars. Mid-lateral band projecting anteriorly to orbit and many specimens with a black occipital bar. Black dorso-medial blotches present in most specimens. Dorsal fin hyaline with pale grey lappets tipped with orange-brown; submarginal band narrow and dark grey; inter-ray membranes sometimes spotted, either yellow on hyaline background or hyaline on yellow background. Caudal and anal fins hyaline with numerous small bright yellow spots on posterior angle of anal fin. Pelvic fins hyaline with whitish leading edges and narrow grey submarginal bands.

**Habitat.** Members of this species occur over all rock types from 2 to 27 m and are particularly abundant between 5 and 10 m depth.

**Territoriality.** Males defend territories against conspecific males. Females, non-territorial males and juveniles are solitary.

**Feeding.** Individuals feed in the manner typical of this genus.

### 9. *Petrotilapia* 'likoma variable'

**Synopsis.** Territorial males vary in coloration from sky-blue to navy-blue but always have a metallic sheen. Females are off-white with two longitudinal black bands.

**Distribution.** This species occurs at all the rocky shores of Likoma Island.

**Coloration. Males:** Body sky-blue to navy-blue with metallic sheen and ochre chest and belly. Head sky-blue to navy-blue with metallic sheen, normally with ochre cheek, chin, gular region and branchiostegal membranes; interorbital bar dark grey. Dorsal fin sky-blue, but

sometimes with ochre hue; lappets pale blue anteriorly, pale blue tending to orange posteriorly; trailing edge orange. Caudal fin sky-blue with black rays and an orange trailing edge. Anal fin dark blue with orange trailing edge and 3–4 yellow egg-dummies. Some specimens with anal fin entirely ochre coloured. Pelvic fins ochre with pale blue leading edges.

**Females.** Head and body off-white with 8–9 pale grey bars and narrow black mid-lateral and dorso-lateral bands, the former extending anteriorly to form an opercular blotch. In some specimens the ground colour darker and markings less obvious. Dorsal fin hyaline with columns of yellow spots on posterior inter-ray membranes. Caudal fin with pale grey rays and hyaline inter-ray membranes. Anal fin hyaline with yellow spots on posterior angle in some specimens. Pelvic fins hyaline with white leading edges.

**Habitat.** This species is most common in the shallows, its full depth range is from the extreme shallows to at least 34 m. Most individuals live among medium-sized and large rocks.

**Territoriality.** Males defend territories against conspecific males. Females, non-territorial males and juveniles are solitary.

**Feeding.** Individuals feed in the manner typical of members of this genus.

### 10. *Petrotilapia* 'likoma barred' (Plate 10d)

**Synopsis.** Males are sky-blue to navy-blue and have 7–9 distinct dark vertical bars on their flanks.

**Distribution.** This species occurs at all the rocky shores of Likoma Island.

**Coloration. Males:** Body sky-blue to navy-blue with 7–9 dark blue to black bars on flanks; belly blackish; chest dark brown tending to black. Head dark blue dorsally, but blackish-brown below the level of the orbit. Dorsal fin blue-grey with a broad, black submarginal band; lappets pale blue with orange tips in most individuals though some may have either pure blue or pure orange lappets. Caudal fin lilac-blue with black rays and an orange-brown trailing edge. Anal fin bluish-grey with a broad, black submarginal band and a pale blue leading edge; 1–6 bright yellow egg-dummies. Pelvic fins grey-brown with black submarginal bands and pale blue leading edges.

**Females:** Head and body brown with 7–9 dark brown to black bars; between the bars a series of dark brown to black mid-lateral and dorso-lateral blotches along the flanks. The mid-lateral blotches extending anteriorly to form an opercular blotch. Dorsal fin brown with lappets and trailing edge orange-brown; black submarginal band narrow. Caudal fin with orange-brown trailing edge, dark brown rays and brown inter-ray membranes. Anal fin dark brown. Pelvic fins brown-orange with pale blue leading edges and black submarginal bands.

**Habitat.** Typically occurs over a wide range of rock sizes as well as inhabiting weed beds. Common in water less than 6 m deep and rarely found below 10 m except at Mazimbwe Islet where it penetrates to 15 m.

**Territoriality.** Males defend territories against conspecific

males. Females and non-territorial males are usually solitary but when plankton is abundant they hover in the water column, usually next to projecting boulders, in schools of more than 100 individuals.

*Feeding.* Individuals feed in the manner typical of members of this genus.

### 11. *Petrotilapia* 'orange pelvic'

*Synopsis.* Males are predominantly sky-blue and have bright orange pelvic fins.

*Distribution.* Chisumulu I. (C).

*Coloration. Males:* Body dark blue dorsally, but light blue ventrally; 5–7 blue-grey bars traversing the flanks. Head blue-grey dorsally but cheeks, chin, gular region and branchiostegal membranes bluish-brown; lips light blue. Dorsal fin blue with a narrow but conspicuous black submarginal band; lappets bluish-white with orange tips; rays black, inter-ray membranes blue with numerous orange ocelli along the trailing edge. Caudal fin rays dark grey, inter-ray membranes lilac, trailing edge orange, upper and lower edges black. Anal fin bluish with black rays and a black leading edge; 1 or 2 large orange-yellow egg-dummies. Pelvic fins bright orange with narrow, black submarginal bands and bluish-white leading edges. *Females:* Head and body normally dark brown but varying from pale brown to chocolate-brown. Opercular spot black. A series of mid-lateral black wedge-shaped blotches on flanks. Certain specimens also with a series of narrow dorso-lateral blotches. Dorsal fin hyaline brown with orange-brown lappets and a narrow black submarginal band. Caudal fin rays dark brown; inter-ray membranes hyaline brown. Anal fin hyaline brown. Pelvic fins brown with an orange hue and white leading edges.

*Habitat.* Members of this species were found most commonly among medium-sized and large rocks. They appear to favour sediment-free zones in the shallows and are rare below 3 m depth.

*Territoriality.* Males defend territories against conspecific males. Females, non-territorial males and juveniles are solitary.

*Feeding.* Individuals feed in the manner typical of members of this genus.

### 12. *Petrotilapia* 'retrognathous'

*Synopsis.* This species differs from all of its congeners in that it has a ventrally directed gape owing to the fact that the premaxilla extends anteriorly beyond the dentary.

*Distribution.* Chisumulu I. (C).

*Coloration. Males:* Body sky-blue with 8–9 navy-blue bars; belly with variable amount of ochre-brown; in some specimens the hue covers the entire flank region, but in others it is restricted to the chest. Head navy-blue dorsally with ochre-brown cheeks. Dorsal fin sky-blue with a variable amount of ochre-yellow anteriorly; trailing edge has numerous orange ocelli in most specimens. Caudal fin rays navy-blue, inter-ray membranes sky-blue; trailing edge orange; upper and lower edges whitish. Anal fin sky-blue, but suffused with ochre-yellow anteriorly; 1–4 bright yellow egg-dummies.

Pelvic fins sky-blue with heavy suffusion of ochre-yellow and with white leading edges.

*Females:* Head and body dark brown with faint ochre hue; belly paler brown than flanks. Dorsal fin dark brown with hyaline spots in inter-ray membranes; trailing edge orange-brown. Caudal fin dark brown with ochre trailing edge. Anal fin with dark brown rays, grey inter-ray membranes and 1–2 small orange egg-dummies. Pelvic fin rays dark brown, inter-ray membranes ochre-yellow; submarginal bands dark grey; leading edges whitish-blue.

*Habitat.* Members of this species exhibit no apparent preferences for rocks of a particular size. Furthermore, they may also occur in areas where pockets of sand are interspersed among the rocks. Most individuals occur at about 2 m depth, but this species was found to at least 10 m.

*Territoriality.* Males defend territories against conspecific males. Females, non-territorial males and juveniles are solitary.

*Feeding.* Feeds in the manner typical of members of this genus.

### 13. *Petrotilapia* 'yellow ventral'

*Synopsis.* Males are blue with yellow ventral surface. Common in deep water.

*Distribution.* Chisumulu I. (C).

*Coloration. Males:* Body pale sky-blue with 5–6 darker blue bars on flanks; ventral half of flanks, the chest and belly yellow. Head sky-blue dorsally, but yellow-orange below the level of the orbit. Dorsal fin sky-blue with scattered orange-blue flecks. Caudal fin rays yellow and inter-ray membranes lilac-blue. Anal fin navy-blue with a narrow black submarginal band and whitish leading edge; 13 orange-yellow egg-dummies. Pelvic fins yellow. *Females:* Head and body pale brown with rows of thin black dorso-medial, dorso-lateral and mid-lateral blotches. Mid-lateral blotches extending anteriorly to form an opercular blotch. Flanks also with 8 narrow, brown bars. Dorsal fin hyaline with orange lappets. Caudal fin inter-ray membranes hyaline and rays brown. Anal fin hyaline. Pelvic fins hyaline with white leading edges.

*Habitat.* It is common in water deeper than 10 m, and occurs from 8 m to at least 30 m depth. Members of this species were found most often among medium-sized and large rocks.

*Territoriality.* Males defend territories against conspecific males. Females, non-territorial males and juveniles are solitary.

*Feeding.* Feeds in the manner typical of members of this genus.

### 14. *Petrotilapia* 'small blue'

*Synopsis.* This is the smallest *Petrotilapia* species known (Table 10). Males are predominantly sky-blue with a yellow ventral surface and females are predominantly golden.

*Distribution.* Nkhata Bay (C), Lion's Cove (C), Cape Manulo (U). It probably occurs along the entire coastline between Nkhata Bay and Cape Manulo.

*Coloration. Nkhata Bay males:* Body sky-blue with 5–9

dark blue vertical bars; chest and belly yellow. Head blue with yellow chin, gular region and branchiostegal membranes. Dorsal fin sky-blue, though anterior basal portion orange; a broad, black submarginal band runs the length of the fin; lappets bright yellow. Caudal fin sky-blue with grey rays and an orange-yellow trailing edge. Anal fin hyaline grey with a broad black leading portion; 1–6 yellow egg-dummies. Pelvic fins greyish, sometimes with orange flecks; leading edges pale blue.

*Nkhata Bay females:* Ground colour brilliant gold in most individuals, but body and head varying from brown to golden; a series of dark brown to black blotches running mid-laterally along body, a similar series of blotches running dorso-laterally along the body. Dorsal fin golden with a narrow dark grey-brown submarginal band. Caudal fin golden with brown rays. Anal fin golden. Pelvic fins golden with dark grey submarginal bands.

*Habitat.* Members of this species are found over most rock types from 2 to at least 42 m depth with most individuals in the middle depths.

*Territoriality.* Males defend territories against conspecific males, seldom chasing heterospecifics. Females, non-territorial males and juveniles are usually solitary.

*Feeding.* Individuals feed in the manner typical of members of this genus.

#### 15. *Petrotilapia* 'ruarwe'

*Synopsis.* Males are predominantly blue with most fins, the gular region and belly yellow.

*Distribution.* Ruarwe (C), Chilumba at Chitande I. (C) and Mpanga Rocks (C).

*Coloration. Ruarwe males:* Body and head light blue with faint darker blue bars visible in some specimens; the chin, gular region, ventral part of the chest and the belly are yellow. Dorsal fin yellow with a faint blue hue in some individuals; lappets bright yellow; inter-ray membranes lilac-blue. Caudal fin lilac-blue with blue-grey rays and 2–5 bright yellow egg-dummies. Pelvic fins orange-yellow with light blue leading edges.

*Ruarwe females:* Head and body yellow-buff with 9 khaki bars and thin black mid-lateral and dorso-lateral bands on flanks. All fins hyaline with yellowish hue.

*Geographical variation.* The population at Chilumba differs slightly from that at Ruarwe. Chilumba males have orange-brown caudal fin rays. Females have a darker brown ground colour which has the effect of obscuring the vertical flank bars; all the fins are hyaline, with a brownish hue.

*Habitat.* Occurs over all rock sizes with an apparent preference for larger rocks. It has a broad depth range from 2 to 35 m at Ruarwe with its maximum abundance at 15 m.

*Territoriality.* Males defend territories against conspecific males. Females appear to be solitary.

*Feeding.* Individuals feed in the manner typical of members of this genus.

#### 16. *Petrotilapia* 'black flank'

*Synopsis.* Males are almost entirely black or deep purple. Females have a distinctive pattern of black criss-crossing

bands and bars on their flanks.

*Distribution.* Chilumba at Mpanga Rocks (C).

*Coloration. Males:* Head and body deep purple or black.

Dorsal fin grey with orange lappets and a broad black submarginal band. Caudal fin deep purple or black with an orange trailing edge. Anal fin black with 1–5 bright yellow egg-dummies. Pelvic fins purple or black with pale blue leading edges.

*Females:* Head and body colour varying from pale grey to dull brown with 8 black bars crossed by black mid-lateral and dorso-lateral bands; the vertical bars penetrating the dorsal fin. Dorsal fin hyaline with a narrow black submarginal band and orange-tipped lappets. Caudal, anal and pelvic fins hyaline.

*Habitat.* Occurs over all rock sizes in the shallows between 2 and 8 m depth, but is essentially a fish of large rocks.

*Territoriality.* Males defend territories against conspecific males. Females, non-territorial males and juveniles are solitary.

*Feeding.* Individuals feed in the manner typical of members of this genus.

#### 17. *Petrotilapia* 'chitande'

*Synopsis.* Only found at Chitande Island, Chilumba. Males are predominantly sky-blue with a distinctive yellow patch on their ventral surface.

*Distribution.* Chilumba at Chitande I. (C).

*Coloration. Males:* Body sky-blue with yellow chest and belly; 5 blue-grey bars traversing the anterior half of the flanks. Head sky-blue dorsally, but yellow below the orbit. Dorsal fin sky-blue with orange flecks and a narrow black submarginal band; lappets yellow. Caudal fin blue with orange-brown rays, a yellow-orange trailing edge and blackish-grey upper and lower borders. Anal fin grey with a black leading edge and 2–4 yellow egg-dummies. Pelvic fins yellow with grey leading edges.

*Females:* Head and body yellow-buff with 8 brown bars on the flanks and a series of black mid-lateral and dorso-lateral blotches. All fins are hyaline.

*Habitat.* Occurs over all rock sizes in the shallows and extreme shallows, but territorial males occur most commonly among medium-sized and large rocks. The maximum depth recorded for this species was 6 m.

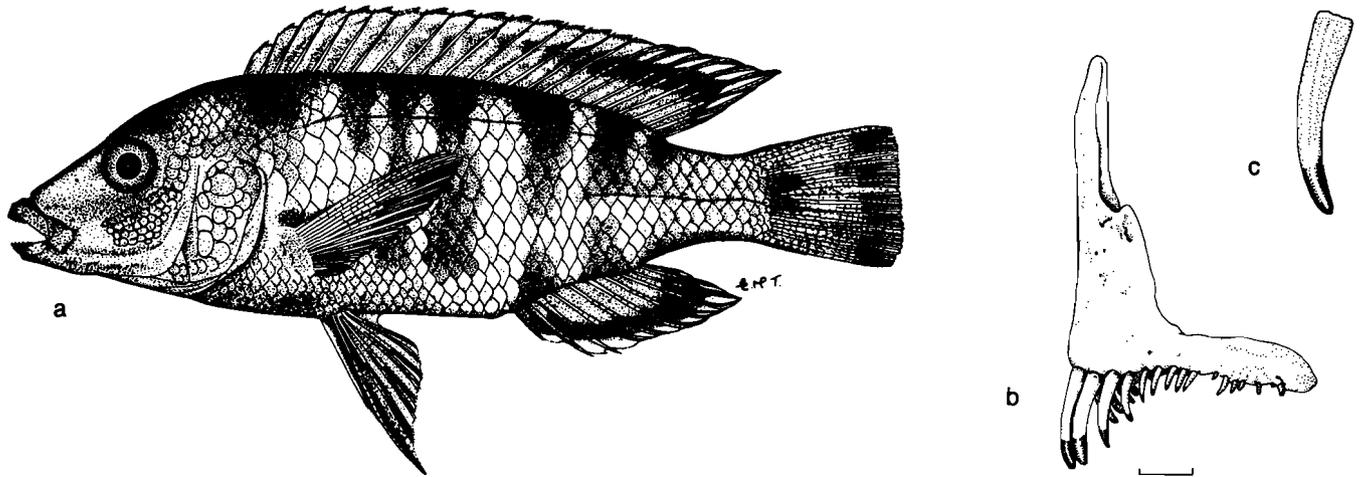
*Territoriality.* Males defend territories against conspecific males. Females appear to be solitary.

*Feeding.* Individuals feed in the manner typical of members of this genus.

Genus *Labidochromis* Trewavas 1935 (Figure 13a – c)

Members of this genus are distinguished from other genera by their long, pointed, unicuspid, forwardly directed anterior teeth (Trewavas 1935). Lewis (1982) has broadened the diagnosis of the genus to include three previously undescribed species, the members of which possess unevenly bicuspid anterior teeth, and a fourth species in which the teeth in the outer row are both bicuspid and unicuspid.

Lewis (1982) redescribed three species and described 13 new species giving illustrations and colour notes of all. As a consequence of this revision the genus *Labidochromis* is



**Figure 13** (a) *Labidochromis shiranus*, Nkudzi Point, 66 mm SL. (b) Lateral aspect of left premaxilla of *Labidochromis vellicans* (Scale = 1 mm). (c) Anterior outer row tooth of *L. vellicans*.

**Table 11** The members of the genus *Labidochromis*. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-), introduced (i)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	Ila	Ilb	Ilc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Labidochromis vellicans</i>	83	Chinyankwazi I.	+	+	-	+	+	+	+	+	-	-	+	-	-	-
2. <i>L. shiranus</i>	78	Nkudzi	-	+	-	-	-	-	-	-	-	-	-	-	-	-
3. <i>L. heterodon</i>	73	Boadzulu I.	-	-	+	-	-	-	-	-	-	-	-	-	-	-
4. <i>L. pallidus</i>	67	Thumbi West I.	-	-	-	-	-	+	-	+	-	-	-	-	-	-
5. <i>L. 'blue bar'</i>	84	Thumbi West I.	-	-	-	-	-	+	-	-	+	-	-	-	-	-
6. <i>L. mylodon</i>	69	Mumbo I.	-	-	-	-	-	-	+	-	-	-	-	-	-	-
7. <i>L. mbenjii</i>	64	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
8. <i>L. ianthinus</i>	71	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
9. <i>L. gigas</i>	100	Likoma I.	-	-	-	-	-	i	-	-	-	-	+	-	-	-
10. <i>L. freibergi</i>	64	Likoma I.	-	-	-	-	-	i	-	-	-	-	+	-	-	-
11. <i>L. lividus</i>	71	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
12. <i>L. zebroides</i>	68	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
13. <i>L. strigatus</i>	69	Chisumulu I.	-	-	-	-	-	i	-	-	-	-	+	-	-	-
14. <i>L. flavigulus</i>	68	Chisumulu I.	-	-	-	-	-	i	-	-	-	-	+	-	-	-
15. <i>L. chisumulae</i>	66	Chisumulu I.	-	-	-	-	-	-	-	-	-	-	+	-	-	-
16. <i>L. maculicauda</i>	64	Ruarwe	-	-	-	-	-	-	-	-	-	-	-	+	+	+
17. <i>L. caeruleus</i>	81	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	+

well understood taxonomically and only one of the 17 species listed in Table 11 is undescribed. Lewis (1982) discusses the validity of five other descriptions of species of *Labidochromis* which appeared mainly in the aquarist literature. Of these, only the description of *L. textilis* Oliver, 1975 appears to be valid, despite its inadequacy and the fact that four distinct species were included in the type series (Lewis 1980, 1982). However, as *L. textilis* occurs on the Mozambique coast it was not included in our survey.

As detailed colour descriptions are given by Lewis (1982), only the most notable of the species-specific colours and markings are given below. We also comment on the geographical variation of colour where appropriate.

**1. *Labidochromis vellicans* Trewavas, 1935 (Plate 10e)**

**Synopsis.** A small lithophilous species in shallow waters in the southern parts of the lake.

**Distribution.** Nkudzi (U), Mpandi I. (R), Kanchedza (U), Monkey Bay (C), Nankumba Peninsula (C), Domwe I. (U), Zimbabwe I. (C), Thumbi West I. (C), Otter Point (C), Mumbo I. (C), Maleri Is. (C), Namalenje I. (C), Chinyankwazi I. (C), Masinje Rocks (U), Makanjila Point (R). Although Lewis (1982) records the presence of *L. vellicans* at Chinyamwezi Island (p.198), elsewhere in his text (p.197) its distribution is given as Chinyankwazi Island. We found *L. vellicans* at Chinyankwazi Island and not Chinyamwezi Island.

**Coloration. Monkey Bay males:** Purple-brown with a rusty-brown hue. All fins have orange-brown edges or are predominantly orange-brown.

**Monkey Bay females:** Greenish-grey with orange-brown edges to all fins. Both sexes with grey vertical bars, but these are faint in males.

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**Geographical variation.** The populations along the western coast from Nkudzi to the northern tip of Domwe Island are very similar in colour to the Monkey Bay forms. However, those at Chinyankwazi Island, Zimbabwe Island, Mumbo Island, Masinje Rocks and Makanjila Point are predominantly reddish-brown in colour. The populations at Thumbi West Island and at Otter Point are paler than the Monkey Bay form. The Maleri Island and Namalenje Island forms were not included in the recent revision by Lewis (1982). These populations are pale brown, almost beige, with faint vertical bars.

**Habitat.** *L. vellicans* is most common in sediment-free rocky zones, on exposed shores. It favours medium-sized and large rocks. It is usually found in less than 7 m depth but an individual was seen at 15 m at Nakantenga Island (Maleri group) and another at 19 m at Chinyankwazi Island.

**Territoriality.** This species is not territorial, but occurs singly, in pairs or small groups usually not numbering more than 5 individuals.

**Feeding.** *L. vellicans* feeds mainly from the upper surfaces of rocks where it appears to pluck Aufwuchs from cracks and grooves. Stomachs of 12 individuals caught at Monkey Bay contained almost 90% C2, while loose Aufwuchs, C1, benthic Invertebrata and plankton comprised the remainder. Stomachs of 6 individuals caught at Maleri Island, contained 70% C1, 23% C2 and loose Aufwuchs, insects, plankton and benthic crustaceans. Lewis (1982) found that the diet of *L. vellicans* consists predominantly of filamentous algae, insect larvae and benthic crustaceans.

**Notes:** (i) The *Labidochromis* studied by Fryer (1959a) was not the *L. vellicans* of Lewis (1982) and so the feeding habits attributed to *L. vellicans* by Fryer do not apply to this species. (ii) The small dark brown fishes resembling *L. vellicans* at Likoma Island (Lewis 1982: 198) are now believed to be juvenile *L. gigas* (Lewis pers. comm.).

## 2. *Labidochromis shiranus* Lewis, 1982

**Synopsis.** The snout of *L. shiranus* is longer than in any other known species of *Labidochromis* (Lewis 1982). It lives among small rocks in less than 4 m depth. Males are olive-brown with orange markings; females are pale olive with grey bars and bands.

**Distribution.** Upper Shire River at Mangochi (C), Nkopola (C), Nkudzi (U), Mpandi (U).

**Coloration. Males:** Olive-brown with bluish cast, with narrow bands on the flanks and 7–9 bars. Dorsal fin pale olive with orange-brown spots which run together to form a reticulate pattern on the rayed portion; prominent black dorsal fin-spot.

**Females:** Pale olive with 7–9 grey bars and 2 longitudinal bands. Lower part of caudal fin and distal half of anal fin orange.

**Habitat.** *L. shiranus* occurs among small rocks in 0–4 m depth.

**Territoriality.** Members of this species are apparently not territorial and usually occur singly or in pairs, but sometimes slightly larger groups were seen.

**Feeding.** As the gut contents consist mainly of loose Aufwuchs, Lewis (1982) suggests that the spaced anterior teeth

might be used to comb unicellular components from the filamentous Aufwuchs.

## 3. *Labidochromis heterodon* Lewis, 1982

**Synopsis.** *L. heterodon* is the only member of the genus at Boadzulu Island. This little brown species is numerous among the rocks of the shallows.

**Distribution.** Boadzulu I. (N).

**Coloration. Males:** Yellowish-brown with a mauve cast and a black submarginal band in the dorsal fin.

**Females:** Brown with darker brown barring and a less prominent submarginal band in the dorsal fin than found in males.

**Habitat.** This species is numerous among medium-sized and small rocks in less than 3 m depth, but does penetrate to 10 m.

**Territoriality.** *L. heterodon* is a non-territorial species which occurs in large schools, often numbering more than 100 individuals.

**Feeding.** The Aufwuchs in the shallows at Boadzulu Island is particularly luxuriant, possibly because nutrients washed in from the cormorant colony of the island increase algal productivity. *L. heterodon* feeds mainly from this rich algal growth, nipping and jerking at the filamentous algae. The stomach contents of 10 specimens comprised wads of C1 (85%), loose Aufwuchs, crustaceans and C2.

## 4. *Labidochromis pallidus* Lewis, 1982

**Synopsis.** An almost white, lithophilous species of the shallows of the Maleri Islands and Thumbi West Island.

**Distribution.** At all three Maleri islands: Nakantenga (C), Maleri I. (C), Nankoma I. (C), and Thumbi West I. (U).

**Coloration. Males and females:** Totally white, but males may have a mauve cast.

**Habitat.** This species is most numerous in the shallows among medium-sized rocks, but it has been recorded from surface waters to a depth of 25 m, over other rock types and occasionally in intermediate areas.

**Territoriality.** It is not territorial, occurring singly, in pairs or in small groups usually numbering less than 6 individuals.

**Feeding.** *L. pallidus* feeds by nipping at the rock surface. Lewis (1982) found arthropod remains, filamentous algae and loose Aufwuchs in the stomachs of specimens of this species. Loose Aufwuchs was the dominant food item of some stomachs, which is unusual for members of this genus.

**Note:** Lewis (1982) suggests that the *L. pallidus* at Thumbi West Island may have been introduced there by an exporter of aquarium fishes. It does, however, occur all around the island and its increased density in the vicinity where exporters deposited fishes from other parts of the lake may be the result of some other factor. Unfortunately we shall never know whether *L. pallidus* occurs naturally at Thumbi West Island.

## 5. *Labidochromis* 'blue bar' (Plate 10f)

**Synopsis.** A rare blue fish with 10 to 12 dark vertical bars. It occurs among medium-sized and large rocks in sediment-free, shallow areas.

**Distribution.** Thumbi West I: at Mitande Rocks (R), Namalenje I. (U) and perhaps on the Nankumba Peninsula (unconfirmed observation).

**Coloration. Males:** Body metallic blue with 10–12 dark grey bars; chest and belly whitish; dorso-medial ridge blue-grey. Head blue-grey; chin, lower cheeks, gular region and branchiostegal membranes white; interorbital bar light blue. Dorsal fin blue with narrow, black submarginal band and whitish-blue lappets. Caudal fin blue-grey with orange trailing edge. Anal fin light blue at base, black submarginal band, white leading edge and hyaline trailing edge; 1–2 yellow egg-dummies. Pelvic fins pale blue with black submarginal bands and white leading edges.

**Females:** Pale blue-grey with the same markings as males.

**Habitat.** This species occurs among medium-sized and large rocks in less than 10 m depth in sediment-free areas.

**Territoriality.** Members of this species appear to be non-territorial and are usually solitary, but occasionally occur in pairs.

**Feeding.** It has been seen to nip at the Aufwuchs on the upper surface of rocks.

#### 6. *Labidochromis mylodon* Lewis, 1982

**Synopsis.** A white species endemic to Mumbo Island.

**Distribution.** Mumbo I. (U).

**Coloration. Male and female:** Creamy white.

**Habitat.** It lives in a variety of habitats, being found on the open faces of boulders and slabs, among medium-sized and small rocks, in the intermediate zones and in beds of *Vallisneria aethiopica*. It occurs from the surface to at least 15 m depth, but is most numerous between 1 and 8 m.

**Territoriality.** Neither sex of *L. mylodon* is territorial. The species occurs singly, in pairs or occasionally in groups of 3–6 individuals.

**Feeding.** The members of this species feed from crevices and cracks in the rock surface, apparently selecting their food items with care (Lewis 1982). They also feed from the sand and among *V. aethiopica* where they thrust their heads among the leaves and roots of these plants. Lewis (1982) identified several different species of insect larvae, ostracods of the genus *Cypridopsis* and the gastropod *Gabiella stanleyi* in the stomachs of *L. mylodon*. He considers the hypertrophy of the pharyngeal bones and teeth to be adaptations to cope with the molluscan components of the diet of these fishes.

#### 7. *Labidochromis mbenjii* Lewis, 1982

**Synopsis.** A brown barred lithophilous species of Mbenji Island.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Brown with numerous grey-brown bars and 2 longitudinal bands. Dorsal and caudal fins yellowish with black rays; anal and pelvic fins yellowish with black submarginal bands.

**Females:** Similar to males, but paler, and the rays in dorsal and caudal fins not as dark.

**Habitat.** It inhabits all the rocky shores of Mbenji Island, being most numerous in water less than 7 m deep but occurring to at least 18 m.

**Territoriality.** Members of this species are not territorial, but occur singly, in pairs or in small groups.

**Feeding.** Members of this species were seen to nip at the Aufwuchs. Lewis (1982) found filamentous algae and loose Aufwuchs in the stomachs.

#### 8. *Labidochromis ianthinus* Lewis, 1982

**Synopsis.** Pale brown species with a mauve cast. It is endemic to the rocky and intermediate habitats of Mbenji Island.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Pale olive or fawn with a mauve cast and 6–7 grey-brown bars. Prominent mauve iridescence on cheeks.

**Females:** Paler than males with less intense mauve iridescence.

**Habitat.** *L. ianthinus* lives in a variety of rocky habitats and in the intermediate zones, usually in less than 10 m depth. At Fuawe Islet, which is part of the western reef around Mbenji Island (Figure 52), it was found to 18 m.

**Territoriality.** The members of this species are not territorial and occur most often in small groups of up to 8 individuals.

**Feeding.** It feeds from both rock and sand substrata. Lewis (1982) found that some specimens had fed almost exclusively on chironomid larvae whereas in others the gut contents consisted entirely of detritus and sand grains. He also found a number of other insect larvae and nymphs were included in the diet of this species.

#### 9. *Labidochromis gigas* Lewis, 1982

**Synopsis.** A large relatively deep-bodied, lithophilous species. Males are cobalt-blue; females are brown.

**Distribution.** Likoma I. (C), Chisumulu I. (C). An introduced population occurs at Thumbi West I. (U) and another at Otter Point (U).

**Coloration. Males:** Cobalt-blue, sometimes with faint black barring and a black interorbital bar.

**Females:** Uniformly brown.

**Habitat.** *L. gigas* is present on virtually every type of rocky shore, but appears to favour medium-sized rocks. It is most numerous between 6 and 12 m depth and usually absent from the extreme shallows (except at Ndomo Point and Machili Islet). It occurs to at least 30 m depth.

**Territoriality.** Males defend territories against conspecifics, but females are not territorial and are usually solitary.

**Feeding.** It feeds by nipping and jerking at the Aufwuchs. Stomach contents of 14 specimens caught at Maingano contained C2 (90%), C1 (3%), plankton and benthic Invertebrata. Lewis (1982) notes that the diet consists solely of filamentous algae.

**Notes:** (i) *L. gigas* at Thumbi West Island occupies the same preferred habitat as at Likoma Island and Chisumulu Island. Territorial males may be found between 5 and 14 m depth among medium-sized rocks at Mitande Rocks.

(ii) While generally uncommon or rare at Thumbi West, it is common at Mitande Rocks, the rocky reef just off Thumbi West. It is believed that the introduced population was released at Mitande Rocks.

#### 10. *Labidochromis freibergi* Johnson, 1974

**Synopsis.** A deep-bodied, lithophilous species of the shallows of the north-eastern regions of Likoma Island. Males are blue with grey barring; females are olive-brown with dark brown barring.

**Distribution.** Endemic to the north-eastern part of Likoma Island: Mbako Point (U), Maingano (C), Membe Point (C), Madimba Bay (C), White Rock (U) and Mbuji Point (U). A small population was found at the south-eastern tip of Thumbi West Island where this species is rare (no more than 15 individuals were seen in 1980). This population was almost certainly introduced to Thumbi West Island.

**Coloration. Males:** Bright blue with 7 grey bars. Head bright blue, except for snout which is grey. Dorsal fin pale blue.

**Females:** Olive-brown with darker brown vertical bars.

**Habitat.** *L. freibergi* inhabits areas of small rocks usually in less than 6 m depth, though occasionally individuals penetrate to about 12 m.

**Territoriality.** Males are territorial in 2 to 6 m depth and are aggressive towards conspecifics, but they occasionally chase other species also. Females are not territorial and are normally solitary.

**Feeding.** *L. freibergi* feeds by nipping at the Aufwuchs mat and on plankton. Stomach contents of 11 individuals comprised 51% C1, 34% C2, 11% plankton and 4% loose Aufwuchs. Lewis (1982) found only filamentous algae in the stomachs of those specimens he examined.

**Note:** The populations at Thumbi West Island occupied the areas of small rocks in the shallows which is consistent with the habitat preference of this species at Likoma Island.

#### 11. *Labidochromis lividus* Lewis, 1982

**Synopsis.** A small, cryptic, darkly coloured species found among small and medium-sized rocks, in shallow waters at Likoma Island.

**Distribution.** It occurs along the northern and western shores of Likoma I. at Mbako Point (U), Makulawe Point (C), Khuyu (C), Ndomo Point (U). Its presence on Masimbwe Islet is unconfirmed.

**Coloration. Males:** Dark blue, almost black, with 8 narrow blue bars. Head blackish with two bright blue inter-orbital bars. Dorsal fin black with blue-white lappets. Caudal, anal and pelvic fins mainly dark grey.

**Females:** Olive-brown with grey barring.

**Habitat.** *L. lividus* lives among small and medium-sized rocks, but sometimes occurs among large rocks (at Makulawe Point) and in the intermediate zones (at Khuyu Bay). It is most numerous between 1 and 3 m and rare beyond 6 m.

**Territoriality.** Males are territorial, defending areas which are centred around holes or gaps among the rocks. They tend to remain hidden and seldom display in the open.

**Feeding.** It feeds by nipping at the Aufwuchs and appears

to favour vertical rock surfaces. Stomach contents of 6 individuals caught at Makulawe Point contained, in varying proportions, C1, C2 and loose Aufwuchs.

#### 12. *Labidochromis zebroides* Lewis, 1982

**Synopsis.** A deep-bodied, broad-banded, blue lithophilous species endemic to Masimbwe Islet.

**Distribution.** Likoma I. at Masimbwe Islet (U).

**Coloration. Males:** Bright blue with 5–6 wide black bars running the full depth of flanks and extending onto dorsal fin. Head blue. Fins pale blue with black markings.

**Females:** Colours unknown.

**Habitat.** This species lives among medium-sized and large rocks in water less than 6 m deep.

**Territoriality.** Males defend sites among the rocks, but like *L. lividus* they tend to remain hidden, or to display at the entrances of their refuges.

**Feeding.** Not recorded.

#### 13. *Labidochromis strigatus* Lewis, 1982

**Synopsis.** A small, elongate fish of small or pebble-sized rocks in shallow water. Males are blue with vertical bars. Females are greenish-olive with orange bands.

**Distribution.** Chisumulu I. (C). It also occurs at Likoma Island at Madimba Bay (U) and near to White Rocks (U). As both of these sites are close to where exporters of aquarium fishes maintain holding facilities, it is considered likely that the Likoma Island populations arose from escapees of Chisumulu origin. Similarly, a small introduced population occurs at the south-eastern tip of Thumbi West I. (R–U).

**Coloration. Males:** Royal blue with prominent grey-black bars.

**Females:** Greenish-olive with vertical barring and numerous thin orange bands.

**Habitat.** The preferred habitat of *L. strigatus* is among pebble-sized or small rocks in water of 1–4 m depth. It does, however, venture into intermediate zones and occurs among larger rocks. Its full depth range is from the surface to at least 10 m.

**Territoriality.** Males defend territories against conspecifics, occasionally also chasing heterospecific intruders. Territorial males of the intermediate zones construct sand-scrape nests. Females are not territorial and occur singly; sometimes in small groups.

**Feeding.** Stomachs of 3 individuals were examined and all contained predominantly C1, some C2 and a small proportion of loose Aufwuchs. Two of these individuals also had remains of insects in their stomachs, but these constituted a small fraction of the whole contents.

**Note:** The introduced populations occupy essentially the same habitat as they do in their native environment.

#### 14. *Labidochromis flavigulus* Lewis, 1982

**Synopsis.** A small species found among pebbles and small rocks over sandy areas where burrows may be constructed. Members of this species have orange-brown bands and a

yellow gular region.

**Distribution.** Chisumulu I. (C) and Likoma I. (R). It was probably introduced to Likoma Island where it is found in the vicinity of the holding facilities of exporters of aquarium fishes at Madimba Bay and at Mbuji Island. However, a small population is established on a submerged reef near White Rock which is between the sites used by exporters for storage of fishes.

**Coloration. Males:** Olive-grey with scalloped, orange-brown longitudinal bands; gular region and branchiostegal membranes bright golden-yellow. Fins with orange-brown blotches. Anal fin with prominent black submarginal band and 1–4 orange-yellow egg-dummies. **Females:** Paler than males with less intense submarginal band in anal fin and fainter yellow gular and branchiostegal region, but more prominent orange-brown longitudinal bands.

**Habitat.** *L. flavigulus* lives among small rocks and pebbles which have accumulated on sandy areas. It is most numerous in the extreme shallows, but it does penetrate to 15 m depth though it is rare beyond 8 m.

**Territoriality.** Territorial males excavate spawning sites wherever the habitat permits burrowing. The excavated sand which is deposited in a small mound at the burrow entrance marks the centre of each territory. Territories are defended against conspecifics most aggressively, but occasionally *L. flavigulus* chases heterospecific intruders. Females are not territorial, occurring singly or in small groups of 10–15 individuals.

**Feeding.** This species nips at the epilithic Aufwuchs when feeding.

#### 15. *Labidochromis chisumulae* Lewis, 1982 (Plate 10g)

**Synopsis.** A white, lithophilous species endemic to Chisumulu Island.

**Distribution.** Chisumulu I. (C).

**Coloration. Males:** White, sometimes with a blue hue; dorso-medial aspect black with incomplete black bars. **Females:** Uniform creamy white, sometimes with faint brownish bars below the dorsal fin.

**Habitat.** *L. chisumulae* occurs over a variety of rocky habitats ranging from small rocks in intermediate zones to large rocks in purely rocky environments. Its depth distribution extends from the extreme shallows to at least 25 m.

**Territoriality.** Members of this species occur singly, in pairs and in small groups usually numbering fewer than 5 individuals. No territorial individuals were found.

**Feeding.** Individuals remain close to the rocks, feeding from small cracks and crevices in the rock surface. They pluck insect larvae, nymphs, pupae and also ostracods and freshwater mites from these crevices (Lewis 1982).

#### 16. *Labidochromis maculicauda* Lewis, 1982

**Synopsis.** An elongate lithophilous species of the north-western shores of the lake. Males are darkly coloured; females have orange-brown bands.

**Distribution.** Chirombo Point (R), Nkhata Bay (C), Lion's Cove (U), Mara Rocks (R), Dankanya Bay (C), Usisya (U),

Ruarwe (C), Mpanga R), Chitande (C).

**Coloration. Males:** Dark brown with darker brown barring. Dorsal fin yellowish with a black or dark brown submarginal band and white lappets with yellow tips. All other fins pale brown, with dark brown blotches.

**Females:** Pale olive-grey with 9–11 dark brown bars and 7–8 narrow, orange-brown bands.

**Habitat.** It occurs mainly among small and medium-sized rocks, but also among large rocks (Mpanga Rocks, Mara Rocks, Chirombo Point) and in intermediate habitats. It usually occupies the shallows, being most numerous between 2 and 7 m, but it has been found to 12 m depth.

**Territoriality.** This is a non-territorial species occurring singly and in small groups.

**Feeding.** It feeds upon invertebrates collected from the Aufwuchs (Fryer 1959a, as *L. vellicans*).

**Note:** Fryer (1959a) described the biology of this species as that of *L. vellicans*.

#### 17. *Labidochromis caeruleus* Fryer, 1959

**Synopsis.** A deep-bodied, essentially white species from a variety of habitats of the rocky shores of the north-western regions of Lake Malawi.

**Distribution.** Chirombo Point (R), Nkhata Bay (R), Lion's Cove (R), Ruarwe (R). Exporters of aquarium fishes report its occurrence at Chilumba, but we cannot confirm this.

**Coloration. Nkhata Bay males and females:** White with prominent black submarginal bands in dorsal, anal and pelvic fins. Males developing a blue hue when in courtship.

**Geographical variation.** Specimens south of Nkhata Bay to Chirombo Point and also those at Ruarwe are white without black submarginal bands. Most individuals at Lion's Cove are white with the black fin markings, but a lime-yellow form was also seen there.

**Habitat.** *L. caeruleus* occupies a variety of rocky and intermediate habitats, also occurring in *Vallisneria aethiopica* beds. It occurs from the surface down to at least 40 m.

**Territoriality.** This is a non-territorial species. The fish are usually solitary or form pairs.

**Feeding.** It feeds by wresting insect larvae and nymphs, ostracods and mites from the rocks (Fryer 1959a). Lewis (1982) found that two individuals had enlarged pharyngeal bones and dentition and that these enlargements correlated with a diet of gastropods, probably *Gabiella stanleyi*. He suggested that these molluscs had been collected in beds of *V. aethiopica*.

**Note:** Although Fryer (1956a) described the colour of *L. caeruleus* as 'cobalt-blue' no individuals of this colour were seen during our survey.

#### Genus *Cynotilapia* Regan, 1921 (Figure 14a–c)

Members of this genus possess long, widely spaced, sharp conical outer teeth and have several irregularly spaced, smaller inner teeth. There is, however, considerable interspecific variation in body depth and coloration.

The genus was originally considered to be monotypic, with *C. afra* (Gunther, 1893), the type species. Recently,

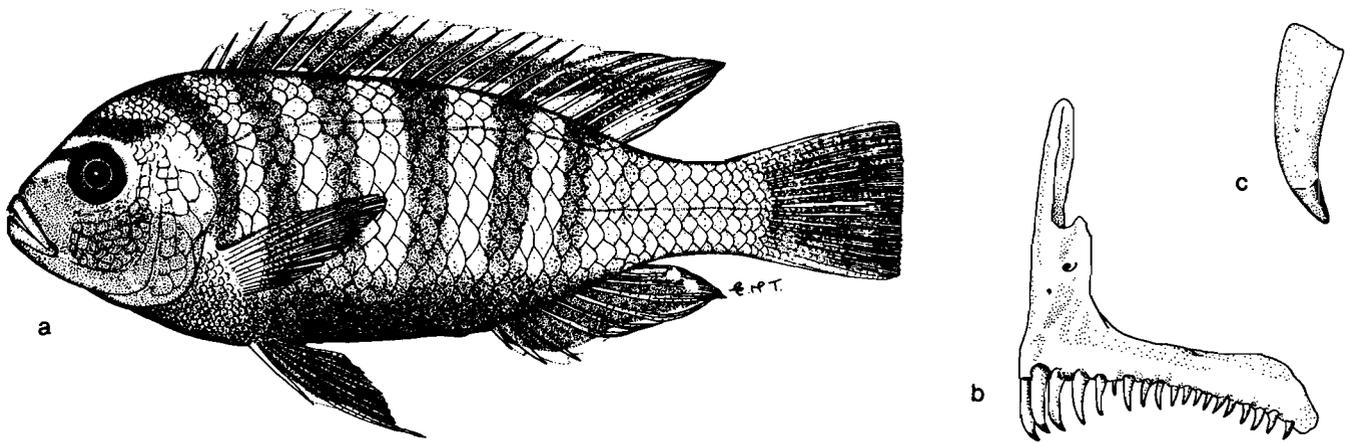


Figure 14 (a) *Cynotilapia afra*, Likoma Island, 93 mm SL. (b) Lateral aspect of left premaxilla of *C. afra* (Scale = 1 mm). (c) Anterior outer row tooth of *C. afra*.

**Table 12** The members of the genus *Cynotilapia*. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-), introduced (i)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	Ia	Ib	Ic	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Cynotilapia</i> 'chinyankwazi'	95	Chinyankwazi I.	-	-	-	-	+	-	-	-	-	-	-	-	-	-
2. <i>C.</i> 'maleri'	86	Maleri I.	-	-	-	-	-	-	-	+	-	-	-	-	-	-
3. <i>C.</i> 'yellow dorsal'	71	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
4. <i>C.</i> 'black dorsal'	83	Mbenji I.	-	-	-	-	-	-	-	-	-	+	-	-	-	-
5. <i>C. afra</i>	101	Likoma I.	-	-	-	-	-	i	-	-	-	-	+	+	+	+
6. <i>C.</i> 'mbamba'	105	Likoma I.	-	-	-	-	-	-	-	-	-	-	+	+	+	+
7. <i>C.</i> 'ndumbi'	none	caught	-	-	-	-	-	-	-	-	-	-	+	-	-	-
8. <i>C. axelrodi</i>	77	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	-
9. <i>C.</i> 'lion'	69	Lion's Cove	-	-	-	-	-	-	-	-	-	-	-	+	-	-
10. <i>C.</i> 'mpanga'	82	Mpanga Rocks	-	-	-	-	-	-	-	-	-	-	-	-	-	+

a second species, *C. axelrodi* Burgess, 1976 was described and we recognize a further eight species (Table 12).

### 1. *Cynotilapia* 'chinyankwazi' (Plate 10h)

**Synopsis.** A large member of the genus which closely resembles *Pseudotropheus zebra* in coloration, markings and general appearance.

**Distribution.** Chinyankwazi I. (C), Chinyamwezi I. (N).

**Coloration.** *Chinyankwazi males:* Body pale blue with 7–8 black bars. Head black with pale blue occipital bar and 2 interorbital bars. Dorsal fin pale blue with black bars of the body extending across the fin to merge with the black submarginal band; lappets white with yellow-orange tips. Caudal fin dark blue with white edges. Anal fin black with a white leading edge and 2–6 yellow egg-dummies. Pelvic fins black with white leading edges.  
*Chinyankwazi females:* Similar to males but with grey-blue ground colour.

**Habitat.** This species is found in greatest numbers among medium-sized rocks, but also occurs among rocks of other sizes. It occurs from 3 m to at least 40 m depth with the greatest number living between 10 and 20 m.

**Territoriality.** Males hold territories among medium-sized

rocks which they defend aggressively against conspecifics and less vigorously against heterospecifics. Females, juveniles, and non-territorial adults form large schools, comprising hundreds of individuals, in the water column 1–4 m above the rocks.

**Feeding.** Non-territorial individuals feed almost exclusively on plankton. Stomachs of 17 individuals caught in Jan./Feb. 1980 contained on average 97% phytoplankton and 3% zooplankton; stomachs of 8 individuals caught in December 1980, contained on average 78% zooplankton and 22% phytoplankton. The differences in stomach contents reflect the differences in availability of zoo- and phytoplankton at the time of our visits. Five territorial males caught in Jan./Feb. 1980 had more variable stomach contents for, in addition to the dominating phytoplankton and zooplankton, small proportions of loose Aufwuchs, filamentous algae and some insect larvae were found.

### 2. *Cynotilapia* 'maleri'

**Synopsis.** A deep-bodied, darkly coloured species living in deep water at Maleri Island.

**Distribution.** The south-eastern corner of Maleri I. (U).

**Coloration.** *Males:* Body dark blue, almost black, with

pitch-black bars. Head black with iridescent blue forehead and occipital region and a blue interorbital bar. In some individuals the forehead has a yellow tinge. Dorsal and caudal fins dark blue. Anal fin black with a white leading edge and 2–4 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Body and head grey with darker grey barring. Fins grey with black submarginal bands on all except caudal fin.

**Habitat.** It lives among medium-sized and small rocks in the sedimented areas from 17 to 27 m depth.

**Territoriality.** Males hold territories which they defend against conspecifics. Females, juveniles and non-territorial adult males form schools in the water column 2–4 m above the substratum.

**Feeding.** Observations of feeding behaviour suggest that this species feeds on plankton.

### 3. *Cynotilapia* 'yellow dorsal'

**Synopsis.** A blue and black barred lithophilous species with a yellow dorsal fin.

**Distribution.** Mbenji I. (A).

**Coloration. Males:** Body light blue with 7–8 black bars; belly and chest black ventrally. Head black with a light blue occipital bar and two light blue interorbital bars. Dorsal fin mainly yellow tending to orange posteriorly and blue anteriorly; black body bars penetrate base of fin. Caudal fin light blue with yellow rays and yellow trailing edge. Anal fin hyaline with a black submarginal band and white leading edge; 2–9 yellow egg-dummies. Pelvic fins hyaline with black submarginal bands and white leading edges.

**Females:** Similar in markings to males, but with grey ground colour and yellow fins.

**Habitat.** This species is abundant among small and medium-sized, sediment-free rocks between 5 and 15 m depth. It is uncommon in sheltered sediment-rich areas and rare in intermediate habitats. Its full depth range is from 2 to 20 m.

**Territoriality.** Males hold territories which are centred around small caves or holes among the rocks. They are aggressive to most intruders, but particularly hostile towards conspecific intruders. Females, juveniles and non-territorial adult males form large schools in the water column from 2 to about 10 m above the rocks.

**Feeding.** Members of this species were observed feeding upon plankton. Territorial individuals also feed from the Aufwuchs mat.

### 4. *Cynotilapia* 'black dorsal' (Plate 10i)

**Synopsis.** A secretive, blue and black barred, lithophilous species from Mbenji Island with a predominantly black dorsal fin.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Body light blue with 5 pitch-black bars on the flanks and 2 or 3 faint bars on the caudal peduncle. Head black with 2 light blue interorbital bars, a light blue occipital bar and several light blue patches on the occipital region. Dorsal fin pale blue with the black body bars crossing its base to merge with the prominent black

submarginal band which runs most of the length of the fin; lappets pale blue sometimes white; trailing edge orange; a variable number of yellow ocelli in rayed portion. Caudal fin slate-blue with light blue rays and orange trailing edge. Anal fin blue-grey with a black submarginal band and a white leading edge; 3–5 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Body and head grey with black markings similar to those of males.

**Habitat.** This species lives in caves among medium-sized or large rocks and in gaps between rocky pillars. It is most common between 3 and 8 m depth in sediment-free zones.

**Territoriality.** Males are territorial, but remain close to their sites of refuge, and encounters between conspecific males are uncommon. Non-territorial individuals are usually solitary and remain close to the rocks, but sometimes several may be seen together in the water column.

**Feeding.** Males feed on plankton, but seldom venture more than a metre or two from their caves to do so. Females also remain close to the rocks while feeding in the water column. This species also feeds on Aufwuchs.

### 5. *Cynotilapia afra* (Gunther, 1893) (Plates 10j & 11a)

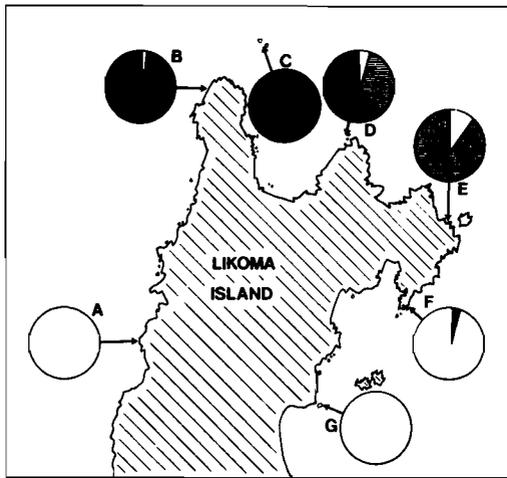
**Synopsis.** A blue and black barred, lithophilous species which is abundant throughout most of its distribution.

**Distribution.** Likoma I. (N–A), Chisumulu I. (N–A), Chirombo Point (N), Nkhata Bay (A), Lion's Cove (A), Mara Rocks (A), Dankanya Bay (A), Usisya (A), Mpandi Point (U), Ruarwe (A), Mpanga Rocks (A), Chitande (A).

**Coloration. Ndumbi Rocks (Likoma Island) males:** Body light blue with 8–9 black bars and a black chest and belly. Head black with a blue occipital bar that runs half-way down the operculum and two light blue interorbital bars. Dorsal fin orange-yellow, but penetrated along its base by black body bars and in some individuals two or three of these bars join distally to form a short black submarginal band; 3–12 red ocelli on trailing edge. Caudal fin inter-ray membranes pale blue, rays black, upper and lower edges orange and trailing edges orange-yellow. Anal fin black with white leading edge and 5–17 yellow-orange egg-dummies. Pelvic fins black with white leading edges.

**Ndumbi Rocks (Likoma Island) females:** Ground colour grey with similar markings as males.

**Geographical variation.** At Likoma Island the populations at Makulawe Point, Mbako Point and Maingano have black bars which traverse the flanks and enter the dorsal fin where they merge to form a black submarginal band. In the populations to the south of these sites, however, the black bars penetrate the dorsal fin but remain unconnected. Furthermore, in the northern populations at Likoma Island, the dorsal fin above the submarginal band is either entirely yellow, or entirely white, or yellow anteriorly and white posteriorly. Between 127 and 174 territorial males were examined at each of seven stations to establish what proportion of each population had a yellow dorsal fin, a white dorsal fin or a yellow-and-white dorsal fin. At Ndumbi Rocks and Makulawe Point virtually every male had a yellow fin, but the proportion decreased progressively towards White Rock where males have entirely white fins (Figure 15). It is conceivable that a similar clinal gradation in dorsal fin



**Figure 15** The proportion of the male populations of *Cynotilapia afra* at seven sites (A – G) around the northern sector of Likoma Island which had yellow (= black), yellow-white (= hatched) and white (= white) dorsal fins. A = Khuyu, B = Makulawe, C = Ndumbi, D = Mbako, E = Maingano, F = Membe Point, G = White Rock.

colour occurs between Khuyu Bay (Site A), where *C. afra* has white dorsal fins, and Makulawe Point (Site B), where 96% of the males were found to have yellow dorsal fins.

These differences in fin coloration and markings may reflect inherent differences between proximate populations, indicating that gene flow between these populations is retarded. Until this contention is proven, however, one cannot discount the possibility that the differences in fin colour are phenotypic responses to differing environmental conditions.

Adult *C. afra* at Chisumulu Island are smaller than those of Likoma Island, but are otherwise very similar morphologically. Both yellow and mixed yellow-white finned forms were found at Chisumulu though the proportion of these colour forms at each locality was not assessed.

Similarly, the populations of *C. afra* along the north-western coast of Lake Malawi have both white and yellow dorsal fins with a black submarginal band. Although it was noted that the proportion of each colour form varied between populations, the variation was not quantified.

**Habitat.** The preferred habitat of *C. afra* is among small and medium-sized rocks, in sediment-free areas which are exposed to currents, but it also lives over large rocks and boulders and in sheltered sediment-rich areas and may even be found in intermediate zones. It is most abundant between 5 and 20 m, but has a total depth range from the surface to at least 40 m.

**Territoriality.** Male *C. afra* are fiercely territorial though most of their aggression is directed intraspecifically. Territories are usually centred around holes or gaps among the rocks and these fishes tend to remain within their territories and close to the substratum. By contrast, non-territorial individuals are usually found in the water column, 1–4 m above the rocks, where they form large mixed schools with other Mbuna species, particularly *Pseudotropheus zebra*.

**Feeding.** Fryer (1959a) found that the vast majority of *C. afra* stomachs which he examined contained only plankton, but a small proportion (perhaps territorial males) also contained material from the Aufwuchs mat. We found that stomach contents are dominated by zoo- and phytoplankton

in non-territorial individuals, but that territorial males also eat loose Aufwuchs, C1, C2, insect larvae and nymphs, and benthic crustaceans.

*Note:* In his description of the preferred habitat of this species Fryer (1959a) correctly indicates that most individuals live in the water column a short distance away from the rocks. He suggests further, that the species is evolving habits which are emancipating it from the rocks. This gives the impression that *C. afra* is not closely tied to the rocks. Our observations indicate, however, that territorial males are strictly lithophilous and do not venture from their territories even when feeding on plankton, that spawning occurs among the rocks, that refuge is sought among the rocks by most and perhaps all members of the species at night and that fry live among the rocks until large enough to avoid being eaten by other fishes.

## 6. *Cynotilapia 'mbamba'* (Plates 11b & 11c)

**Synopsis.** A deep-bodied, large member of the genus which lives in deep water. Males are mainly black with narrow blue bars and a blue or yellow flare on the head. Females are grey.

**Distribution.** Likoma I. at Mbamba Islet (C), Membe Point (U), Maingano (C), Mbako Point (R), Ndumbi Rocks (R), Makulawe Point (C), Ndomo Point (U), Masimbwe Islet (C), Mbuzi Islets (U). Chisumulu I. at Mkanila Bay (C), Machili Islet (C), Membe Islet (C), Same Bay (U). The north-western shores from Chirombo Point to Nkhata Bay (U – C). Lion's Cove (C), Dankanya Bay (C), Ruarwe (N), Mpanga Rocks (N), Chitande (N).

**Coloration.** *Mbamba Islet males:* Body black with 4–6 narrow, light blue wedges of colour projecting downwards onto the flanks. Head black with 2 bright blue interorbital bars and a blue flare on the occipital region. Dorsal fin black with whitish-blue lappets. Caudal fin black with whitish-blue upper and lower edges. Anal fin black with whitish-blue edges and 2–6 yellow egg-dummies. Pelvic fins black with white leading edges.

*Mbamba Islet females:* Body and head dark grey; light grey where males are whitish-blue.

**Geographical variation.** The amount of blue and whitish-blue varies between Likoma Island populations; populations in the south have a greater amount of blue and a more conspicuous flare on the forehead than those in the north. The Chisumulu Island populations have very little blue relative to any Likoma population. From Chirombo Point to Dankanya Bay males have 5–8 blue wedges of colour and a bright blue flare on the head which extends onto the dorsal fin. At Ruarwe, Mpanga Rocks and Chitande both the flare and the dorsal fin are yellow (Plate 11c). Females are similarly marked and coloured throughout the distribution of this species.

**Habitat.** It lives among medium-sized and large rocks in sediment-rich areas, usually in water deeper than 10 m. This species is most numerous between 10 and 25 m, but occurs from 3 m to at least 40 m depth.

**Territoriality.** Males defend territories aggressively against conspecifics, but they also evict other intruders which penetrate deeply into their territories. The territories centre around holes in, and gaps among, the rocks. Females,

juveniles and non-territorial adults form schools of up to 40 individuals which remain 1 to 5 m above the rocks.

**Feeding.** Non-territorial individuals were seen to feed almost entirely from the water column, but territorial fishes fed from the water column and from the Aufwuchs within their territories. Stomach contents of 12 individuals (both territorial and non-territorial fishes) caught at 15 m depth at Membe Point (Likoma Island), contained on average 80% zooplankton, 15% phytoplankton, and the remaining 5% comprised filamentous algae and benthic invertebrates.

### 7. *Cynotilapia* 'ndumbi'

At Ndumbi Rocks a deep-bodied, darkly coloured, cave-dwelling species of *Cynotilapia* was seen between 3 and 15 m. It is uncommon and by virtue of its cryptic behaviour none was caught. We were nevertheless able to view the teeth and assign the specimens with confidence to the genus *Cynotilapia*.

### 8. *Cynotilapia axelrodi* Burgess, 1976

**Synopsis.** An elongate, light blue fish of the intermediate habitats.

**Distribution.** Chirombo Point to Nkhata Bay (C), Lion's Cove (R).

**Coloration. Males:** Body pale blue, with yellowish-pink belly and chest; 7–9 black bars. Head blue tending to grey ventrally with yellowish chin and gular region; one light blue interorbital bar crossing the grey-blue snout. Dorsal fin whitish-blue with white lappets and yellow edges to the rayed part. Caudal fin blue with a blackish base, yellow-orange distal edge and black upper and lower borders with yellowish-white edges. Anal fin hyaline with a broad black submarginal band and a whitish-yellow leading edge; 1–4 golden egg-dummies. Pelvic fins hyaline with black submarginal bands and white leading edges.

**Females:** Body and head blue with very faint black barring; belly, chest and ventral part of caudal peduncle brownish-blue. Fins pale blue with yellowish tinge; black upper and lower borders to caudal fin; black submarginal bands on anal and pelvic fins.

**Habitat.** This species lives in intermediate zones and may also be found over sand at least 12 m away from rocks. *C. axelrodi* is most numerous in 4–10 m depth, but it has been found to 20 m.

**Territoriality.** Males either dig saucer-shaped spawning sites 8–12 cm in diameter and 5 cm deep alongside rocks, or burrow beneath the rocks depositing the excavated sand in a ring around the entrance. These spawning sites usually mark the centre of the territory. Males are aggressive in the defence of their territories chasing conspecific and heterospecific intruders. Non-territorial individuals of both sexes form schools numbering between 20 and 150 members which usually remain in the water column 1–2 m above the sand substratum, but sometimes descend onto the sand.

**Feeding.** *C. axelrodi* feeds on plankton and also from sandy and rocky substrata onto which the schools periodically descend.

### 9. *Cynotilapia* 'lion' (Plate 11d)

**Synopsis.** A small, elongate, yellowish-blue species which

lives at the rock-sand interface at Lion's Cove.

**Distribution.** Lion's Cove (C).

**Coloration. Males:** Body yellowish-blue dorsally, yellowish-brown ventrally with 6 black bars on the flanks and 2–3 faint grey bars on the caudal peduncle. Head bluish-grey over occipital region, snout dark grey; cheeks, chin and gular region ochre-yellow; 2 light blue interorbital bars. Dorsal fin yellowish-blue with 6 black bars of the flanks crossing its base; lappets whitish-blue. Caudal fin blue at base, but black distally with black upper and lower borders and white edges. Anal fin black with a light blue leading edge; 2–6 bright golden-yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Markings similar to males, but ground colour sombre greenish-yellow with dark grey barring.

**Habitat.** This species lives over sand along the rock-sand interface from 2 to at least 30 m depth.

**Territoriality.** Males are aggressively territorial, usually defending sites alongside or among rocks, but some individuals were found guarding territories over sand as far as 5 m from the rocks. They construct saucer-shaped nests of about 10 cm diameter. Females and non-territorial males occur singly or in small groups over the sand and among the rocks in the intermediate habitats.

**Feeding.** This species was seen to feed from the water column, the sand and the rocks.

### 10. *Cynotilapia* 'mpanga'

*C. 'mpanga'* is a shy, blue and black barred fish that occurs at Mpanga Rocks between 5 and 15 m depth. This species differs from *C. afra* in its cryptic behaviour, its larger adult size and by having an almost entirely black dorsal fin. This species is rare and only one specimen was caught.

**Genus *Labeotropheus* Ahl, 1927. (Figures 16a–c)**

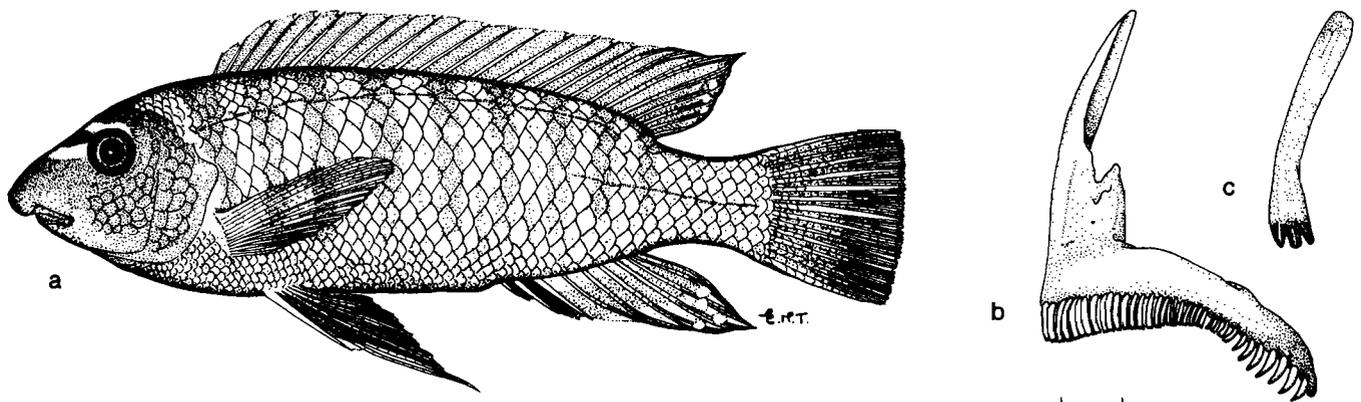
This genus was originally described by Ahl (1927) who distinguished its members from other cichlids by their possession of large protuberant fleshy snouts. The mouth is inferior-subterminal (Trewavas 1935) which enables the members of this genus to crop algae while swimming almost parallel to the rock surface (Fryer 1956b, 1959a). Only two species are currently recognized (*L. fuelleborni* Ahl, 1927 and *L. trewavasae* Fryer, 1956b) although considerable geographical variation occurs (Ribbink, Marsh, Marsh & Sharp in press, see also below). Both species exhibit polychromatism. *L. trewavasae* has a disjunct distribution, but *L. fuelleborni* occurs in all the major study areas (Table 13).

#### 1. *Labeotropheus fuelleborni* Ahl, 1926 (Plate 11e)

**Synopsis.** This is the deeper-bodied member of the genus. It inhabits the shallows, favouring medium-large rocks.

**Distribution.** *L. fuelleborni* is one of the most widely distributed species of Mbuna and was found at every rocky shore visited, except Chemwezi Rocks and the submerged reef at Mazinzi. It is a common species on virtually all rocky shores.

**Coloration. Monkey Bay males:** Body blue with 8–10 dark blue bars varying in intensity from almost black to hardly discernible; chest and belly whitish-blue. Head blue with 2 blue-black occipital bars and 2 blue-black interor-



**Figure 16** (a) *Labeotropheus trewavasae*, Maleri Island, 90 mm SL. (b) Lateral aspect of left premaxilla of *L. trewavasae* (Scale = 1 mm). (c) Anterior outer row tooth of *L. trewavasae*.

**Table 13** The members of the genera *Labeotropheus*, *Gephyrochromis*, *Iodotropheus*, *Genyochromis* and *Cyathochromis*. The maximum size in mm of each species and the locality at which the largest specimen was caught. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Details of distribution are given for each species in the text. Present (+), absent (-)

Species	Maximum size		Distribution													
	mm (SL)	Locality	I	Ila	Ilb	Ilc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Labeotropheus fuelleborni</i>	122	Zimbabwe I.	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2. <i>L. trewavasae</i>	121	Zimbabwe I.	+	-	+	+	-	+	+	+	+	-	-	+	+	+
3. <i>Gephyrochromis lawsi</i>	89	Nkhata Bay	-	-	-	-	-	-	-	-	-	-	-	+	-	+
4. <i>Genyochromis mento</i>	108	Chinyamwezi I.	+	+	+	+	+	+	+	+	+	+	+	+	+	+
5. <i>Cyathochromis obliquidens</i>	112	Nkhata Bay	+	+	-	+	-	+	+	+	-	+	+	+	+	+
6. <i>Iodotropheus sprengerae</i>	94	Chinyamwezi I.	-	-	+	-	+	-	-	-	-	-	-	-	-	-

bitar bars; lower part of snout, cheeks and opercular regions dark blue; chin, gular region and branchiostegal membranes whitish. Dorsal fin pale blue with black rays and orange-red inter-ray membranes. Caudal fin pale blue with black rays and an orange trailing edge. Anal fin pale blue at base, orange distally with 2–5 yellow egg-dummies. Pelvic fins orange with black submarginal bands and whitish-blue leading edges. The blue-blotch (male OB) forms are very rare in Monkey Bay.

**Monkey Bay females:** Normal females are brown or grey-brown with dark grey barring. Orange-blotch (OB) forms constitute less than 5% of the female population.

**Geographical variation.** *L. fuelleborni* exhibits geographical variation, particularly with regard to male fin colours. Unless stated otherwise only male colours are given below as geographical variation in female colours is less obvious. Ground colours of the body and head are given and as barring is present in all populations it is mentioned only where it is particularly intense or virtually absent. For comparisons the reference population is that of Monkey Bay.

**Zimbabwe Rocks:** Pale blue body and head. Dorsal fin blue with orange-red rayed section and yellow ocelli. Caudal fin blue with dusky grey rays and a bright orange trailing edge. Anal fin blue at base, but otherwise grey to hyaline with 3–9 yellow egg-dummies. Females almost entirely black and no OB forms were found.

**Nkopola:** Slate-blue with yellowish fins.

**Nkudzi:** Body, head and fins very pale blue with an orange trailing edge to dorsal fin.

**Mpandi Island:** Pale sky-blue with orange anal and pelvic fins. Dorsal fin whitish-blue with orange trailing edge.

**Boadzulu Island:** Body and head pale blue. Dorsal fin blue with yellowish-orange hue, tending to reddish posteriorly; rayed portion black with yellow-orange trailing edge and orange ocelli. Caudal fin blue with black rays and yellow trailing edge. Anal fin orange with a black patch distally and orange egg-dummies. Pelvic fins orange with black submarginal bands and white leading edges.

**Makanjila Point:** Body and head blue. Dorsal fin orange-red, caudal fin blue with black rays. Anal fin dark blue-grey with an orange trailing edge and yellow egg-dummies. Pelvic fins orange with blue leading edges.

**Masinje Rocks:** Body and head blue with yellowish fins.

**Eccles Reef and West Reef:** Body and head blue. Fins blue with yellow-orange trailing edges.

**Chinyankwazi Island:** Body and head lavender-blue with prominent black bars dorsally, but fading ventrally. Dorsal fin yellowish-orange cast on blue background, but dominated by a broad black submarginal band. Caudal fin-rays blue with yellow-orange inter-ray membranes. Anal fin blue with yellowish cast and bright golden-yellow egg-dummies. Pelvic fins orange with black submarginal bands and whitish-blue leading edges. About 97% of females are black and 3% OB.

**Chinyamwezi Island:** Body and head lavender-blue with black bars prominent mid-laterally on the flanks, but fading both dorsally and ventrally; lower half of the head black,

with a light blue chin and gular region. Dorsal fin whitish-blue with black rayed section. Caudal fin rays black with blue inter-ray membranes. Anal fin black with blue-white leading edge and yellow egg-dummies. Pelvic fins black with blue-white leading edges. The number of normal (black) relative to OB and O females was counted along depth contours in the 3–10 m depth range by three divers working separately; 53% were normal-coloured and 47% were OB/O ( $N=427$ ). The OB/O morphs at Chinyamwezi ranged from speckled, through blotched to an almost pure tangerine-orange.

**Thumbi West Island:** Body and head blue. Dorsal fin blue with orange trailing edge and yellow ocelli, but less black in the rayed portion than Monkey Bay form. Anal fin blue at base, otherwise orange-pink with 3–8 yellow egg-dummies. Pelvic fins mainly orange with narrow black submarginal bands and whitish-blue leading edges.

**Mumbo Island:** Body and head dark blue. Dorsal fin pale blue with orange-red rayed region. Caudal fin rays blue with orange inter-ray membranes and yellow trailing edge. Anal fin orange with yellow egg-dummies. Pelvic fins orange-red with light blue leading edges. Females dark blue-grey and OB, but the OB form is rare.

**Maleri Island:** Body and head very pale, powder-blue. Dorsal and caudal fins whitish-blue with yellow trailing edges. Anal fin pale yellow-orange. Pelvic fins pale yellow-orange with white leading edges. It is estimated that between 2 and 5% of the males at the south-eastern corner of Maleri Island were the blue-blotched form.

**Nakantenga Island:** Body and head pale blue, but with a golden-yellow flush on the flanks, extending onto the head in some individuals. This is the only population with yellowish flanks. Dorsal fin blue with a faint golden hue, orange trailing edges and yellow ocelli. Caudal fin blue with an orange trailing edge. Anal fin blue with yellow egg-dummies. Pelvic fins blue with orange trailing portions.

**Mbenji Island:** Body and head pale blue. Dorsal and caudal fins whitish-blue with bright orange trailing sections. Anal fin blue along posterior basal region, but otherwise bright yellow-orange with yellow egg-dummies. Pelvic fins orange with broad, black submarginal bands and blue-white leading edges. The female OB and O morphs were quite common at Mbenji Island and were heavily exploited for the aquarium trade until 1978, but are now protected.

**Likoma Island:** Body and head blue. Dorsal fin pale blue with a pinkish-orange hue, bright yellow-orange trailing edge, orange ocelli and purple rays. Caudal fin rays blue with black inter-ray membranes and an orange-yellow trailing edge. Anal fin blue with orange cast and 2–5 large yellow egg-dummies. Pelvic fins orange-blue with black submarginal bands and pale blue leading edges. The OB form is uncommon and the O form is rare.

**Chisumulu Island:** The populations are similar to those of Likoma Island but have less pink in the dorsal fin. The OB female is rare and only one O female was seen.

**Chirombo Point to Ruarwe:** Body and head sky-blue. Dorsal fin pale blue with black rays and yellow-orange ocelli. Caudal fin rays black with pale blue inter-ray membranes; trailing edge orange. Anal fin pale blue with yellowish-orange egg-dummies. Pelvic fins pale blue with broad black

submarginal bands and whitish leading edges.

**Chitande:** This population is similar to those of the other regions of the north-western shores, but it has a rusty-orange chest, an orange hue to the dorsal fin and the rayed part of the pelvic fins is orange-red.

**Habitat.** *L. fuelleborni* shows a preference for medium-large rocks (Ribbink *et al.* in press), but occurs in a wide variety of habitats and in the intermediate zones. It is most common in the shallows, but may penetrate to 18 m.

**Territoriality.** Males are aggressively territorial towards conspecifics, but pay little attention to heterospecific intruders unless they enter the centre of the territory. Females, juveniles and non-territorial males congregate in the extreme shallows.

**Feeding.** Non-territorial fish feed from the upper surfaces of rocks, and by virtue of their ventrally directed jaws they are able to feed in water which would be too shallow for fishes of a similar size, but which feed at right angles to the rock surface. Furthermore, since *L. fuelleborni* individuals feed parallel to the rock surface it appears that they are better able to cope with the turbulence which prevails in the extreme shallows than fishes which feed at right angles to the rock face. They favour the upper surfaces of rocks as feeding sites and have a varied diet which comprises mainly loose Aufwuchs, C1, C2, benthic Invertebrata and plankton (Ribbink *et al.* in press).

**Note:** A small population of the yellow-flanked form from Nakantenga Island was introduced to the island of Thumbi West. It has not been established whether this introduced population is breeding with the native population, but no intermediate forms were recognized.

## 2. *Labeotropheus trewavasae* Fryer, 1956 (Plate 11f)

**Synopsis.** *L. trewavasae* is the slender-bodied member of the genus.

**Distribution.** Boadzulu I. (C), Thumbi West I. (C–N), Zimbabwe I. (C), Mumbo I. (C), Nakantenga I. (C), Maleri I. (C), Nankoma I. (C), Namalenje I. (C), Masinje Rocks (U), Chirombo Point to Nkhata Bay (U–C), Lion's Cove to Chitande (U–C).

**Coloration.** *Boadzulu males:* Body and head pale powder-blue. Dorsal fin yellow with pale blue trailing portion and yellow ocelli. Caudal fin pale blue with yellow trailing edge. Anal fin pale blue with 2–5 bright yellow egg-dummies. Pelvic fins pale blue with a dark blue submarginal band.

*Boadzulu females:* Normal females pale brown or light grey-brown; OB females beige with brownish-black blotches.

**Geographical variation.** Considerable geographic variation in dorsal fin colour was found and the basic coloration of the body and head of the populations along the north-western shores is different from that of the southern populations.

**Thumbi West Island:** Males are similar to the Boadzulu form, but are a deeper blue, tending to royal blue, with 9–10 dark blue bars and a dark blue head. Dorsal fin orange-red; caudal fin blue with a yellow-orange trailing edge. Anal fin blue with a black leading edge and 2–7

yellow egg-dummies. Pelvic fins pinkish with white leading edges. Females are normal (brown to grey-brown), OB and O (reddish-orange).

**Zimbabwe Rocks:** This colour form is very similar to the Thumbi West form, but the rays of the dorsal and caudal fins are black; anal fin has a large orange-yellow central portion and the pelvic fins are orange-red.

**Mumbo Island:** Males are blue with a blue dorsal fin and yellow ocelli. Caudal fin blue with yellow trailing edges. Anal fin blue with a yellow antero-dorsal patch. Pelvic fins yellow with a black submarginal band. Females: brown form or pale OB form are present in approximately equal proportions.

**Masinje Rocks:** Males are metallic-blue with light blue fins. Females are brown or OB.

**Nakantenga Island:** Males are blue; fins mainly pale blue. Females are brown to grey-brown forms and OB forms.

**Maleri and Nankoma Islands:** Males are very similar to the Boadzulu Island form, but deeper blue with yellow-orange dorsal fins. Only pale OB females were found.

**Namalenje Island:** Males are similar to those of Maleri Island, but the dorsal fin is a deeper orange-red. Both normal and OB females were seen.

**Nkhata Bay, Mara Rocks and Mpanga Rocks:** Males are blue with blue fins. The only noticeable difference is that the Nkhata Bay form has a purple-blue dorsal fin whereas the other two populations have whitish-blue dorsal fins and the Mara Rocks form is deeper blue with 8–10 dark blue bars.

**Lion's Cove:** Males are purple dorsally on the head and body, with a rusty tint, but blue-grey ventrally and khaki-yellow mid-laterally. The fins are predominantly light blue, but with black submarginal bands on the anal and pelvic fins. Normal and OB females occur.

**Ruarwe:** The upper half of the body and head of males is khaki-yellow; belly, chest, chin and gular region purple to mauve. A light violet-blue interorbital bar is bordered by two dark brown interorbital bars. Dorsal fin mauve-blue with orange-brown rays, blue inter-ray membranes and orange ocelli. Caudal fin rays orange-brown, inter-ray membranes light blue and trailing edge orange. Anal fin mauve with a black submarginal band, and yellow-orange egg-dummies. Pelvic fins ochre-red with black submarginal bands and white leading edges. At Ruarwe OB females outnumbered normal females 14:1 (Ribbink *et al.* in press).

**Chitande:** The Chitande form is very similar to the Ruarwe population, but the khaki-yellow extends onto the dorsal fin and further onto the belly in males. Both OB and normal females were seen.

**Habitat.** *L. trewavasae* favours large rocks, but also occurs in other habitats and is usually fairly evenly distributed from the surface waters down to about 20 m. It has been found to 34 m depth.

**Territoriality.** Relative to its congener, *L. trewavasae* is weakly territorial. Males hold large, poorly defended territories among large rocks, normally favouring caves and crevices formed by these rocks. They quite frequently vacate the territories to feed elsewhere. Females, juveniles and non-

territorial males usually occur singly or in small groups.

**Feeding.** At the island of Thumbi West *L. trewavasae* feeds principally from the under-surfaces of rocks (Ribbink *et al.* in press) and it is assumed that other populations also favour these surfaces. This species feeds on loose Aufwuchs, C1, C2, C3, benthic crustacea and plankton in varying proportions (Ribbink *et al.* in press).

### Genus *Gephyrochromis* Boulenger, 1901

This genus exhibits numerous resemblances to the genus *Pseudotropheus* with which it may be confused (Fryer 1957). The only real structural difference between *Gephyrochromis* and *Pseudotropheus* is that the teeth in the outer series of both jaws in *Gephyrochromis* may, and often do, become conical and are longer and more slender than in any of the *Pseudotropheus* (Fryer 1957) (Figure 17a–b). There are only two described species in the genus: *G. moorii* Boulenger, 1901 and *G. lawsi* Fryer, 1957. Only *G. lawsi* was found by us (Table 13).

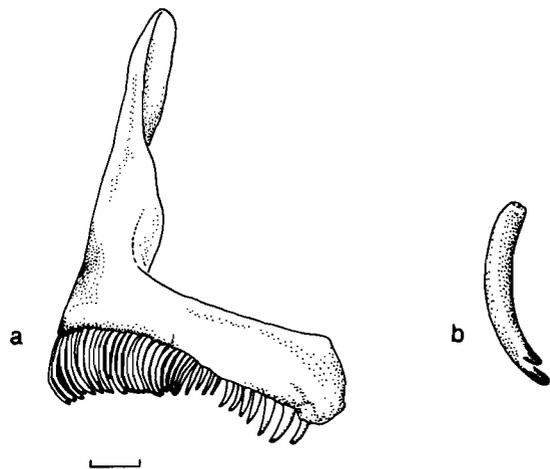


Figure 17 (a) Lateral aspect of left premaxilla of *Gephyrochromis lawsi* (Scale = 1 mm). (b) Anterior outer row tooth of *G. lawsi*.

#### 1. *Gephyrochromis lawsi* Fryer, 1957

**Synopsis.** A rare fish on the shores we studied, being found in the intermediate zones below 8 m. Both sexes are light in colour and can be identified by the protruding teeth of the lower jaw.

**Distribution.** Nkhata Bay (R), Lion's Cove (R). Fryer (1957) found this species at Chitimba Bay (previously Florence Bay). *G. lawsi* is rare on the rocky shores we studied, but Fryer (1957) had little difficulty collecting specimens on a beach consisting of coarse shingle and rocks. This suggests that it may be more common in other habitats.

**Coloration. Males:** Body fawn to bronze dorsally, bluish mid-laterally with a silvery-white chest and belly, but the anterior part of the chest may be black ventrally; 7 faint grey bars traversing the flanks. Head grey-bronze dorsally with a dark grey snout and a light blue interorbital bar; cheeks and opercula silvery-blue; chin and gular region black. Dorsal fin lemon-yellow with whitish-blue flecks on the spines and fin rays. Caudal fin yellowish with blue-white rays and a white lower border. Anal fin whitish-blue with a black submarginal band and 1–3

yellow-orange egg-dummies. Pelvic fins grey with black submarginal bands and white leading edges.

**Females:** Body and head pale grey-brown dorsally, but silvery-white ventrally with 7–8 faint grey bars. Dorsal fin whitish-grey with a faint yellow hue. Caudal fin pale grey. Anal fin greyish, darker submarginally, with small orange egg-dummies. Pelvic fins white with grey submarginal bands.

**Habitat.** At Nkhata Bay and Lion's Cove, *G. lawsi* was found in sediment-rich intermediate zones at depths of 8–25 m. Fryer (1957) found this species in 4–5 m on the shingle beach at Chitimba Bay, but at Nkhata Bay he found it on the outer fringe of the rocky shore and in water deeper than that frequented by most Mbuna. Fryer (1959a) suggested that this species could not compete successfully with other Mbuna on the truly rocky shores of Nkhata Bay, except in deeper water where the population density is low.

**Territoriality.** Males are weakly territorial, chasing away some intruders. Females are solitary.

**Feeding.** *G. lawsi* feeds mainly upon loose Aufwuchs and has protruding teeth on the lower jaw which are well suited for 'scooping loose material from rock surfaces' (Fryer 1959a).

#### Genus *Iodotropheus* Oliver & Loisel, 1972

This genus has only one species, *I. sprengerae* (Figure 18a), which is most easily recognized in the field by its rusty-red coloration, a slightly projecting lower jaw and the possession of a frenum which connects the upper lip to the snout. The outer row teeth are bicuspid and the inner rows tricuspid (Figure 18b–c). *I. sprengerae* occurs in the south-eastern parts of the lake (Table 13).

#### 1. *Iodotropheus sprengerae* Oliver & Loisel, 1972 (Plate 11g)

**Synopsis.** A small, reddish-brown non-territorial lithophilous species.

**Distribution.** Boadzulu I. (C), Chinyamwezi I. (C), Chinyankwazi I. (U).

**Coloration.** *Boadzulu males:* Body and head reddish-brown with purple-violet spots in the centre of each scale. Dorsal fin reddish-brown with orange lappets and trailing

edges. Caudal fin reddish-brown with narrow blue streaks in the inter-ray membranes and an orange trailing edge. Anal fin brown with a purple cast, orange trailing edge and usually 2, sometimes 3, yellow egg-dummies. Pelvic fins orange-brown with narrow black submarginal bands and white leading edges.

**Boadzulu females:** Females brown with less red and purple than males.

**Geographical variation.** The populations at Chinyankwazi Island and Chinyamwezi Island have a little more red, but less purple than the Boadzulu Island form.

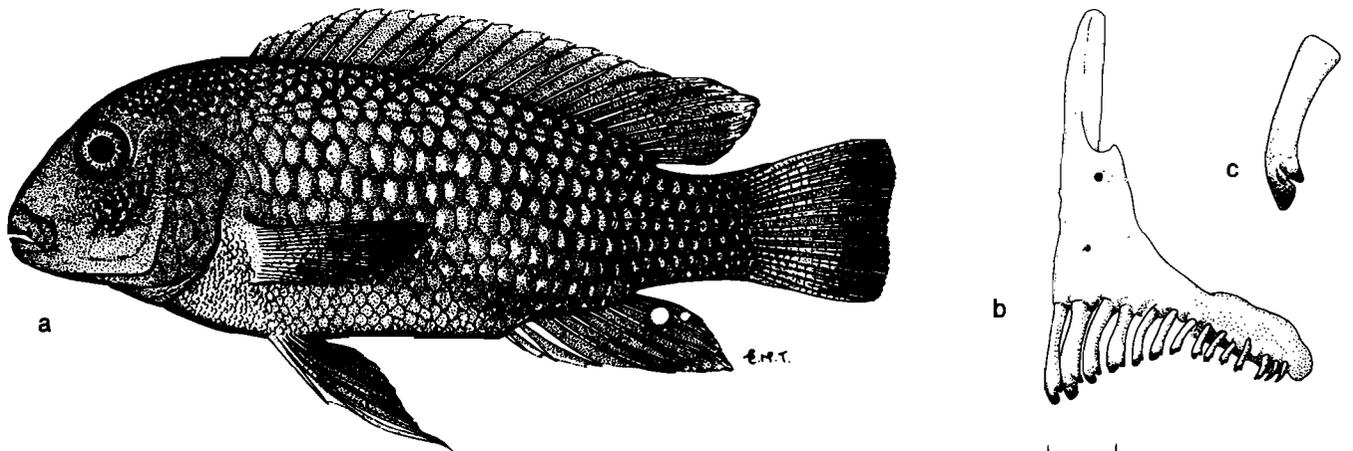
**Habitat.** *I. sprengerae* lives in a variety of rocky habitats being found over large rocks and slabs, among medium-sized rocks and among small rocks. It also occurs in areas where detritus and organic ooze accumulate in pockets among the rocks and occasionally in the intermediate zones at Boadzulu Island. It is most numerous between 3 and 15 m depth, but occurs from the surface to at least 40 m.

**Territoriality.** Members of this species are not territorial, occurring singly, in pairs or in small groups which seldom exceed 5 individuals.

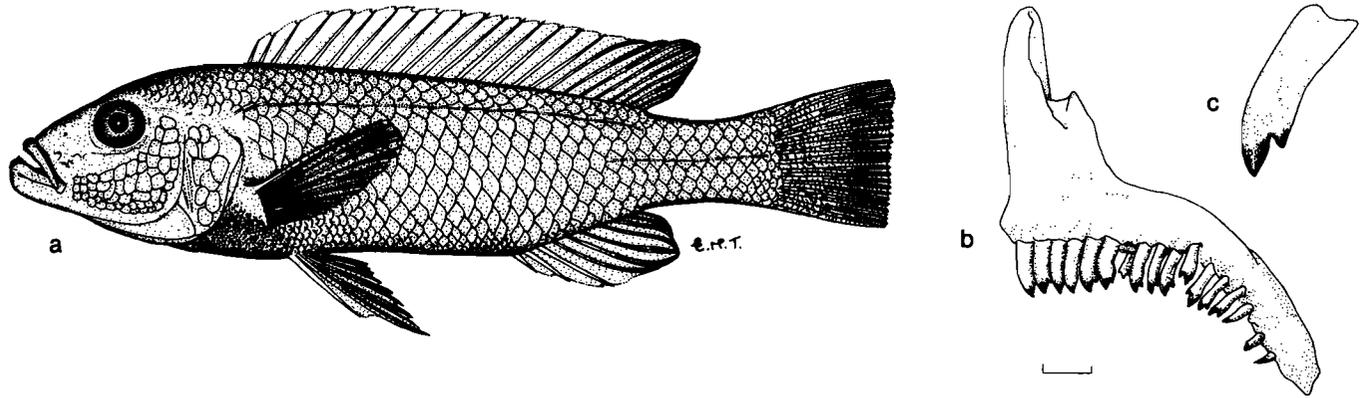
**Feeding.** The members of this species feed by nipping at the Aufwuchs and upon plankton. Stomach contents of 9 specimens caught in 3–10 m depth at Chinyamwezi contained principally loose Aufwuchs (73%), insect larvae and nymphs (11%), phytoplankton (10%), zooplankton (4%) and C2 (2%). Stomach contents of 8 specimens caught in 5–12 m depth at Boadzulu Island all differed from one another and each contained a variety of food substances: 6 stomachs contained a high proportion of loose Aufwuchs; 3 contained insect larvae, 3 contained C2; 3 contained benthic crustaceans; 3 had pieces of leaves of terrestrial macrophytes; 2 contained phytoplankton, and part of a cormorant feather was found in the stomach of one individual.

#### Genus *Genyochromis* Trewavas, 1935

This genus is currently considered to be monotypic, but as the species shows so much variability with regard to coloration, it may eventually prove to be polytypic. *G. mento* is a lepidophage and fin-eater (Fryer, Greenwood & Trewavas 1955) and is readily recognized by its prominent lower jaw and broad mouth (Figure 19a–c). *G. mento* enjoys lake-wide distribution (Table 13).



**Figure 18** (a) *Iodotropheus sprengerae*, Chinyankwazi Island, 82 mm SL. (b) Lateral aspect of left premaxilla of *I. sprengerae* (Scale = 1 mm). (c) Anterior outer row tooth of *I. sprengerae*.



**Figure 19** (a) *Genyochromis mento*, Monkey Bay, 85 mm SL. (b) Lateral aspect of left premaxilla of *G. mento* (Scale = 1 mm). (c) Anterior outer row tooth of *G. mento*.

### 1. *Genyochromis mento* Trewavas, 1935 (Plate 11h)

**Synopsis.** A lithophilous Mbuna which is specialized to feed upon scales and fins. It exhibits polychromatism.

**Distribution.** *G. mento* is present at every rocky shore we visited except Senga Point and Rifu. This fish is easily overlooked because it is usually solitary and has dark coloration, but can be readily located when searched for and is considered to be uncommon verging on common.

**Coloration.** We were normally unable to distinguish between males and females in the lake and so the notes given could refer to one or both sexes. Several different colour forms are present at each rocky shore:

- (i) Pure black specimens at every site where the species occurs.
- (ii) A fawn-coloured form with 10–11 grey bars, 2 grey bands and whitish fins at all sites.
- (iii) A chocolate-brown form with prominent black submarginal bands in the dorsal, anal and pelvic fins, and with orange-tipped white lappets on the dorsal fin at Masinje Rocks, Makanjila Point, Eccles Reef, West Reef, Chinyankwazi I., Chinyamwezi I. and Chemwezi I.
- (iv) An olive-green form with black submarginal bands in the dorsal, anal and pelvic fins at Nkopola.
- (v) A dark grey form with 3 broken longitudinal bands of black patches at Likoma I. and Chisumulu I.
- (vi) A khaki-green form with 2 dark grey longitudinal bands and 8–10 dark grey bars. Along the rocky shores of the north-western parts of the lake.
- (vii) A plain grey form at Ruarwe, Chitande and Mpanga Rocks.
- (viii) The orange-blotch (OB) form is rare — found at Boadzulu I., Nkudzi, Monkey Bay, Thumbi West I., Maleri I., Likoma I., Chisumulu I., Nkhata Bay and Chitande.
- (ix) A tangarine-orange form at Chisumulu I. and at Mpanga Rocks.

The relation of the various colour forms to one another is unknown at present.

**Habitat.** *G. mento* occurs on all rocky shores and appears to be most numerous over large rocks and boulders. It occurs from the extreme shallows to at least 40 m depth and is most common in 3–12 m. It rarely ventures onto sandy substrata.

**Territoriality.** This species is apparently not territorial. In-

dividuals are normally solitary and frequently when conspecifics are encountered, intraspecific aggression occurs.

**Feeding.** It feeds by darting towards passing cichlids, particularly the larger species, and biting pieces from their caudal and anal fins. Consequently, many lithophilous fishes have pieces missing from their fins (Plate 10i). Fryer (1959a) records that it feeds principally on the scales of *Labeo cylindricus* Peters, but while this may be correct we have never seen it removing scales from this species. We have, however, seen it rasp scales from the caudal peduncle and flanks of cichlids, though such feeding on scales is infrequent. *G. mento* is attracted to fighting cichlids and snaps up dislodged scales as they drift towards the substratum. Furthermore, while combatants are engaged in battle *G. mento* may approach more closely than normally permitted and tear pieces from the protagonists. *G. mento* has been seen harassing *Petrotilapia* spp. and also *Labeotropheus fuelleborni* combatants to such an extent that the protagonists ceased fighting to chase off the opportunistic lepidophage.

Many fishes respond to *G. mento* by chasing it before it can approach close enough to attack. Consequently, *G. mento* frequently hides in ambush until a prey species approaches closely and then darts out to bite a piece from the victim. *G. mento* was also observed feeding upon Aufwuchs and plankton. Analyses of stomach contents revealed that C1, C2, loose Aufwuchs, insects, plankton and benthic crustaceans are all included in the diet. We have never seen *G. mento* eat scales or fins of conspecifics.

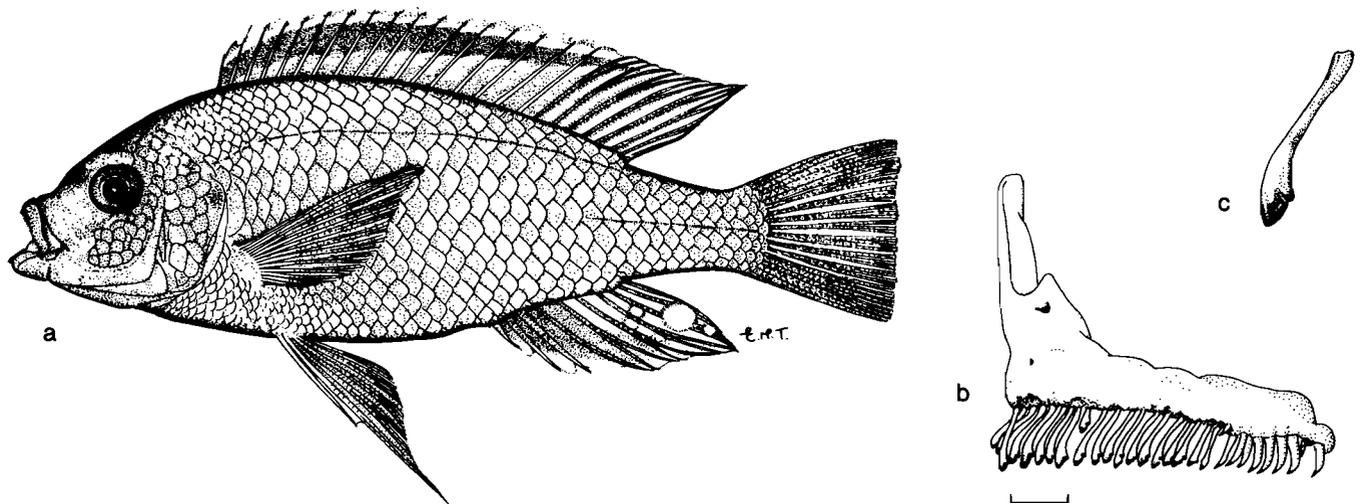
**Genus *Cyathochromis* Trewavas, 1935 (Figure 20a–c)**

This monotypic genus superficially resembles members of the *Pseudotropheus zebra* species-complex, but it differs from all other Mbuna in its dentition. *Cyathochromis obliquidens* possesses teeth which have slender shafts and compressed spoon-like crowns; those of the outer series sloping obliquely towards the symphysis (Figure 20b & c). *C. obliquidens* is widely distributed in intermediate habitats (Table 13).

### 1. *Cyathochromis obliquidens* Trewavas, 1935 (Plate 11i)

**Synopsis.** A large Mbuna of the intermediate habitats in shallow water.

**Distribution.** Upper Shire River (U), Mangochi (C), Nkopola (C), Nkudzi (C), Mpandi I. (C), Kanchedza I. (C),



**Figure 20** (a) *Cyathochromis obliquidens*, Monkey Bay, 102 mm SL. (b) Lateral aspect of left premaxilla of *C. obliquidens* (Scale = 1 mm). (c) Anterior outer row tooth of *C. obliquidens*.

Chigubi (C), Monkey Bay (C), Mvunguti (C), Domwe I. (U), Chemwezi I. (U), Makanjila Point (U), Masinje (U), Thumbi West I. (U), Otter Point (C), Mumbo I. (C), Maleri I. (U), Nankoma I. (C), Mbenji I. (U), Likoma I. (N), Chisumulu I. (U), Nkhata Bay (C), Lion's Cove (U), Usisya (U), Chitande (U). Exporters of ornamental fishes have told us that *C. obliquidens* also occurs in Lake Malombe. As our survey concentrated upon the rocky zones it is possible that this species is present at sites such as Ruarwe where the shallow-water intermediate zone (its preferred habitat) was not studied.

**Coloration. Nkhata Bay males:** Body olive-green with brown shoulder and chest. Head olive-green with iridescent purple edges to the opercula. Dorsal fin green with a prominent black submarginal band running through the spinous region; lappets blue along their bases, but otherwise bright yellow; rayed region bluish with yellow trailing region. Caudal fin olive-green at base, greyish distally with blue inter-ray membranes. Anal fin turquoise, but black anteriorly and purple posteriorly; 2–3 large yellow egg-dummies. Pelvic fins purple with black submarginal bands and white leading edges.

**Nkhata Bay females:** Body and head olive-green, almost khaki, with 10–11 dark brown bars, a narrow, brown mid-lateral band and a similar dorso-lateral band. Fins pale brown with whitish-brown spots.

**Geographical variation.** The other populations of *C. obliquidens* found along the north-western coast were similar in coloration and markings to the Nkhata Bay form, but at Likoma I. the ground colour is slate-blue with only a hint of olive-green. At Mbenji I. and Maleri I. it is similar to the Likoma I. form. At Monkey Bay, males are blue-green with olive-green shoulders, yellow-green chests and bellies; 5 grey bars are apparent anteriorly on the flanks. Head olive-green, tending to yellow dorsally, but greyish ventrally with a yellow tinge to the chin and gular region. South of Monkey Bay, towards Mangochi, the chin, gular region, chest and belly become increasingly yellow until they are bright yellow in the southernmost populations. The Chemwezi population is similar to that of Mangochi but not quite as yellow. At Masinje Rocks and Makanjila Point, *C. obliquidens* is not as yellow as the southern populations and

the bodies are a deep slate-blue. Females showed virtually no geographical variation.

**Habitat.** Throughout its distribution *C. obliquidens* occupies intermediate habitats where sand and rock are mixed. It is also common in beds of *Vallisneria aethiopica* which are close to rocks. It is most numerous between 1.5 and 4 m, but has been seen to 6 m depth.

**Territoriality.** Males are aggressively territorial chasing conspecifics and other Mbuna species with which it shares the intermediate habitat, but other cichlids are attacked less often. Spawning sites are excavated either among the *V. aethiopica* or beneath rocks. In dense *V. aethiopica* beds some plants may be uprooted to accommodate the spawning site. Females, juveniles and non-territorial males occur singly or in small groups.

**Feeding.** Fryer (1959a) described the manner in which *C. obliquidens* brushes loose Aufwuchs from the rocks and from *V. aethiopica* fronds, and he found that stomach contents consisted almost entirely of loose Aufwuchs. We also found that stomach contents are dominated by loose Aufwuchs, and small proportions of C1, C2, plankton, insect larvae and benthic crustaceans were also present.

#### Genus *Microchromis* Johnson, 1975

A single species of an eleventh genus *Microchromis* was briefly and inadequately described in the aquarist literature and purported to come from Likoma Island. No such fish was found at Likoma Island nor was it recognized anywhere else during our survey. D.S.C. Lewis (pers. comm.) considers the description of this genus to be of doubtful validity.

#### OTHER CICHLIDS OF ROCKY HABITATS

In addition to the Mbuna, numerous other cichlids are sold as aquarium fishes. Table 14 lists some of the more common or colourful species which occur on the rocky shores. Where available, data on the distribution, coloration and role of these fishes within the rock-frequenting fish community are presented, but as the survey concentrated on the Mbuna many of the descriptions of the non-Mbuna are brief. Notes on piscivores, most members of the Utaka species-flock, and on several fishes which are adapted to

**Table 14** Distribution of some of the non-Mbuna of the rocky shores. The distribution of each species is given according to the 14 major study areas which are depicted in Figure 4. Present (+), absent (-)

Species	Distribution													
	I	Ila	Ilb	Ilc	III	IV	V	VI	VII	VIII	IX	Xa	Xb	Xc
1. <i>Aristochromis christyi</i>	+	+	+	+	+	+	+	+	-	+	+	+	-	+
2. <i>Astatotilapia calliptera</i>	+	+	-	+	-	+	+	+	-	-	+	-	-	-
3. <i>Aulonocara</i> 'yellow collar'	+	-	-	-	-	+	-	-	-	-	+	-	-	-
4. <i>Aulonocara</i> 'blue collar'	+	-	-	-	-	+	-	-	-	-	+	+	-	-
5. <i>Aulonocara</i> 'maleri gold'	-	-	-	-	-	-	-	+	-	-	-	-	-	-
6. <i>Aulonocara</i> 'mbenji blue'	-	-	-	-	-	-	-	-	-	+	-	-	-	-
7. <i>Chilotilapia rhoadesii</i>	+	+	-	-	-	-	-	-	-	-	-	-	-	-
8. <i>Cyrtocara taeniolata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
9. <i>C. fenestrata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
10. <i>C.</i> 'pink dorsal'	-	-	-	-	-	+	-	-	-	-	-	-	-	-
11. <i>C. picta</i>	+	-	-	-	-	+	-	-	-	-	-	-	-	-
12. <i>C. intermedia</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-
13. <i>C. euchila</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
14. <i>C.</i> 'labrosa'	+	+	+	-	-	+	+	+	-	+	-	-	-	-
15. <i>C.</i> 'maleri thick lip'	-	-	-	-	-	-	-	+	-	-	-	-	-	-
16. <i>C.</i> 'mbenji thick lip'	-	-	-	-	-	-	-	-	-	+	-	-	-	-
17. <i>C. ornata</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-
18. <i>C.</i> cf. <i>borleyi</i>	+	-	-	-	-	+	-	-	-	+	+	+	-	+
19. <i>C. chrysonota</i>	+	+	-	+	+	+	+	+	+	+	+	+	-	+
20. <i>C. quadrimaculata</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-
21. <i>C. eucinostoma</i>	+	-	-	-	-	+	-	-	-	-	-	+	-	-
22. <i>C. kiwinge</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
23. <i>C. macrostoma</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
24. <i>C. woodi</i>	+	+	-	-	+	+	-	-	-	-	-	-	-	-
25. <i>C. polyodon</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-
26. <i>C. pardalis</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-
27. <i>C. spilorhyncha</i>	+	+	-	+	-	+	-	-	+	-	-	-	-	-
28. <i>C. fuscotaeniata</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-
29. <i>C. linni</i>	+	+	+	+	+	+	+	+	-	+	+	+	-	+
30. <i>C. polystigma</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
31. <i>C. livingstonii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
32. <i>C. venusta</i>	+	+	-	+	-	+	-	-	-	-	-	-	-	-
33. <i>C. compressiceps</i>	+	+	-	+	-	+	+	+	+	+	+	+	+	+
34. <i>C. rostrata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
35. <i>C. moori</i>	+	+	-	+	-	+	+	+	+	+	+	+	+	+
36. <i>C. sphaerodon</i>	-	-	-	-	+	-	-	-	-	-	+	+	-	-
37. <i>C. electra</i>	-	-	-	-	-	-	-	-	-	-	+	-	-	-
38. <i>C. johnstonii</i>	+	+	-	+	-	+	-	+	+	-	+	+	-	-
39. <i>C. similis</i>	+	+	-	-	-	+	-	-	-	-	+	-	-	-
40. <i>C. placodon</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-
41. <i>C. kirkii</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-
42. <i>C. mola</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-
43. <i>Docimodus evelynae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
44. <i>Hemilitilapia oxyrhynchus</i>	+	+	-	-	-	+	+	+	-	-	-	-	-	-
45. <i>Rhamphochromis longiceps</i>	+	+	+	?	+	+	?	?	?	?	+	-	-	-
46. <i>R. esox</i>	+	+	+	?	+	+	+	+	-	-	+	+	-	-
47. <i>Serranochromis robustus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
48. <i>Trematocranus jacobfreibergi</i>	+	+	-	-	-	+	-	-	-	-	-	-	-	-

live in other habitats but which are regular visitors to the rocky shores, are particularly brief.

The list of non-Mbuna is far from complete and a separate survey of these fishes is required.

#### Genus *Aristochromis* Trewavas, 1935

##### 1. *Aristochromis christyi* Trewavas, 1935

**Synopsis.** A bilaterally compressed, predatory fish which is characterized by large beak-like jaws.

**Distribution.** An uncommon to rare species which was found at most diving stations. It probably has a lake-wide distribution.

**Coloration. Males:** Blue with an oblique black band running from the centre of the caudal fin base to the occipital region and a second black band running dorso-medially from the top of the caudal peduncle to approximately half-way along the spinous portion of the dorsal fin.  
**Females:** Yellowish-white with black bands similar to

males.

**Habitat.** This species has been seen over rocks of all sizes and in rock-sand and vegetated intermediate habitats. It occurs from surface waters down to at least 20 m depth.

**Territoriality.** Only solitary, non-territorial individuals were found.

**Feeding.** Stomach contents of 6 individuals caught in Monkey Bay, all comprised fish fry and 2 contained plant fragments. To catch its prey *A. christyi* approaches slowly, rolls onto its side and suddenly darts forwards. It is not understood how this behaviour helps it catch prey in open water where it was seen hunting on many occasions, but it does enable it to skim over rocks and thrust its bilaterally compressed head and beak into horizontal cracks and crevices among rocks. Since these cracks are the refuges of innumerable cichlid fry, the beak and bilateral compression of the head and body of *A. christyi* may be adaptations for penetrating such sanctuaries.

## Genus *Astatotilapia* (Gunther, 1893)

### 1. *Astatotilapia calliptera* (Gunther, 1893)

**Synopsis.** A generalized omnivore of shallow vegetated areas.

**Distribution.** This species is not endemic to Lake Malawi (Fryer & Iles 1972). In Lake Malawi it occurs at virtually every vegetated intermediate zone on the mainland coast and we found it at the islands of Mpandi, Kanchedza, Thumbi West, Mumbo, Maleri and Likoma.

**Coloration. Males:** Body and head olive-green with a conspicuous purple patch on occipital region and snout. The eye-bar, chin, branchiostegal membranes and anterior chest are pitch-black. Dorsal and caudal fins bluish. Anal fin pale blue with a line of 5–11 yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Body and head yellowish-green. Fins bluish-yellow.

**Habitat.** *A. calliptera* is found most often in beds of *Vallisneria aethiopica*, but also occurs among other plants, in rocky areas and where terrestrial plants hang into the water. It is most common at 2–4 m depth, but has been seen at 9 m.

**Territoriality.** Males hold territories among plants where they excavate saucer-shaped spawning sites. They are intraspecifically aggressive, but are also intolerant of all intruders which approach the spawning sites.

**Feeding.** This species has been observed feeding from the fronds of plants, from rock surfaces, from within the sand between the roots of plants and on plankton. This feeding behaviour and general nature of the jaws and dentition of *A. calliptera* suggest that it is an omnivore, but no stomachs were dissected for analysis. Fryer & Iles (1972) consider *A. calliptera* to be primarily carnivorous, but since it eats both plants and animal matter it qualifies for the designation 'omnivore'.

## Genus *Aulonocara* Regan, 1921

### 1. *Aulonocara* 'yellow collar' (Plate 11j)

**Synopsis.** A yellow-collared fish with cephalic pits. It fre-

quents the sand-rock interface.

**Distribution.** Monkey Bay (C), Nankumba (C), Domwe I. (C), Thumbi West I. (C), Likoma I. (C).

**Coloration. Males:** Body and head yellowish with bright yellow shoulder, occipital region, gular region and chest; 9–11 grey bars. Ventral aspect of head iridescent-blue. Dorsal fin yellow with a black submarginal band. Caudal fin blue. Anal fin grey with a black submarginal band and 5–9 yellow egg-dummies. Pelvic fins grey with black submarginal bands and white leading edges.

**Females:** Whitish-grey with 9–11 dark grey bars.

**Habitat.** This species is found along the sand-rock interface from 4 to at least 40 m depth, but appears to be most numerous between 10 and 20 m.

**Territoriality.** Males construct turret-like spawning sites of sand and all fishes are excluded from this area except gravid conspecific females. Females form schools of up to 30 individuals.

**Feeding.** These fishes were seen feeding from the sand, but as none was caught we cannot comment on their diet.

### 2. *Aulonocara* 'blue collar' (Plate 12a)

**Synopsis.** A dark blue, barred species with cephalic pits. It inhabits the sand-rock interface.

**Distribution.** Monkey Bay (C), Nankumba (C), Domwe I. (C), Thumbi West I. (U), Likoma I. (U), Nkhata Bay (U).

**Coloration. Males:** Body dark blue with 8–9 black bars and brownish-yellow shoulder, pectoral region and chest. Head very dark blue. Dorsal fin black with white lap-pets. Caudal fin dark blue. Anal fin dark blue with numerous large yellow egg-dummies. Pelvic fins black with white leading edges.

**Females:** Body and head grey with dark grey bars.

**Habitat.** This species was found along the rock-sand interface from 6 to at least 40 m.

**Territoriality.** Males defend territories in which they construct turret-like nests. Females are not territorial, but gather in groups.

**Feeding.** This species feeds from the sand.

### 3. *Aulonocara* 'maleri gold' (Plate 12b)

**Synopsis.** A gold fish with cephalic pits. It lives in the intermediate zones.

**Distribution.** Nakantenga I. (C), Maleri I. (C), Nankoma I. (C).

**Coloration. Males:** Golden-yellow with grey-brown bars.  
**Females:** Sandy-grey with dark grey bars.

**Habitat.** It occurs in the intermediate zones and over patches of sand among the rocks from 3 to 25 m depth.

**Territoriality.** Males are aggressively territorial and construct nests which are 8–12 m in diameter. Females are not territorial.

**Feeding.** Members of this species have been observed feeding from both sand and rock substrata, but no data on stomach contents are available.

#### 4. *Aulonocara* 'mbenji blue' (Plate 12c)

**Synopsis.** A metallic royal blue fish with cephalic pits. It lives in the intermediate zones.

**Distribution.** Mbenji I. (C).

**Coloration. Males:** Body and head metallic-blue. Fins blue, but dorsal fin has white lappets with orange tips.

**Females:** Colours not recorded.

**Habitat.** This species occupies the sand-rock interface and other similar intermediate zones in water 3–25 m deep.

**Territoriality.** Males excavate sand-scrape nests alongside or beneath rocks and defend the area immediately around these nests. Females are not territorial but occur in small groups.

**Feeding.** No data are available.

#### Genus *Chilotilapia* Boulenger, 1908

##### 1. *Chilotilapia rhoadesii* Boulenger, 1908

**Synopsis.** A deep-bodied fish with a blunt head.

**Distribution.** Nkudzi (U), Chemwezi I. (N), Mpandi I. (U), Monkey Bay (U).

**Coloration. Males:** Body and head blue with a black mid-lateral band and an oblique black band running from the top of the caudal peduncle to the occipital region.

**Females:** Greenish-brown with two black bands similar to those of males.

**Habitat.** *C. rhoadesii* is normally found over sand and among macrophytes, but is usually uncommon over rocks. At Chemwezi Island, however, it was numerous in the rocky habitat. It occurs from 3 to at least 25 m depth.

**Territoriality.** Males were found defending territories among the rocks at Chemwezi Island. Females are not territorial.

**Feeding.** The stomachs of 33 specimens were examined; 11 were empty and 22 contained the soft remains of the gastropod *Lanistes nyassanus*.

#### Genus *Cyrtocara* Boulenger, 1902

##### (a) The Aufwuchs feeders

##### 1. *Cyrtocara taeniolata* (Trewavas, 1935) (Plate 13a)

**Synopsis.** A small lithophilous member of the genus. It has a narrow mouth and small, widely spaced teeth.

**Distribution.** This species is common or numerous on all rocky shores studied except at Chigubi and Mazinzi Reef where it is rare.

**Coloration. Monkey Bay males:** Body and head bright metallic-blue with very faint traces of bars and bands.

**Monkey Bay females:** Silvery-grey with longitudinal bands and vertical bars.

**Geographical variation.** At Chinyankwazi I., Chinyamwezi I. and Boadzulu I. the chin, gular region and chest of males are yellow. At Namalenje I., Senga Point and Rifu the gular region, chest and belly of males are crimson. At Mbenji I. females are greyish-beige with black bands and bars that are broader than those of populations found elsewhere. These markings are also apparent in males.

**Habitat.** It is found over rocks of all sizes, but appears to favour large rocks for feeding and medium-sized rocks for territoriality. It occurs from the surface waters to at least 28 m depth being most numerous between 5 and 15 m.

**Territoriality.** Males are aggressively territorial, defending the upper surfaces of medium-sized rocks from all intruders. Females are not territorial and although they occur singly they usually form groups which remain close to the rock surfaces.

**Feeding.** *C. taeniolata* feeds by nipping at the Aufwuchs from which it collects mostly loose Aufwuchs and also some C1, C2 and benthic Invertebrata (particularly chironomid larvae). During plankton blooms the entire *C. taeniolata* population may feed in open water, 1–2 m above the substratum.

##### 2. *Cyrtocara fenestrata* (Trewavas, 1935)

**Synopsis.** A black-barred species which frequents sediment-rich zones where it blows away the sediment to take food from the underlying substratum (Plate 13b).

**Distribution.** This species has lake-wide distribution. It is rare at Chinyankwazi I., Chinyamwezi I. and Zimbabwe I. Elsewhere it is uncommon to common on the rocky shores.

**Coloration. Monkey Bay males:** Body blue-grey with broad bars and orange flecks on the flanks; belly yellowish. Head blue with emerald-green sheen. Dorsal fin blue with prominent black submarginal band; lappets orange with white tips. Caudal fin bluish. Anal fin blue with a black submarginal band and yellow egg-dummies. Pelvic fins yellowish-blue, but black anteriorly.

**Monkey Bay females:** Body yellowish-grey with broad black irregularly shaped bars that usually extend into the dorsal fin, but do not always span the full depth of the body. Head yellowish-grey. Fins yellowish-white with black blotches in the dorsal and anal fin. Dorsal fin lappets orange.

**Geographical variation.** Slight differences in coloration and markings were found, but no details were recorded. In general, however, the populations of Likoma I., Chisumulu I. and the north-western shores of the lake are deeper yellow than the southerly populations.

**Habitat.** It is a lithophilous species which is most numerous in areas where sediment accumulates such as deepish water of exposed shores and in the shallows of sheltered areas. *C. fenestrata* also occurs over sand in intermediate zones.

**Territoriality.** Males have been seen defending territories, but they appear to be weakly territorial. Non-territorial individuals are usually solitary.

**Feeding.** It feeds by blowing away the sediment before pecking at the underlying substratum. Specimens caught in the shallows had fed almost exclusively upon chironomid larvae, but those caught in depths greater than 10 m had, in addition, other insect larvae, benthic crustaceans, C3 and loose Aufwuchs in their stomachs.

##### 3. *Cyrtocara picta* (Trewavas, 1935)

**Synopsis.** A small lithophilous species of sediment-rich areas which feeds by sucking up loose material on rock surfaces.

**Distribution.** Monkey Bay (C), Nankumba (U), Domwe I.

(C), Thumbi West I. (C), Otter Point (C). Jackson (1961a) notes that this species also occurs in the northern part of the lake.

**Coloration. Males:** Body and head blue with three distinct black blotches on the flanks.

**Females:** Silvery-white with similar markings.

**Habitat.** *C. picta* occurs in areas where there is a sediment layer. Its depth distribution extends from the shallows to at least 30 m.

**Territoriality.** Only solitary individuals have been found and none was territorial.

**Feeding.** While swimming slowly, *C. picta* sucks up sediment and associated organisms from the rock surfaces by extending its highly protrusible mouth. At no stage during the extension of the mouth, or inward sucking and closing of the mouth, is contact made with the substratum. The fish behaves rather like a vacuum cleaner (Plate 13c). The principal food found in the stomachs of adults is benthic copepods, probably sifted from the ingested sediment by gill-rakers. Juveniles appear to be exclusively planktivorous.

#### 4. *Cyrtocara euchila* (Trewavas, 1935)

**Synopsis.** A fish with markedly hypertrophied lips. It frequents both rocky and sandy shores.

**Distribution.** It has lake-wide distribution, though it is uncommon at all sites except Liwelo Bay (Chisumulu Island) where it is common.

**Coloration. Males:** Body and head blue with a broad black band running mid-laterally from the caudal fin to the posterior part of the orbit; a black dorso-medial band runs from the upper ridge of the caudal peduncle to the occipital region. Occipital bar and eye-band black.

**Females:** Body and head yellowish-brown with black markings similar to those of the males.

**Habitat.** *C. euchila* is a regular inhabitant of the rocky shores, but also occurs over sand and in weeded areas. It has been seen most often in water less than 10 m deep and rarely beyond this depth.

**Territoriality.** Members of this species are usually solitary, though occasionally small groups of less than 5 individuals occur. No territorial individuals were found.

**Feeding.** The large fleshy lips are used during feeding to seal grooves in the rocks, trapping prey which are then sucked and/or scraped into the mouth. *C. euchila* individuals appear to select feeding sites carefully, swimming from one to the next, poising over many, but selecting only a few for feeding. They also feed by nipping at rocky and sandy substrata from which they appear to collect visually located particles. Fryer (1959a) suggested that the hypertrophied lips are sensitive appendages which assist in the detection of prey. We have no data to support or refute this idea. The stomachs examined contained the remains of insect larvae as well as benthic crustaceans, and the intestines contained a high proportion of ostracods. Fryer (1959a) found that *C. euchila* feeds predominantly on insect larvae and nymphs as well as crustaceans. He found small snails in the stomach of one specimen.

#### 5. *Cyrtocara 'labrosa* (Plate 12d)

**Synopsis.** A thick-lipped species characterized by 4–5 broad

vertical bars on the flanks.

**Distribution.** Monkey Bay (U), Boadzulu I. (U), Nkudzii (U), Nankumba (U), Zimbabwe I. (U), Thumbi West I. (U), Mumbo I. (C), Nakantenga I. (C), Maleri I. (C), Mbenji I. (U).

**Coloration. Males:** Blue with dark blue bars.

**Females:** Beige with dark brown bars.

**Habitat.** This species was found only among rocks, apparently favouring medium-large rocks. It is most common between 10 and 20 m depth, but its full depth range is from 4 to at least 35 m.

**Territoriality.** In March/April 1980, at Nakantenga Island a group of 6 males, situated about 4 m apart in 12–15 m depth, was found defending territories. Normally, however, this fish is solitary and not territorial.

**Feeding.** This species appears to feed in the same way as *C. euchila*, but frequents deeper areas and apparently does not feed over sand.

#### 6. *Cyrtocara 'maleri thick lip'* (Plate 12e)

**Synopsis.** A pale brown species with dark brown bars and slightly enlarged lips, it inhabits shallow water in sediment-rich areas.

**Distribution.** This species was found on the western shores of Maleri I. (U) and at Nankoma I. (U).

**Coloration.** Pale brownish-yellow with incomplete, irregular, dark brown barring.

**Habitat.** It lives among small and medium-sized rocks in water less than 10 m deep.

**Territoriality.** The individuals of this species are solitary and no evidence of territoriality was found.

**Feeding.** Members of this species were seen to feed from the rock surfaces.

#### 7. *Cyrtocara 'mbenji thick lip'* (Plate 12f)

**Synopsis.** A dark, brown-and-black fish with thickened lips.

**Distribution.** Mbenji I. (C).

**Coloration. Males and females:** Brownish-grey tending to black ventrally with irregular black bars and mid-lateral and dorso-lateral black bands. Males in breeding dress with a blue cast.

**Habitat.** This species was found most commonly in the intermediate zones of the western shore of Mbenji Island, but it was also present along all rocky shores. Its depth range is from the surface waters to at least 23 m.

**Feeding.** It feeds in a manner similar to that of *C. euchila*, but no data on stomach contents are available.

#### 8. *Cyrtocara ornata* (Regan 1921)

**Synopsis.** A colourful fish (male) of shallow rocky and intermediate habitats. It has an elongate pointed snout and moderately hypertrophied lips.

**Distribution.** Nkhata Bay (U).

**Coloration. Males:** Body dark blue dorsally with orange spots in each scale; light blue ventrally with a grey mid-lateral line; chest and belly yellow. Head iridescent-blue with bright blue lips; chin and gular region yellow. Dor-

sal fin bright blue with orange patches; submarginal band black; lappets white with yellow tips. Caudal fin blue with orange streaks and orange trailing edge. Anal fin grey with yellow edges and 4–8 orange-yellow egg-dummies. Pelvic fins yellow with black submarginal bands and yellow leading edges.

*Females:* No data available.

*Habitat.* It was found among rocks and in the intermediate zones between 2 and 10 m depth.

*Territoriality.* Males hold territories beneath rocks, usually where they can construct small, sand-turret spawning-sites. They chase all intruders. As territorial individuals are far apart intraspecific interactions are rare.

*Feeding.* Fryer (1959a) found chironomid larvae, ostracods, mayfly nymphs, other insect larvae and nymphs as well as mites and algae in the stomachs of *C. ornata*.

## (b) The planktivores (Utaka)

### 9. *Cyrtocara* cf. *borleyi* (Plate 12g)

*Synopsis.* A deep-bodied member of the Utaka group which frequents the rocky shores, and, unlike other members of this species-flock, it apparently does not form large schools.

*Distribution.* Monkey Bay (U), Nankumba (U), Domwe I. (U), Zimbabwe I. (U), Mbenji I. (U), Likoma I. (U), Makulawe Point (C), Nkhata Bay (U), Lion's Cove (U), Ruarwe (U).

*Coloration.* *Males:* Body blue with a khaki-gold cast. Head iridescent-blue. Dorsal fin blue with a narrow black submarginal band and white lappets. Caudal fin blue with pale blue streaks. Anal fin dark red with whitish-yellow egg-dummies. Pelvic fins black with white leading edges. *Females:* Silvery-grey.

*Habitat.* This species is found among medium-sized and large rocks, in sediment-free exposed areas at a depth of 2–25 m, but is most numerous between 3 and 12 m.

*Territoriality.* Males defend territories among the rocks, but are not highly aggressive. Females occur singly or in small groups usually numbering less than 5 individuals.

*Feeding.* It feeds on plankton and also from the Aufwuchs mat.

#### *Notes on other Utaka species*

In addition to *Cyrtocara* cf. *borleyi* a number of other Utaka species periodically move inshore and use the rocky areas for breeding and feeding, and thousands of Utaka fry shelter and feed in rocky zones. Since Utaka males are attractive blue fishes (Plate 12h), many species are popular in the aquarium trade. Important among these are *C. chrysonota* (Boulenger, 1908) and *C. quadrimaculata* Regan, 1921, which are common on the rocky shores and have a wide distribution in the lake. Males hold territories in open water at certain times of the year. These territories are usually near to rocky shores, but may also be over sand and weeded areas (Eccles & Lewis 1981).

A sand-dwelling species *C. eucinostoma* (Regan, 1921), has an unusual impact on the rocky shore communities. In areas close to sand at Monkey Bay, along the Nankumba Peninsula, at Domwe Island and at Otter Point territorial males construct prominent spawning sites by carrying sand

to the top of rocks. Sometimes sand is carried to the top of 4 m high rocks which represents an enormous expenditure of energy. The nests in Monkey Bay were  $23 \pm 1,5$  cm in diameter at the apex ( $N=38$ ). This is the same size as those built on sand by conspecifics. As the defended area extends about 50 cm around the nest, these fishes occupy a part of the rocky shore which is then unavailable to truly lithophilous species. Furthermore, since they cover the Aufwuchs with sand these fishes undoubtedly reduce the productivity of each rocky surface which they cover.

Iles (1960) and Fryer & Iles (1972) noted that Utaka shoals gather in large numbers at submerged reefs. We found that, in addition, these shoals congregate around small exposed rocky islands. At Chemwezi Island, Chinyankwazi Island, Chinyamwezi Island, Zimbabwe Island and also at Ndumbi Rocks and Mazimbwe Islet off Likoma Island, huge shoals were common.

At Chinyamwezi Island Utaka dominate the shallows and sometimes more than 20 individual cichlids were found in every square metre (see p.260). About 25% of the Utaka population at Chinyamwezi are a golden-yellow colour, but it is not known whether these are colour forms of a polychromatic species or whether they are a separate species.

At Likoma Island a popular aquarium fish of the Utaka species-flock is caught at the rock-sand interface, where territorial males build turret nests. Males of this species are predominantly black with a contrastingly blue flare on the head. This species is sold as *C. mloto* but it is not the same fish as that described by Iles (1960).

## (c) Notes on piscivores of the genus *Cyrtocara*

In addition to predatory pressures exerted by other genera, the fishes of the rocky zones are subject to predation by specialized piscivores of the genus *Cyrtocara*. Most predatory species are themselves small and therefore predatory pressure on fry and juveniles is most intense. Pursuit predators, *C. kiwinge* Ahl, 1927, *C. macrostoma* Regan, 1921 and *C. woodi* Regan, 1921, appear to have lake-wide distribution. All three are most numerous in the shallows. *C. polyodon* Trewavas, 1935 and *C. pardalis* Trewavas, 1935 are piscivores of the north-western coast.

The rocky shores are also visited by *C. spilorhyncha* Regan, 1921 and *C. fuscotaeniata* Regan, 1921 which are primarily fishes of the vegetated and sandy zones of the south-eastern arm of the lake, but which also occur at Otter Point.

All ambush predators listed here are popular aquarium fishes by virtue of their attractive markings and interesting behaviour. *C. linni* Burgess & Axelrod, 1975 is a lithophilous species found in less than 10 m depth and appears to have lake-wide distribution. At most sites it is uncommon or rare, but at Thumbi West Island and at Chisumulu Island it is common. *C. polystigma* Regan, 1921 is a fairly common member of the rocky shores, but also occurs commonly on sandy areas and in a variety of intermediate habitats. It is most numerous in the shallows, but has been seen to 28 m depth. It appears to have lake-wide distribution. *C. livingstonii* (Gunther, 1893) is common on the rocky shores of Likoma and Chisumulu Islands, but uncommon in rocky habitats elsewhere. It occurs in sandy and vegetated areas. As well as having lake-wide distribution it inhabits the Upper Shire River and local fishermen report its presence in Lake Malombe. It is most numerous in shallow water, but has been seen at 33 m depth at Chinyankwazi Island.

*C. compressiceps* (Boulenger, 1908) is adapted to catch prey in *Vallisneria aethiopica* beds since its markings mimic the fronds of this plant. However, it frequently hunts over rocks and at Membe Islet, off Chisumulu Island, it was seen in a purely rocky habitat more than 300 m from the nearest vegetated area.

\* \* \*

A great many fishes adapted for life over sand visit the rocky shores to release their fry. Most of the species are unknown to us and few were caught for identification. Other species live along the fringe of the rocks either in sandy or vegetated areas and make excursions onto the rocks to feed or to release fry. A few of the common members are listed below. *C. rostrata* (Boulenger, 1909) frequently spawns among rocks, and females protecting newly released broods occur frequently over the upper surfaces of large rocks in shallow water. *C. moori* Boulenger, 1902 and *C. sphaerodon* Regan, 1921 are sand-dwellers which may occupy rocky sites during the guarding phase of parental care. Both appear to have lake-wide distribution and *C. moori* also occurs in the Upper Shire River and in Lake Malombe.

*C. electra* Burgess, 1979 lives over sand at the edge of the rock-sand interface at Likoma Island. It frequently holds territories in the intermediate zone and its members feed among the rocks. It occurs from 7 to at least 40 m depth. *C. johnstonii* (Gunther, 1893), *C. similis* Regan, 1921, *C. placodon* Regan, 1921, *C. kirkii* (Gunther, 1893), *C. mola* Trewavas, 1935, *C. venusta* Boulenger, 1908 and *C. 'pink dorsal'* usually inhabit sand and intermediate zones (often of vegetated areas), but may also visit rocky shores. Similarly *Hemitilapia oxyrhynchus* Boulenger, 1902 is usually found in weeded areas, but is nonetheless common in intermediate habitats and a frequent visitor to rocky shores in southern Lake Malawi.

#### Genus *Docimodus* Boulenger, 1896

This genus has two species of which one, *D. evelynae* Eccles & Lewis, 1976, is found on the rocky shores. It has lake-wide distribution, but is uncommon or rare on all shores except Thumbi West Island where it is common. It occurs from the surface waters to at least 40 m depth. As juveniles, *D. evelynae* individuals may behave as cleaners, but as they grow their diet changes so that they feed on scales, skin and fins of other species (Ribbink in press).

#### Genus *Rhamphochromis* Regan, 1921

This is a group of silvery, elongate fishes which are essentially pursuit predators, but which also ambush their prey among the rocks. At least one species and sometimes as many as four species (e.g. at Chinyankwazi Island) were found at each rocky shore. While it is possible to recognize that species are different, positive identification is a problem. Probably the two most common species associated with rocky zones are *R. longiceps* (Gunther, 1864) and *R. esox* (Boulenger, 1908).

#### Genus *Serranochromis* Regan, 1920

*S. robustus* (Gunther, 1864) is the only member of this genus found in Lake Malawi. It is a non-endemic piscivore which frequents a variety of habitats, preferring vegetated areas. It is, nevertheless, frequently found on the rocky shores. It has lake-wide distribution and is also found in numerous other water bodies (Greenwood, 1979b).

#### Genus *Trematocranus* Trewavas, 1935

Those members of this genus which inhabit intermediate zones in shallow water are colourful fishes which are currently popular in the aquarium trade.

##### 1. *Trematocranus jacobfreibergeri* Johnson, 1974

**Synopsis.** This species is found in rocky caves over sand in shallow water. Its members have cephalic pits. Males are golden-red, females are grey-brown with dark grey bars.

**Distribution.** Nkudzi (R), Monkey Bay (R), Nankumba (R), Domwe I. (R), Otter Point (U – C).

**Coloration.** *Males:* Body light blue with a reddish-gold patch over the shoulder, pectoral region and along the dorsal part of the body; 9 grey bars. Head light blue ventrally, golden-red dorsally, with grey snout and black eye-bar. Dorsal fin pale bluish-white with orange interspine membranes, but black inter-ray membranes. Caudal fin light blue. Anal fin orange-red with a light blue leading edge. Pelvic fins black with red submarginal bands and white leading edges.

*Females:* Greyish-brown with 8 – 10 dark grey bars.

**Habitat.** This species inhabits the rock-sand interface where it lives over sandy substrata in rocky caves or beneath rock overhangs. It is most often associated with large rocks. It follows the rock-sand interface from about 2 m to at least 35 m depth, but appears to be most numerous between 4 and 12 m.

**Territoriality.** Males are territorial, but females form small schools of up to 30 individuals which also occur in rocky caves.

**Feeding.** It feeds from the sand. Stomachs of two specimens were examined, both contained insect larvae and one had a few ostracods.

\* \* \*

A number of similar species, but of different coloration have been seen occasionally on various coasts, but these fishes are rare and by virtue of their tendency to remain hidden in rocky caves they are difficult to catch. Consequently, very little is known about them.

\* \* \*

In addition to the fishes listed above many other non-Mbuna species which feed from the rock surface, presumably taking components of the Aufwuchs or its invertebrate inhabitants, are permanent members of the rocky communities. Some of these such as *Cyrtocara intermedia* of Monkey Bay, Nankumba and Thumbi West Island are described, but most, such as the elongate blue-fish with the red dorsal fin (Plate 12i) are undescribed. Very little is known about any of these fishes.

#### The cichlid communities of the rocky shores

In this section we describe the various areas studied and list the Mbuna species found at each, noting the habitat preference of these species. Where possible an indication of numerical abundance is given for each species. The non-Mbuna are dealt with briefly.

##### Area 1: Monkey Bay, Nankumba, Domwe Island and Zimbabwe Island

The area that forms the focus for this section of the paper

extends from Harbour Island, at the southerly entrance of Monkey Bay, to Zimbabwe Island, just north of Cape Maclear which is the northern-most point of Domwe Island (Figure 21). Most of the shoreline within this study area is rocky, but its continuity is broken by sandy beaches at Monkey Bay, Chizali, Zambo and Mvunguti and by the short stretches of open water which separate islands. The rocky shores of this region shelf steeply and, with the exception of Zimbabwe, all reach sand in less than 40 m depth (Figure 21). A characteristic of this entire area, particularly Domwe Island and Zimbabwe Island is that it is dominated by medium-large and large rocks; boulders and slabs are also common. Pockets of small rocks are found only occasionally.

Aquatic macrophytes (*Vallisneria aethiopica*, *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Potamogeton pectinatus* and *P. schweinfurthii*) grow in shallow sandy areas and are particularly abundant in Monkey Bay. Shallow wave-washed regions are free of sediment, but in deep water and in sheltered bays a layer of organic sediment covers the rocks and sand. In the deeper central parts of Monkey Bay (15 – 17 m) the organic ooze overlying the sand is at least a metre deep. *C. demersum* and *P. schweinfurthii* may grow in this soft sediment, but *V. aethiopica* is found in cleaner, shallow areas. Within the shallow sheltered waters of Monkey Bay the rocky zones quite frequently give way to weeded areas.

The fishes of this area were studied at 24 diving stations indicated by the arrows on Figure 21. Line transects were laid at the island of Thumbi East, at Tsano Rock and at Mvunguti. Point transects were conducted at the Ilala Gap, Cape Maclear and Zimbabwe.

*Diving stations*

**Monkey Bay.** The rocky shores of Monkey Bay considered here include not only those within the bay itself, but also those adjacent to Chizali and Zambo and those of Harbour Island and Thumbi East Island. Transect A was laid on the exposed shore of Thumbi East Island (Figure 21). Medium-large broken rocks predominated, but at 2 – 8 m pockets of small rocks were also included in the transect. The rocks gave way to sand at 36 m, but sandy patches occurred among the rocks from 29 m.

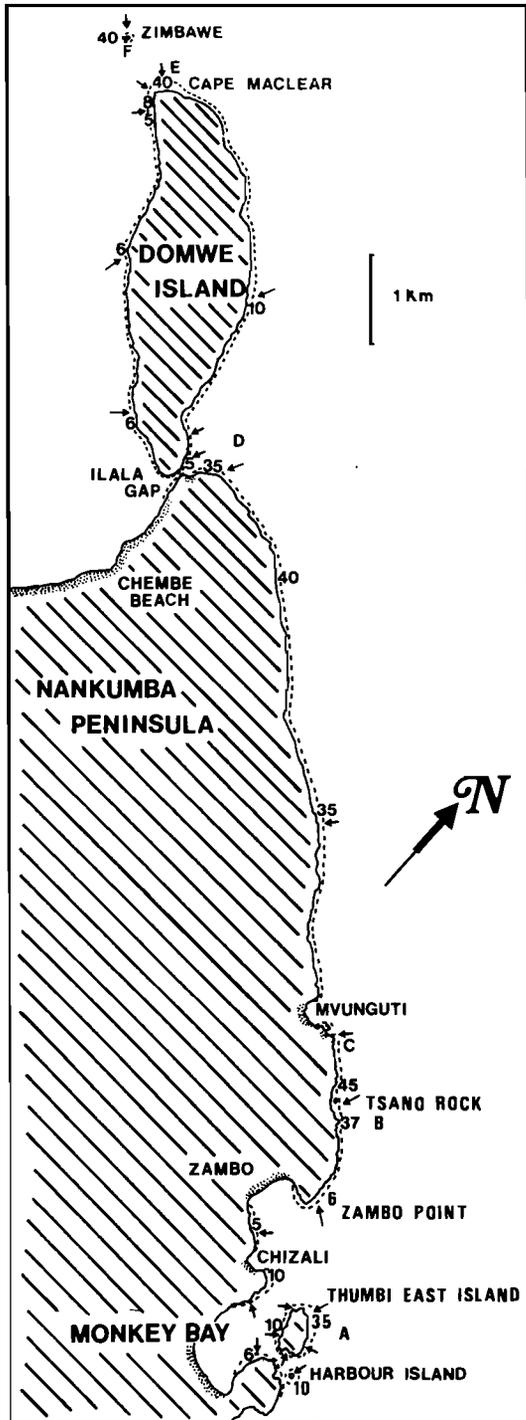
**Tsano Rock.** The rocky region included in this section runs from Zambo Point, which gives way to a coarse gravel at 6 – 8 m, to Tsano Rock where rocks give way to sediment-covered sand at about 40 m. Transect B was laid approximately 70 m south of Tsano Rock, over broken medium-sized rocks. A patch of small rocks was encompassed by the shallowest transect markers and a few pockets of sand were included in the 10 m transect contour. At 20 m the transect included 12 m<sup>2</sup> of a rocky slab.

**Mvunguti.** The stretch of rocky shore from Tsano Rock to the beach at Mvunguti is considered here. In addition to the Mvunguti Beach, a considerably smaller beach lies just south of Mvunguti Point. The transect was conducted approximately 40 m south of this beach (C, Figure 21). The habitat comprises medium-sized and large rocks from the surface to the sand-rock interface at 24 m.

**Nankumba Peninsula.** The rocky shores from Mvunguti to the south-western portion of the Ilala Gap are characterized by large rocks. There are two tiny beaches, one on each side of the Ilala Gap. The eastern coast of Nankumba shelves very steeply to the sandy plains. A point transect was conducted within the funnel of the Ilala Gap (D, Figure 21) where boulders give way to coarse gravel at 33 m depth.

**Domwe Island.** With the exception of the northern-most point, which is 40 m deep, the large rocks and boulders of Domwe Island reach sand in less than 12 m. A point transect was conducted at site E on the northern tip of Domwe Island (Figure 21).

**Zimbabwe Island.** Zimbabwe Island is a rocky pinnacle situated about 500 m west of Domwe Island. It comprises horizontal and vertical slabs, boulders and large rocks with very few smaller rocks. It shelves very steeply, sometimes



**Figure 21** The study sites in area I are indicated by arrows. Letters A – F show the positions of transect sites. The dotted lines indicate the extent of the rocky shore and the numerals within these lines give the depth at which rocks meet the sandy plain. Sandy beaches are stippled.

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vertically, to a depth which is greater than 40 m. The point transect (F, Figure 21) was conducted on its north-eastern side.

*The communities*

The Mbuna community of this study region comprises 25 species of which 14 have been previously described (Table 15). Nineteen of the Mbuna are essentially lithophilous, four occur mainly in intermediate habitats and two are sand-dwellers (Figure 28).

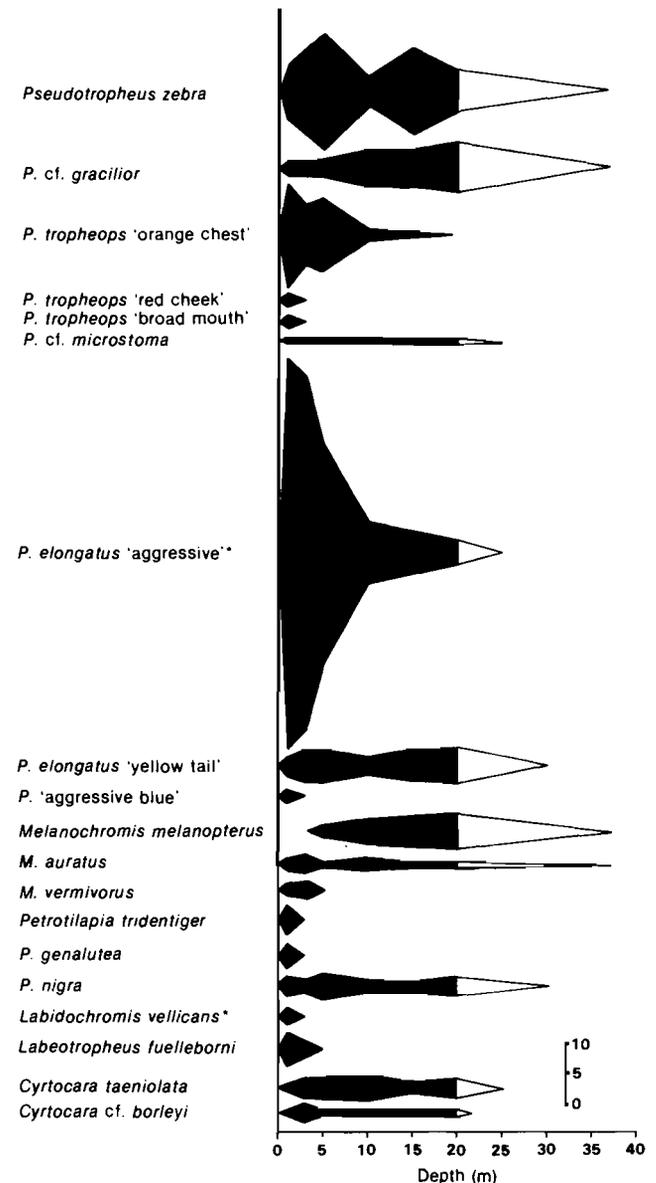
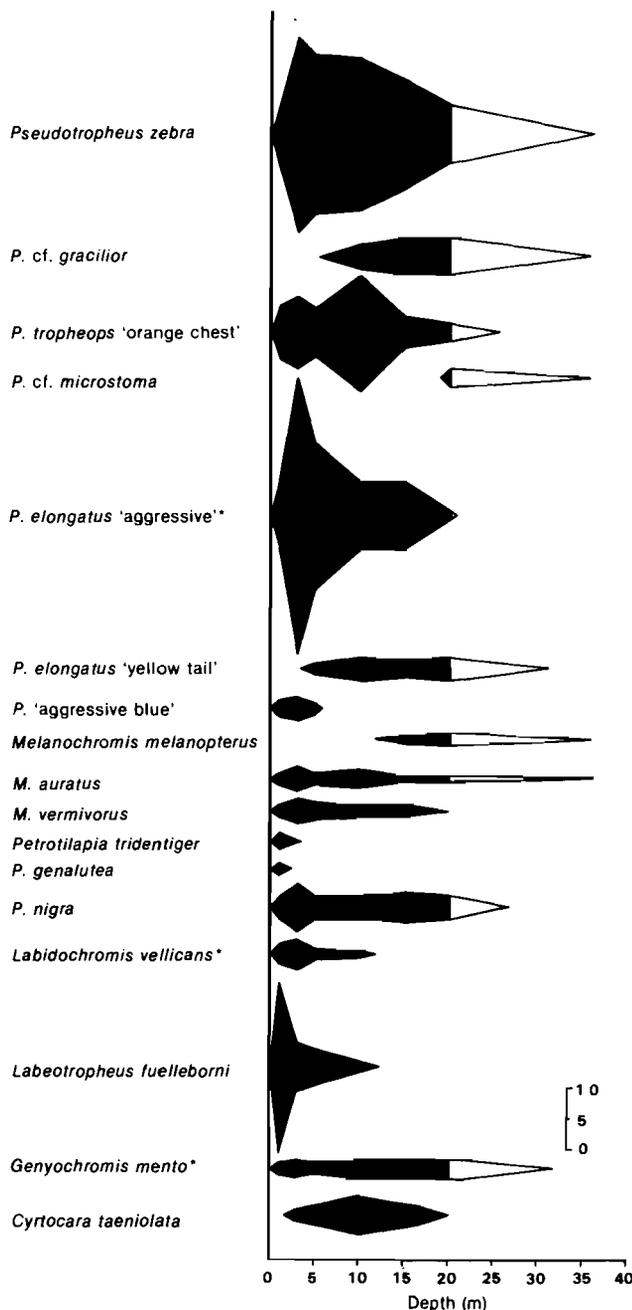
At Monkey Bay 23 Mbuna species were found of which 16 occurred in the transect (Figure 22). Of the 18 species found at Tsano Rock 17 are recorded in the transect (Figure 23). Only 13 of the 19 species which inhabit the Mvunguti area were recorded in the transect (Figure 24). At the Ilala Gap 13 species were recorded in the transect (D, Figure 25).

The other species found there all occurred in the intermediate habitats of the shallows adjacent to the beaches. At Cape Maclear 14 of the 18 Mbuna of Domwe Island were represented in the point transect (Figure 26). In about 40 diving hours at Zimbabwe Island we found only nine Mbuna species all of which are represented in the transect (Figure 27). Zimbabwe proved to be the only rocky site in the lake without a representative of the genus *Petrotilapia*. *Labeotropheus trewavasae* is present at Zimbabwe, but absent from the other sites in this area.

An indication of the number of territorial male *Cyrtocara taeniolata* is given in transects A and B (Figures 22 & 23).

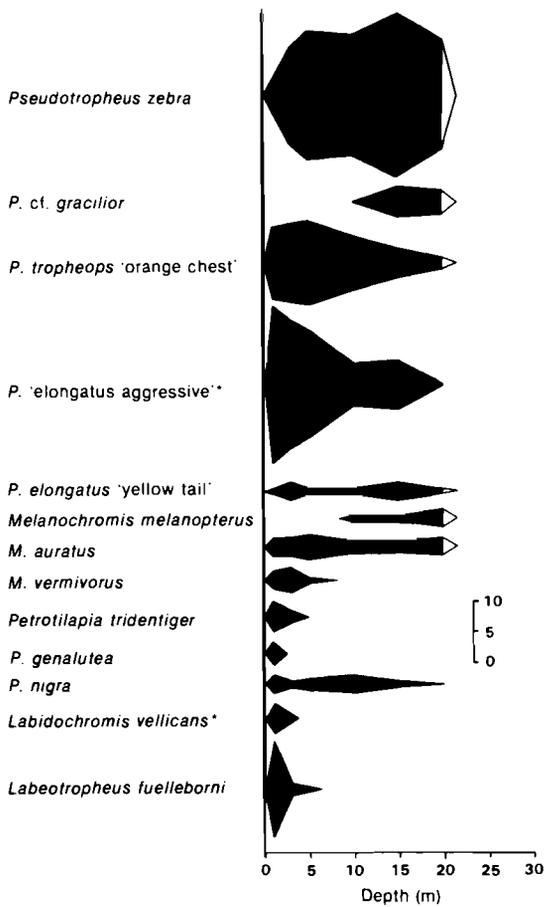
More species of Mbuna inhabit the shallows than deeper water, and in general the numerical density of cichlid individuals also decreases with depth (Table 16). At Thumbi East, however, a shoal of Utaka was present at 20 m at the time the transect was laid, elevating the number of cichlid fishes recorded at that depth.

In addition to the territorial fishes depicted in the transect figures there are numerous non-territorial Mbuna living

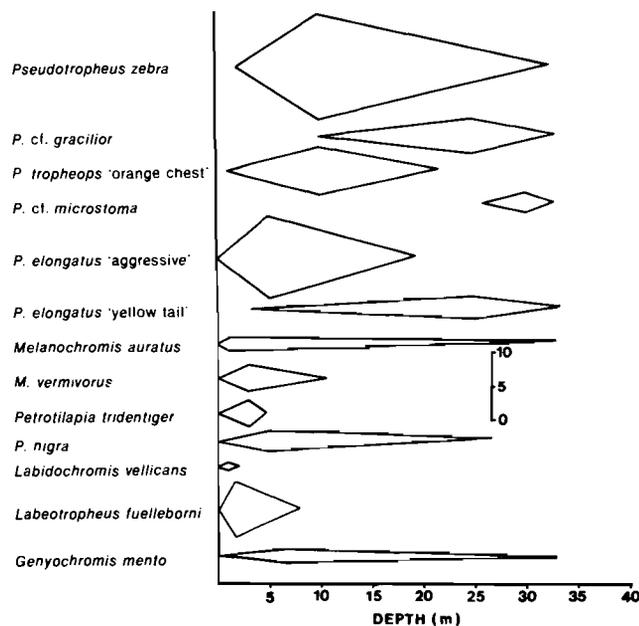


**Figure 22** Transect A at Thumbi East Island, Monkey Bay, giving the depth distribution and numerical abundance of Mbuna species and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

**Figure 23** Transect B at Tsano Rock, Nankumba Peninsula, giving the depth distribution and numerical abundance of Mbuna species and of two species 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<sup>-2</sup>.

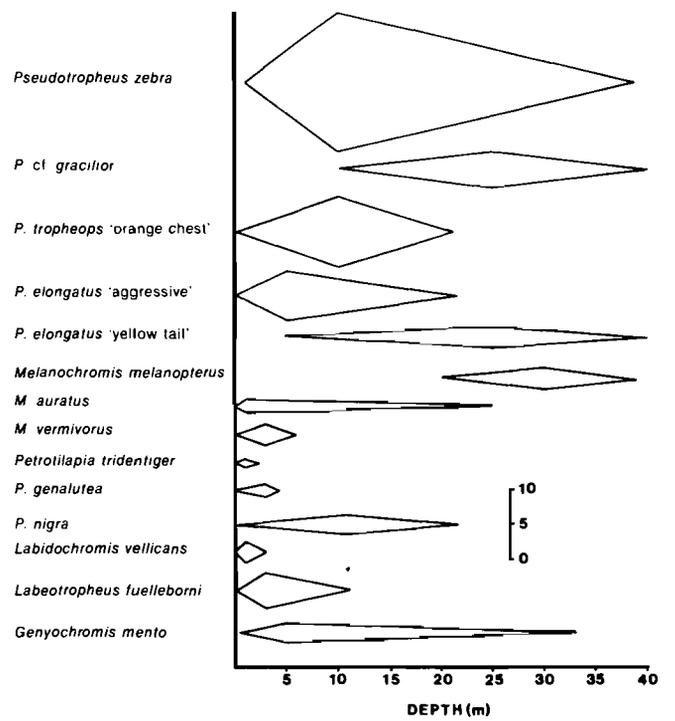


**Figure 24** Transect C at Mvunguti, Nankumba Peninsula, giving the depth distribution and numerical abundance of Mbuna species. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

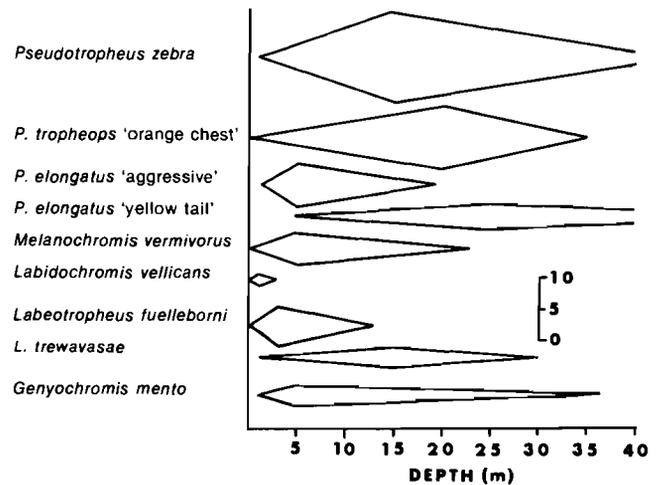


**Figure 25** The point transect at the Ilala Gap (site D, Figure 21) giving the depth distribution and an estimate of numerical abundance of Mbuna species. Estimated numerical abundance is expressed as the number of individual fishes in 50 m<sup>2</sup>.

among the rocks. The extreme shallows are dominated by large groups of juvenile and subadult *Labeotropheus fuelleborni* and *Pseudotropheus tropheops* 'orange chest'. In the



**Figure 26** The point transect at Cape Maclear (site E, Figure 21) giving the depth distribution and an estimate of numerical abundance of Mbuna species. Estimated numerical abundance is expressed as the number of individual fishes in 50 m<sup>2</sup>.



**Figure 27** The point transect at Zimbabwe Island (site F, Figure 21) giving the depth distribution and an estimate of numerical abundance of Mbuna species. Estimated numerical abundance is expressed as the number of individual fishes in 50 m<sup>2</sup>.

shallows, among medium-sized and large rocks there are many adult females, juveniles of both sexes and supernumerary adult male *Petrotilapia* spp., *Labeotropheus fuelleborni*, *Pseudotropheus tropheops* 'orange-chest', *P. cf. gracilior*, *Melanochromis auratus* and *M. vermivorus*. Indeed, *Petrotilapia tridentiger* and *P. genalutea* are considerably more common in these habitats than the census of territorial males suggests (Figures 22 – 24). All of these species feed from the rocks and congregate in mixed groups over the upper surfaces of large rocks, boulders and slabs, often in the company of *Cyrtocara taeniolata* and *C. fenestrata*. A striking feature of the rocky shores of this area is that

**Table 15** The distribution of the Mbuna in area 1. Present (+), absent (-)

Species	Transect stations					
	Monkey Bay	Tsano Rock	Mvunguti	Ilala gap	Domwe Island	Zimbabwe
1. <i>Pseudotropheus zebra</i>	+	+	+	+	+	+
2. <i>P. livingstonii</i>	+	-	+	+	+	-
3. <i>P. elegans</i>	+	-	-	-	-	-
4. <i>P. cf. gracilior</i>	+	+	+	+	+	-
5. <i>P. tropheops</i> 'orange chest'	+	+	+	+	+	+
6. <i>P. tropheops</i> 'red cheek'	-	+	-	-	-	-
7. <i>P. tropheops</i> 'broad mouth'	+	+	+	+	+	-
8. <i>P. cf. microstoma</i>	+	+	+	+	+	-
9. <i>P. cf. novemfasciatus</i>	+	-	+	+	-	-
10. <i>P. williamsi</i> 'nkudzi'	+	-	-	-	-	-
11. <i>P. elongatus</i> 'aggressive'	+	+	+	+	+	+
12. <i>P. elongatus</i> 'yellow tail'	+	+	+	+	+	+
13. <i>P.</i> 'aggressive blue'	+	+	-	-	-	-
14. <i>Melanochromis melanopterus</i>	+	+	+	+	+	-
15. <i>M. auratus</i>	+	+	+	+	+	-
16. <i>M. vermivorus</i>	+	+	+	+	+	+
17. <i>M. cf. brevis</i>	+	-	-	-	-	-
18. <i>Petrotilapia tridentiger</i>	+	+	+	+	+	-
19. <i>P. genalutea</i>	+	+	+	+	+	-
20. <i>P. nigra</i>	+	+	+	+	+	-
21. <i>Labidochromis vellicans</i>	+	+	+	+	+	+
22. <i>Labeotropheus fuelleborni</i>	+	+	+	+	+	+
23. <i>L. trewavasae</i>	-	-	-	-	-	+
24. <i>Genyochromis mento</i>	+	+	+	+	+	+
25. <i>Cyathochromis obliquidens</i>	+	-	+	+	+	-
Totals	23	18	19	19	18	9

**Table 16** The number of Mbuna species and the number of individual cichlids of all species counted at different depths in transects A - C in area 1. Dashes indicate depths at which counts of individuals were not made

	Depth (m)									
	1	3	5	10	15	20	25	30	35	40
<b>Transect A</b>										
No. Mbuna species	12	10	11	11	11	10	9	7	5	-
No. individuals all cichlids	370	340	330	320	340	380	-	-	-	-
No. individuals m <sup>-2</sup>	7,4	6,8	6,6	5,4	6,8	7,6	-	-	-	-
<b>Transect B</b>										
No. Mbuna species	18	18	12	9	9	8	6	4	4	4
No. individuals all cichlids	305	274	230	210	240	140	-	-	-	-
No. individuals m <sup>-2</sup>	6,1	5,5	4,6	4,2	4,4	2,8	-	-	-	-
<b>Transect C</b>										
No. Mbuna species	13	13	12	8	8	8	7			
No. individuals all cichlids	260	280	275	230	140	140	-			
No. individuals m <sup>-2</sup>	5,2	5,6	5,5	4,6	2,8	2,8	-			

shoals of several hundred non-territorial *Pseudotropheus zebra* individuals are always to be found in the water column above the rocks which are tenanted by conspecific territorial males. At times of plankton blooms these shoals may be joined by other species of Mbuna, but most of these

species do not rise more than a metre or two above the substratum whereas *P. zebra* has been seen 8 - 12 m above the rocks.

*Pseudotropheus tropheops* 'broad-mouth' and *P. cf. microstoma* occur among the rocks, but are usually most

numerous in intermediate habitats and are therefore poorly represented in the transects. *P. williamsi* 'nkudzi' and *Melanochromis* cf. *brevis* were found at Harbour Island and Thumbi East Island, but they are rare and were not represented in the transects.

The sand-rock interface is frequented by *Pseudotropheus* cf. *microstoma*, *P. cf. gracilior*, *Aulonocara* 'yellow collar', *A.* 'blue collar' and *Trematocranus jacobfreibergi* which are distributed all along this intermediate zone as it extends from 3 m to 40 m depth. None of these fishes are numerous in this zone, though large groups of female *Aulonocara* spp. sometimes occur under rocky overhangs.

*Pseudotropheus* cf. *novemfasciatus* and *Cyathochromis obliquidens* inhabit the shallow intermediate areas, particularly where macrophytes are present, and as the transects were laid over rocky habitats these species were not represented. Both of these species are common in suitable habitats, and become numerous within the sheltered, vegetated regions of Monkey Bay.

All Zimbabwe species are unique in coloration and are, in general, darker and more sombre than conspecifics elsewhere in this study area. Furthermore, all adult territorial Mbuna, *Cyrtocara taeniolata* and *C. fenestrata* are larger at Zimbabwe than conspecifics at the other sites in this area (unpubl. data).

The preferred habitat, depth distribution and degree of territoriality of most Mbuna species of Monkey Bay and Zimbabwe Island are summarized in Figure 28.

**Area 2: The south-eastern arm**

The south-eastern arm of Lake Malawi is relatively shallow, it is rich in nutrients and supports the major food fishery

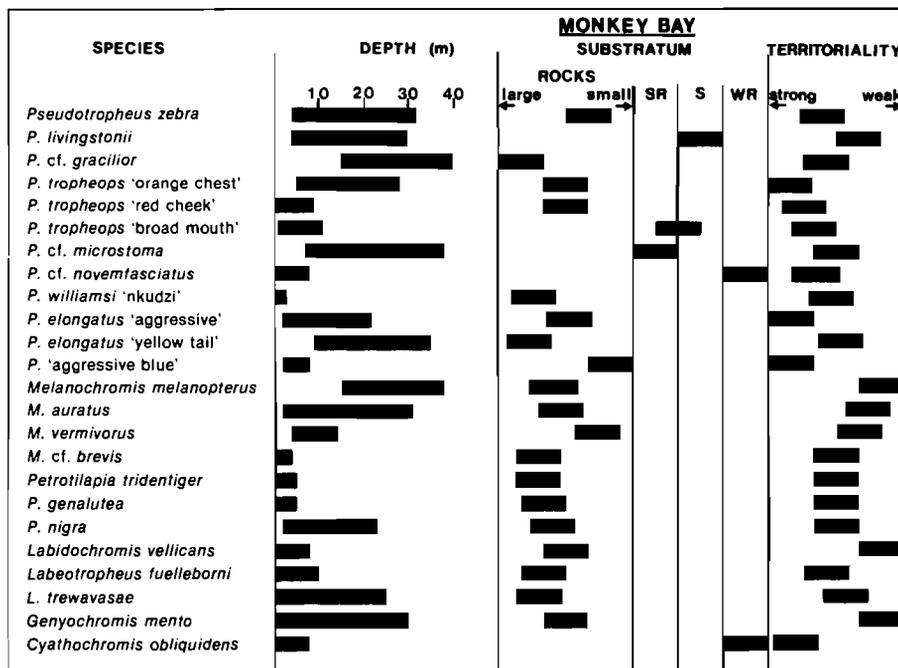
(Fryer & Iles 1972; Turner 1977a, 1977b). Most of the coastline in this area is sandy, although vegetated and marshy areas are also common. Rocky regions are scarce and are usually small, seldom extending to depths greater than 15 m.

**Diving stations**

The fishes were studied at a) the rocky shores of the west coast, b) Boadzulu Island and c) the rocky shores of the east coast.

*The west coast.* Seven rocky zones were studied from Kanchedza Island to Nkopola (Figure 29). In addition to the areas studied, several other small rocky zones occur along the coast between Mpandi Island and Nkopola, the largest of which is Ndala Chikowa (14°14'S).

- (i) Kanchedza is a rocky island of about 70 m diameter which comprises mainly medium-sized rocks in 3 – 8 m of water. *Vallisneria aethiopica* beds surround much of the island and are particularly dense on its north-western shores.
- (ii) Chigubi Point is an area of small broken rocks on a gently shelving sandy bottom. Almost all of the area is of an intermediate habitat which extends to a depth of 6 – 9 m.
- (iii) Mazinzi Reef is a rocky area of about 200 m<sup>2</sup> which was at a depth of 3 – 8 m below the surface in 1980.
- (iv) Nkudzi is the largest rocky shore in this study area being 2,2 km in length. It is a rocky peninsula which is flanked by a long sandy beach to the north, but to the south there is a small marsh and then a long sandy beach. Rocks on this shore are of a variety of sizes, but medium-large rocks predominate. At its deepest



**Figure 28** A summary of resource utilization of the Mbuna community in area 1. Blocks indicating preferred depth are based on quantified and observational data. Those indicating a habitat preference are based on unquantified observations. Preferences for habitats of rocks of a particular size, intermediate zones of sand-rock (SR) or weed-rock (WR) or a tendency to favour sandy environs (S) are indicated by the position of the blocks. The positions of blocks do not indicate the full depth range of species, nor do they indicate an absolute restriction to a particular habitat; they give the depths and habitat types in which most individuals are likely to be found.

An assessment of the degree of territoriality is given by the position of blocks in a range from non-territorial fishes (extreme right) to strongly territorial species which possess algal gardens (extreme left). Those species which are centrally placed are aggressive almost entirely to conspecifics. The evaluation of the degree of territoriality is based largely on unquantified observations and the positioning of the blocks on the continuum was made relative to the three reference points given above (i.e. left, right or central).

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point the rocky zone extends to 18 m (1980) before giving way to sand.

- (v) Mpandi Island comprises medium-sized rocks in 3–8 m of water. It has a diameter of about 100 m. Beds of *V. aethiopica* surround the island.
- (vi) Crocodile Rock is actually a group of large rocks submerged in 3–8 m of water.
- (vii) Nkopola is a sandy beach, but to its south there is a gradually shelving rocky shore, comprising mainly small and medium-sized rocks which extend to a depth of 5 m. To the north of the beach there is a group of medium-large rocks in 4 m of water. The Mbuna at both of these rocky shores were studied.

**Boadzulu Island.** This is an elongate island approximately 600 m in length and a little more than 200 m at its widest point (Site 8, Figure 29). It is usually inhabited by a large colony of white-fronted cormorants, (*Phalacrocorax carbo* Linnaeus). The island's western shore consists of large rocks and boulders which plunge steeply to at least 40 m. A few small patches of sand have accumulated among the rocks of the shallows. The point transect was conducted at Site A and an exploratory dive to 40 m at Site B (Figure 29). The eastern side of Boadzulu Island is not as deep as the western coast and it shelves more gradually. A line transect was laid at Site C where medium and medium-large rocks predominate in the extreme shallows; small and medium-small rocks occur between 3–10 m and from 10–15 m the rocks are large. At 20 m the habitat is of an inter-

mediate nature and the bottom is sandy at 24 m. At Site D large rocks and small slabs dominate the shallows, but give way suddenly, at about 5 m, to a gently shelving bed of small rocks. By 12 m an intermediate sand-rock zone predominates giving way at 14 m to a sandy bottom covered by a mantle of filamentous algae (*Lyngbia* spp.) which is 60 cm thick in places.

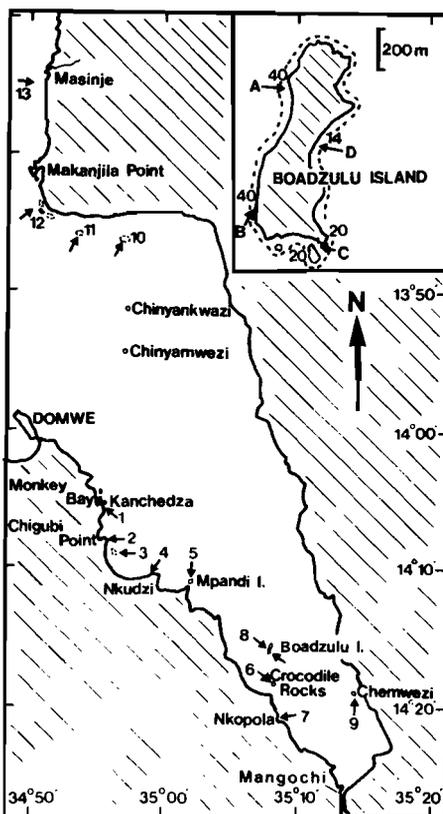
**The east coast.** The eastern shores of the south-east arm are predominantly sandy, but the rocky outcrop of Chemwezi occurs in the south, and numerous rocky reefs which were submerged in 1980 occur off Makanjila Point. In addition, a rocky shore occurs in the northern part of this study region. The stations (9–13; Figure 29) studied in this region are:

- (9) Chemwezi is an outcrop of large rocks and boulders situated on a sandy bottom. In 1980 Chemwezi was about 30 m in diameter at water level and its base was at 10 m depth.
- (10) Eccles Reef is a collection of medium-sized and large rocks: From its base at 15 m in 1980, it rose to within 3 m of the surface.
- (11) West Reef is a smaller submerged reef of large rocks, boulders and slabs. In 1980 its base was at 13 m, its apex 3–4 m below the surface.
- (12) A number of scattered, submerged offshore rocky reefs are included as Makanjila Point (Cape Ngombo). Three different reefs were visited.
- (13) Masinje Rocks is a short stretch of rocky shoreline about 6 km south of Masinje River. This ribbon of rocks is no deeper than 8 m, shelves gradually and is interspersed with many sand patches so that much of the area below 3–4 m is an intermediate habitat.

#### The communities

Forty-two Mbuna species of which 20 have been described, were recorded in this study area, but at no two diving stations were the species assemblages identical (Table 17). The differences between species assemblages increased progressively as the distance between diving stations became greater. A total of 24 species was found at the stations of the western shore and 25 at those along the eastern shores; 11 species are common to both shores. Chemwezi is the southern-most station of the eastern shores (Figure 29), but it has more species in common with the stations of the western shores. Boadzulu Island has 16 Mbuna species, of which 11 are common to the western shores and nine are common to the eastern shores. Only *Genyochromis mento* was found at all diving stations.

Fifteen of the species occurring in the south-eastern arm were not found elsewhere. The Mbuna communities of this study area are unusual in that the *Pseudotropheus* 'aggressive' species-group and the genus *Cynotilapia* are not represented. Furthermore, the *Pseudotropheus* 'miscellaneous' species-group is represented by only one species. In contrast, the genus *Melanochromis* has nine members and is therefore better represented in this region than anywhere else in the lake. The depth distribution and numerical abundance of the Mbuna at Boadzulu Island are indicated by the line and point transects (Figures 30 & 31). *Pseudotropheus zebra*, two members of the *P. tropheops* species-complex, *Labidochromis heterodon* and *Iodotropheus sprengerae* dominate the Mbuna community numerically. A general characteristic of the members of the



**Figure 29** The locations of study sites in area 2 are indicated by the numerals and arrows. 1 = Kanchedza, 2 = Chigubi Point, 3 = Masinje Reef, 4 = Nkudzi Point, 5 = Mpandi Island, 6 = Crocodile Rocks, 7 = Nkopola, 8 = Boadzulu Island, 9 = Chemwezi Rocks, 10 = Eccles Reef, 11 = West Reef, 12 = Makanjila Reef, 13 = Masinje Rocks. The inset of Boadzulu Island shows the positions of diving stations A–D. The positions of Chinyankwazi and Chinyamwezi Islands (area 3) are given in the main map.

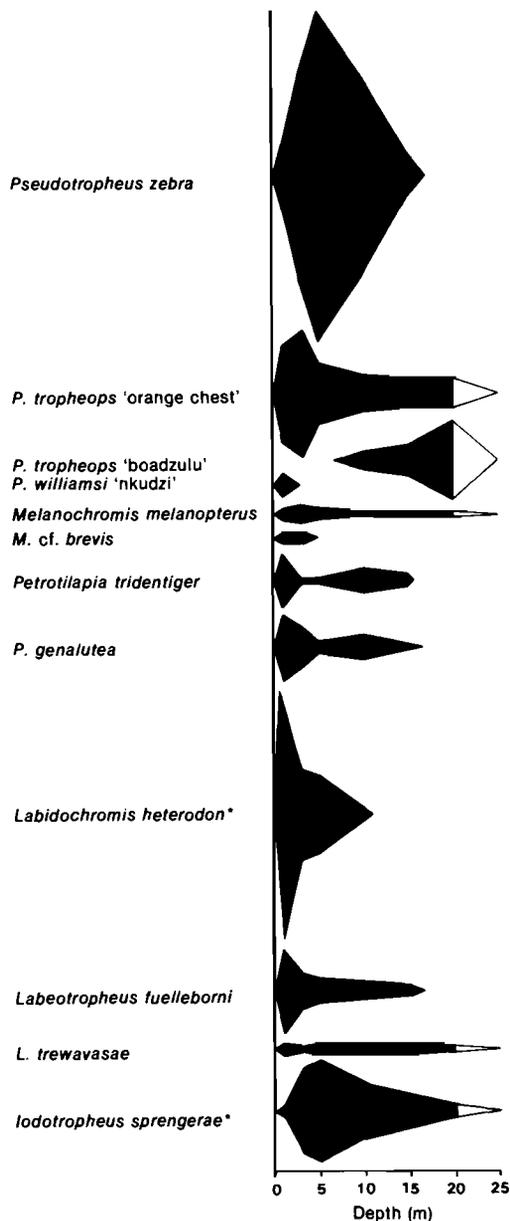
**Table 17** The Mbuna at the principal diving stations in the south-eastern arm of Lake Malawi. Present (+); absent (-); found in this study area only (\*)

Species	Western Shores							Eastern Shores					
	Kanchedza 1	Chigubi 2	Mazinzi 3	Nkudzi 4	Mpandi 5	Croc. Rocks 6	Nkopola 7	Boadzulu Island 8	Chemwezi 9	Eccles Reef 10	West Reef 11	Makanjila Pt 12	Masinje 13
1. <i>Pseudotropheus zebra</i>	+	-	-	+	+	-	-	+	-	+	+	+	+
2. <i>P. livingstonii</i>	+	-	+	+	-	+	-	+	-	-	-	+	-
3. <i>P. zebra</i> 'mazinzi'	*	-	+	-	-	-	-	-	-	-	-	-	-
4. <i>P. elegans</i>	-	-	+	+	-	+	-	+	+	-	+	-	-
5. <i>P. zebra</i> 'fusco'	-	-	+	+	-	-	-	-	-	-	-	-	-
6. <i>P. zebra</i> 'masinje'	*	-	-	-	-	-	-	-	-	-	-	-	+
7. <i>P. cf. gracilior</i>	+	-	-	+	-	-	-	-	-	-	-	-	-
8. <i>P. tropheops</i> 'orange chest'	+	+	-	+	+	+	+	+	+	-	-	-	-
9. <i>P. tropheops</i> 'broad mouth'	+	+	-	+	+	-	+	-	+	-	-	+	-
10. <i>P. cf. novemfasciatus</i>	+	+	-	+	+	-	+	-	-	-	-	-	-
11. <i>P. tropheops</i> 'boadzulu'	*	-	-	-	-	-	-	+	-	-	-	-	-
12. <i>P. tropheops</i> 'black dorsal'	*	-	-	-	-	-	-	-	-	+	+	-	-
13. <i>P. tropheops</i> 'yellow gular'	*	-	-	-	-	-	-	-	-	+	+	+	+
14. <i>P. williamsi</i> 'nkudzi'	-	-	-	+	-	-	-	+	-	-	-	-	-
15. <i>P. williamsi</i> 'makanjila'	*	-	-	-	-	-	-	-	-	-	-	+	+
16. <i>P. elongatus</i> 'aggressive'	+	-	-	+	+	-	-	-	-	-	-	-	-
17. <i>P. elongatus</i> 'yellow tail'	+	-	-	+	+	-	-	-	-	-	-	-	-
18. <i>P. elongatus</i> 'boadzulu'	*	-	-	-	-	-	-	+	-	-	-	-	-
19. <i>P. elongatus</i> 'reef'	*	-	-	-	-	-	-	-	-	+	+	-	-
20. <i>P. elongatus</i> 'brown'	*	-	-	-	-	-	-	-	-	+	+	-	-
21. <i>P. lucerna</i> 'brown'	*	+	+	-	+	+	-	+	-	-	-	-	-
22. <i>Melanochromis melanopterus</i>	-	-	-	+	-	-	-	+	-	+	-	-	-
23. <i>M. auratus</i>	+	+	+	+	+	+	+	-	-	-	-	-	+
24. <i>M. vermicivorus</i>	-	-	-	-	-	-	-	-	-	+	+	-	-
25. <i>M. simulans</i>	*	-	-	-	-	-	-	-	-	-	-	-	+
26. <i>M. johanni</i>	*	-	-	-	-	-	-	-	-	-	-	-	+
27. <i>M.</i> 'blotch'	-	-	-	-	-	-	-	-	-	-	-	-	+
28. <i>M.</i> 'lepidophage'	*	-	-	-	-	-	-	-	-	-	-	+	-
29. <i>M. cf. brevis</i>	-	-	-	+	-	-	-	+	-	-	-	-	-
30. <i>M. crabro</i>	-	-	-	-	-	-	-	-	-	+	+	-	-
31. <i>Petrotilapia tridentiger</i>	+	-	+	+	+	+	+	+	+	-	-	-	-
32. <i>P. genalutea</i>	+	-	+	+	+	+	+	+	-	-	-	+	-
33. <i>P. nigra</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
34. <i>P.</i> 'yellow chin'	-	-	-	-	-	-	-	-	-	+	+	+	+
35. <i>Labidochromis vellicans</i>	+	-	-	+	-	-	-	-	-	-	-	-	-
36. <i>L. shiranus</i>	*	-	-	-	+	+	+	+	-	-	-	-	-
37. <i>L. heterodon</i>	*	-	-	-	-	-	-	+	-	-	-	-	-
38. <i>Labeotropheus fuelleborni</i>	+	+	-	+	+	+	+	+	-	+	+	+	+
39. <i>L. trewavasae</i>	-	-	-	-	-	-	-	+	-	-	-	-	-
40. <i>Genyochromis mento</i>	+	+	+	+	+	+	+	+	+	+	+	+	+
41. <i>Iodotropheus sprengerae</i>	-	-	-	-	-	-	-	+	-	-	-	-	-
42. <i>Cyathochromis obliquidens</i>	+	+	-	+	+	-	+	-	+	-	-	+	+
Totals	15	17	8	8	22	14	9	11	16	6	11	11	12

genus *Labidochromis* is that they occur singly or in small groups and nowhere are they numerous. *L. heterodon* is the exception being the only member which occurs in large schools. *I. sprengerae* occurs singly or in small groups which are normally widely spaced, but at the time the transect was laid several groups had gathered in the area, possibly to feed upon particulate sediment stirred up by divers. The transect

data, therefore, overestimate the abundance of this species.

The bimodal distribution of the two *Petrotilapia* species (Figure 30) is attributed to the presence of small rocks at 3 – 10 m depth, which are unsuitable for habitation by these large Mbuna. It is not known why these two species are found more deeply at Boadzulu Island than elsewhere in their distribution.



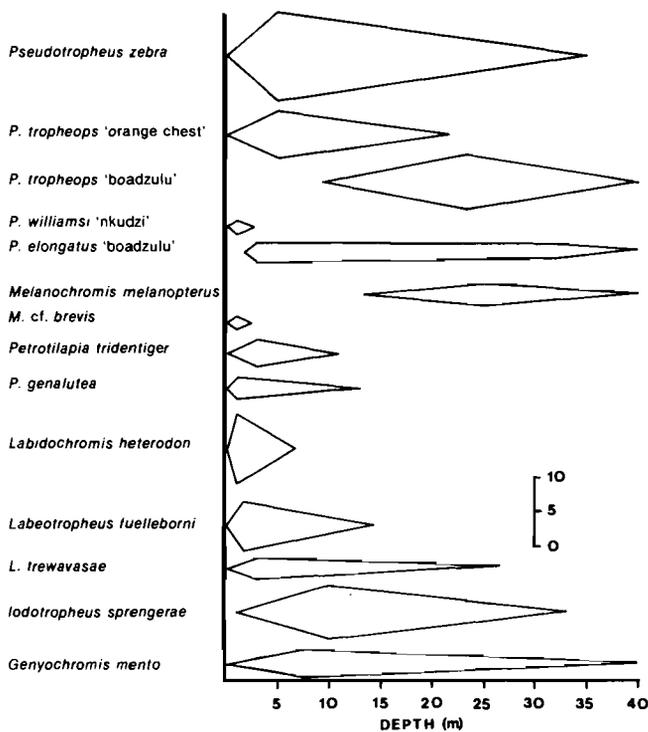
**Figure 30** Transect at site C, Boadzulu Island, giving the depth distribution and numerical abundance of the Mbuna species. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

The shallows at Boadzulu support a larger number of Mbuna species and a greater number of cichlid individuals than the deeper waters (Table 18).

A summary of the habitat and depth preference and an indication of the degree of territoriality of the Mbuna of Boadzulu Island is given (Figure 32). The community is unusual in that none of its members may be classed as an inhabitant of the intermediate zones. *Pseudotropheus livingstonii* and *P. elegans* are rare visitors to the island and both are sand-dwelling Mbuna.

As there are no representatives of the *Pseudotropheus* 'aggressive' species-group at Boadzulu, its Mbuna community has only one interspecifically aggressive territorial fish, *Pseudotropheus tropheops* 'orange chest'.

The non-Mbuna are both speciose and numerically abundant in the south-east arm and often dominate rocky shores and intermediate habitats. For example, some species of the Utaka group are particularly numerous at submerged reefs



**Figure 31** The point transect at site A, Boadzulu Island, giving the depth distribution and an estimate of numerical abundance of the Mbuna species. Estimated numerical abundance is expressed as the number of individual fishes in 50 m<sup>2</sup>.

**Table 18** The number of Mbuna species and the number of individual cichlids of all species recorded at different depths in the transect at Boadzulu Island

	Depth (m)					
	1	3	5	10	15	20
No. Mbuna species	14	14	13	13	13	12
No. of individuals all cichlids	340	370	480	255	159	250
No. of individuals m <sup>-2</sup>	6,8	7,4	9,6	5,1	3,2	5,0

and around islands.

Many of these non-Mbuna are unidentified, but some of the more regular inhabitants of rocky, intermediate and weeded zones are well represented. Among these are the predators *Cyrtocara kiwinge*, *C. macrostoma*, *C. livingstonii*, *C. linni*, *C. venusta*, *C. fuscotaeniata*, *Serranochromis robustus*, *Aristochromis christyi* and several *Rhamphochromis* spp.

The benthic feeders include *Cyrtocara fenestrata*, which was more common than *C. taeniolata* in most areas, possibly owing to higher sediment levels in the south-east arm. *C. euchila* occurred at all sites and *C. labrosa* was found at Boadzulu, Eccles Reef and West Reef. *C. rostrata* is widespread in the study area, even on the rocky reefs. *Astatotilapia calliptera* is common in weeded zones. *Chilotilapia rhoadesii* does not usually venture onto the rocky shore but at Chemwezi it was very common and some males in breeding livery were territorial over the rocks.

A *Trematocranus* sp. from Boadzulu Island and a golden-headed *Cyrtocara* sp. from West Reef are attractive undescribed aquarium fishes of the rock-sand interface.

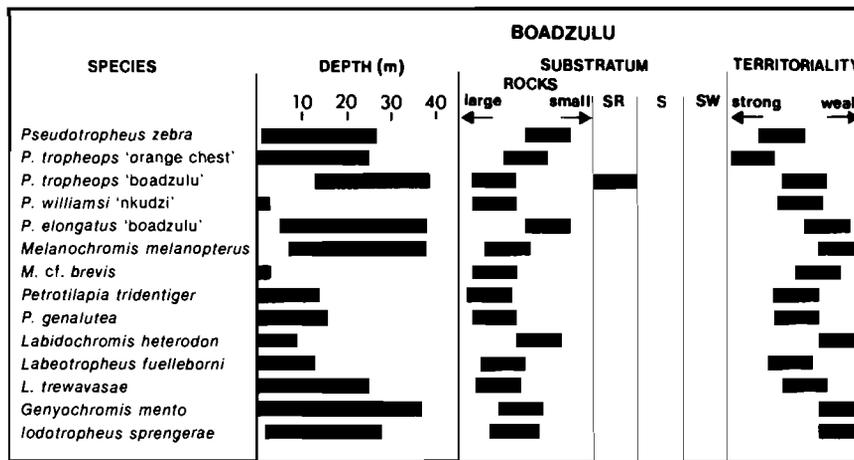


Figure 32 A summary of resource utilization of the Mbuna community at Boadzulu Island. For rest of legend see Figure 28 (p.254).

### Area 3: The islands of Chinyankwazi and Chinyamwezi

Chinyankwazi and Chinyamwezi are small islands between Monkey Bay and Makanjila in the south-east arm of the lake (Figure 29). Chinyankwazi, the larger island, is almost circular in shape with an estimated diameter of 100 m at lake level. It is 8 km from Makanjila, the nearest mainland shore, and a little more than 5 km from Chinyamwezi which is about 12 km from the mainland. The water separating Chinyankwazi from other land is at least 76 m deep. The shallows at Chinyankwazi are dominated by slabs and boulders, but from about 5 m depth smaller broken rocks occur and from 7–10 m small-medium rocks become abundant, though in places, such as the eastern side of the island, slabs and boulders remain a feature of the topography. The shore shelves gradually to about 12 m, then more steeply (about 60° from the horizontal) into deeper water. The island is exposed to wave action and frequently to currents which are so strong at times that divers cannot swim up-current without the aid of ropes. These currents appeared to be wind-generated; they moved in the same direction as the prevailing winds and were particularly strong in the upper 5 m, though still noticeable at 25 m depth. At 40 m depth pockets of sand occur among the rocks, suggesting that the sandy plain is not much deeper than this, though it could not be seen from 40 m. The sediment layers covering the rocks appeared to be thin, presumably being carried away by currents.

Chinyamwezi is oval, about 30 m in length and 10 m in width at water level. Most rocks are medium-large with a few small rocks interspersed among them. The gradient is fairly steep; at about 100 m off-shore the depth was 43 m. This island is also subject to strong currents and wave action. At 43 m depth the sediment layer is negligible and there is no indication that the rocky zone is meeting the sandy plain.

#### Diving stations

One transect was laid on the north-western shore of each island. The entire shore of Chinyamwezi was explored and all but the south-eastern section of Chinyankwazi was studied.

**Chinyankwazi.** The transect at the 1-m contour was laid over slabs with few areas of broken rock in which fish could

find refuge. At 3 m, slabs and medium-sized rocks were encompassed by the transect markers. Medium-sized rocks predominated to 6 m depth, then a gradually shelving area of small and medium-sized rocks continued to 12 m. From 12 m to 40 m medium-sized and medium-large rocks predominated.

**Chinyamwezi.** The entire transect was laid over medium-sized and medium-large rocks.

#### The communities

The species assemblage at each island is unique, each possessing its own endemic species and colour forms. Seventeen species of Mbuna were recorded at the islands of which 10 are endemic, but only nine species are common to both (Table 19). Only six species have been described.

The Mbuna community at Chinyankwazi comprises 14

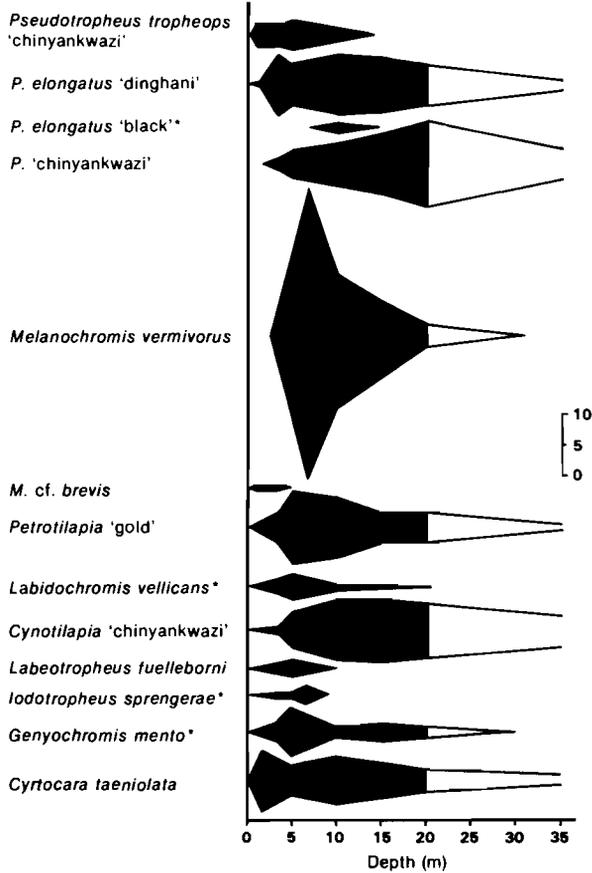
Table 19 The Mbuna found at Chinyankwazi and Chinyamwezi, (+) present, (–) absent and (\*) endemic to the area

Species	Transect stations	
	Chinyankwazi	Chinyamwezi
1. <i>Pseudotropheus tropheops</i> 'chinyankwazi'	*	+
2. <i>P. tropheops</i> 'chinyamwezi'	*	–
3. <i>P. elongatus</i> 'dinghani'	*	+
4. <i>P. elongatus</i> 'chinyamwezi'	*	–
5. <i>P. elongatus</i> 'black'	*	+
6. <i>P.</i> 'chinyankwazi'	*	–
7. <i>Melanochromis vermicorus</i>	+	–
8. <i>M.</i> 'chinyamwezi'	*	–
9. <i>M. crabro</i>	+	+
10. <i>M. cf. brevis</i>	+	+
11. <i>M.</i> 'brown'	*	+
12. <i>Petrotilapia</i> 'gold'	*	+
13. <i>Labidochromis vellicans</i>	+	–
14. <i>Cynotilapia</i> 'chinyankwazi'	*	+
15. <i>Labeotropheus fuelleborni</i>	+	+
16. <i>Iodotropheus sprengerae</i>	+	+
17. <i>Genyochromis mento</i>	+	+
Totals	10	12

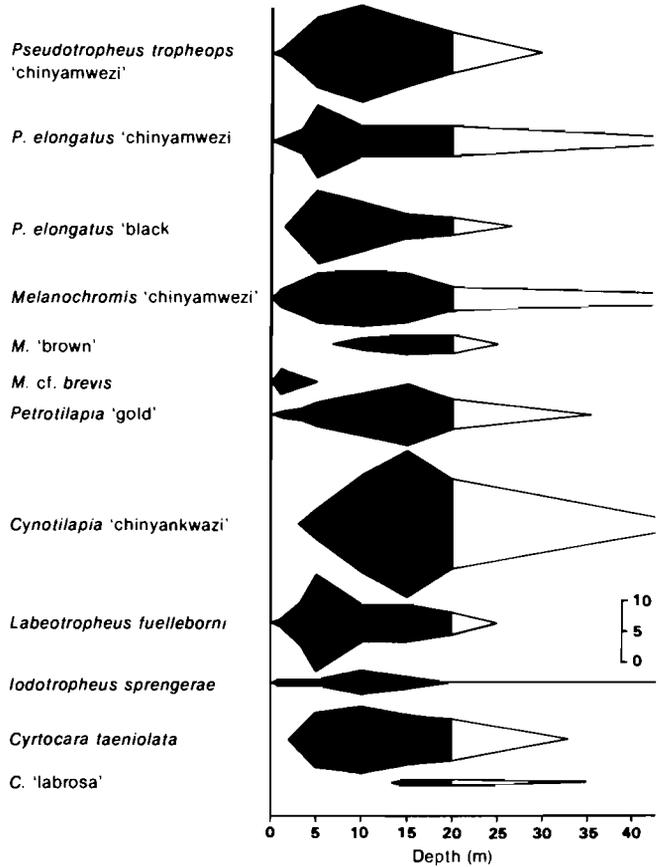
species of which 12 are recorded in the transect (Figure 33). Only *Melanochromis crabro* and a rare reddish-brown *Melanochromis* sp. were not in the transect. There are 12 Mbuna species at Chinyamwezi, 10 of which are recorded in the transect (Figure 34). Only *Genyochromis mento* (few) and *Melanochromis crabro* (1 seen) were not recorded in the transects, but are given in the summary of depth and

habitat preferences (Figure 35).

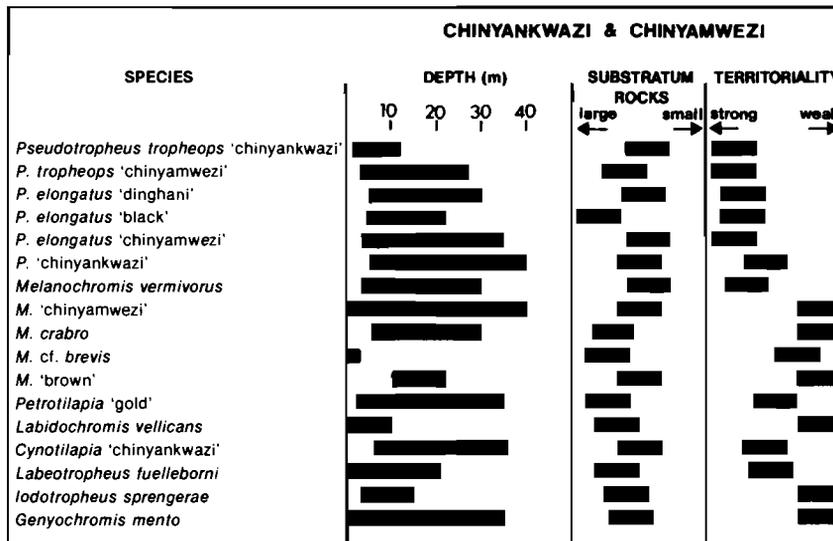
Although there are relatively few species found at each island, the number of individual fishes is high. The greatest number of individual cichlids and also the greatest number of Mbuna species occur in less than 10 m (Table 20). At Chinyamwezi the number of fishes per unit area was very high owing to the presence of large numbers of Utaka and schools of *Melanochromis* 'chinyamwezi'.



**Figure 33** The transect at Chinyankwazi Island 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<sup>-2</sup>.



**Figure 34** The transect at Chinyamwezi Island 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<sup>-2</sup>.



**Figure 35** A summary of resource utilization of the Mbuna communities at Chinyankwazi and Chinyamwezi Islands; all species from Chinyamwezi Island have the suffix 'Chinyamwezi'. For rest of legend see Figure 28 (p.254).

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**Table 20** The number of Mbuna species and the number of all cichlid individuals counted at different depths at Chinyankwazi and Chinyamwezi. Dashes indicate depths at which counts of individuals were not made

	Depth (m)									
	1	3	5	10	15	20	25	30	35	40
<b>Chinyankwazi</b>										
No. Mbuna species	9	11	10	9	7	6	6	4	4	4
No. individuals										
all cichlids in 50 m <sup>2</sup>	122	546	441	483	548	539	–	–	–	–
No. individuals m <sup>-2</sup>	2,4	10,9	8,8	9,7	10,9	10,8	–	–	–	–
<b>Chinyamwezi</b>										
No. Mbuna species	7	8	9	9	9	9	6	5	4	4
No. individuals										
all cichlids in 50 m <sup>2</sup>	ca1200	ca900	570	510	570	630	–	–	–	–
No. individuals m <sup>-2</sup>	ca 24	ca 18	11,4	10,2	11,4	12,6	–	–	–	–

At Chinyankwazi, however, the extreme shallows are characterized by slabs which do not provide refuges for Mbuna and are therefore tenanted by few fishes. Feeding fishes, particularly juvenile *Labeotropheus fuelleborni*, *Pseudotropheus tropheops* 'chinyankwazi', *P. elongatus* 'dinghani' and *Cyrtocara taeniolata*, do frequent the open rocks and were estimated to number 12–14 individuals m<sup>-2</sup> at times, but most of these fishes fled from the exposed regions when approached by divers who were counting fishes; therefore the number of fishes recorded at 1 m depth is low.

A striking feature of the Mbuna community at Chinyankwazi is the high numerical abundance of territorial and especially non-territorial *Pseudotropheus* 'chinyankwazi', *P. elongatus* 'dinghani', *Petrotilapia* 'gold', *Cynotilapia* 'chinyankwazi' and particularly *Melanochromis vermivorus*. Indeed, the number of *M. vermivorus* at Chinyankwazi per unit area is much greater than that at any of the other study areas and concomitantly there is an apparent increase in territorial aggressiveness (see p.203). At Chinyankwazi, where *M. vermivorus* is the most numerous Mbuna species, males are involved in intense, highly active defence of territories and intraspecific interactions are frequent.

At Chinyamwezi Island, large schools of non-territorial *Melanochromis* 'chinyamwezi' were perpetually around divers and frequently nipped at exposed skin and at spots on the diving suits. The presence of these schools led to the impression, which might be correct, that this is the most numerous Mbuna species at the island. *Pseudotropheus tropheops* 'chinyamwezi', *P. elongatus* 'chinyamwezi' and *Cynotilapia* 'chinyankwazi' were also numerous, particularly the non-territorial individuals.

Chinyankwazi and Chinyamwezi are unusual in that not a single member of the *Pseudotropheus zebra* species-complex inhabits them.

Of the non-Mbuna, the Utaka make the largest numerical contribution to the communities at Chinyankwazi and Chinyamwezi. In addition to the Utaka, the following piscivorous species occur at both islands:

*Aristochromis christyi* was more numerous at Chinyankwazi than at any other site studied. *Cyrtocara kiwinge* is the most common piscivore at both islands. The three ambush

predators, *Cyrtocara linni*, *C. polystigma* and *C. livingstonii* are also present, the last two occurring there in a purely rocky habitat which is vastly different from the intermediate habitat with which they are normally associated. Other piscivores recorded are *Cyrtocara woodi*, *C. spilorhyncha*, *Docimodus evelynae*, *Serranochromis robustus*, and at least three species of *Rhamphochromis*.

*Cyrtocara taeniolata* is the most common benthic feeder after the Mbuna. It occupies a relatively wide depth range living from the surface to 35 m, but it is most numerous between 3 and 15 m (Figures 33 & 34). Of the large-lipped species, *C. euchila* is uncommon, but *C. 'labrosa'* is common between 15 and 25 m.

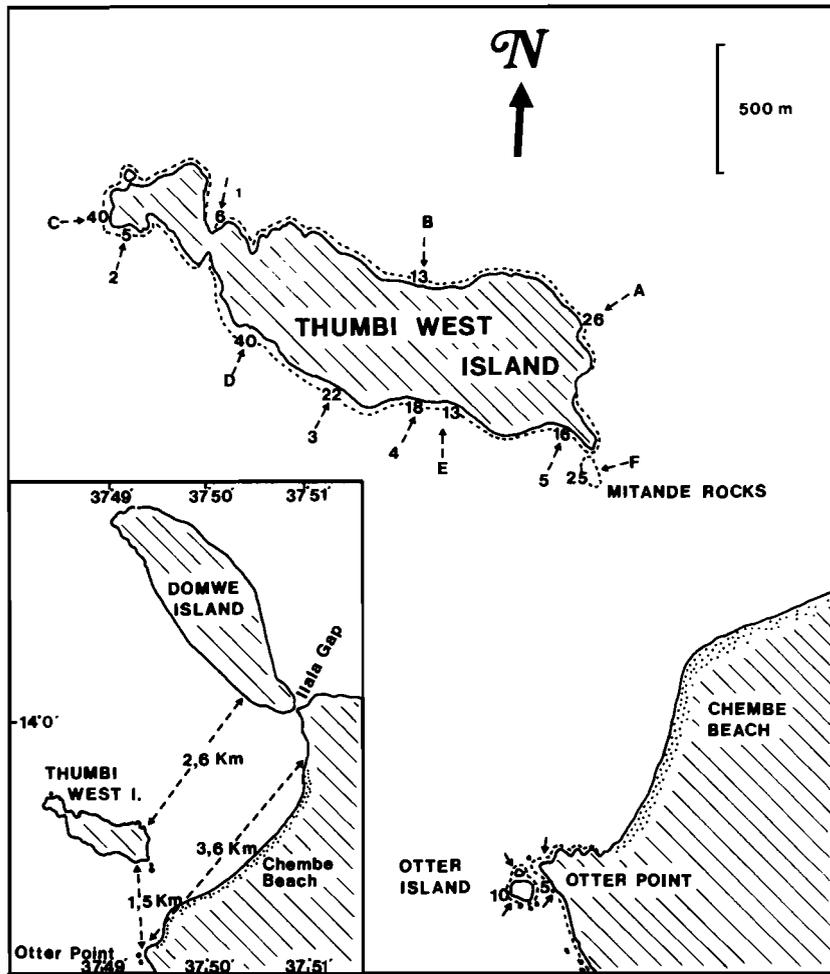
Many other non-Mbuna cichlids were seen among the rocks but not identified.

#### Area 4: Thumbi West and Otter Point

Otter Point, its associated islets, and the island of Thumbi West are the principal foci of the newly declared Lake Malawi National Park. In addition to its primary objectives this study provides information required for a guide to the fishes of the park. Thumbi West is thickly forested. Its shoreline is rocky apart from two tiny sand/weed areas. The rocks at Thumbi West are variable in size and the sand-rock interface occurs from the shallows to about 40 m deep. Otter Point is characterized by large rocks and boulders set in water that is less than 10 m deep. A coarse sandy grit, covered by a thin sediment layer separates the rocky zones at Otter Point. Macrophytes occur in the shallow sandy areas among the rocks.

The mainland rocky shore at the Ilala Gap is separated from the rocks of Otter Point by 3,6 km of sandy beach (Figure 36). Thumbi West is 1,5 km from Otter Point and 2,6 km from Domwe Island. As far as is known the bottom which separates the rocky shores of these areas is entirely sandy. The maximum depth of water between Mitande Rocks and Chembe Beach is at least 40 m; elsewhere the water separating Thumbi West from other nearby land areas is deeper than this.

The fishes were studied at 11 diving stations at Thumbi West and line transects were laid at six of these (Figure 36). At Otter Point the fishes were studied at four stations.



**Figure 36** The diving stations at Otter Point and Thumbi West Island are indicated by arrows. Letters A – F show the positions of transect sites. Numerals 1 – 5 identify the other diving stations at Thumbi West. The dotted lines indicate the extent of the rocky shore and the numerals within these lines give the depth at which rocks meet the sandy plain. Sandy beaches are stippled.

#### Diving stations

**Site A.** In the shallows, the shore shelves steeply and comprises rounded, medium-sized rocks which are covered by a thick green mat of Aufwuchs. The middle depths are characterized by large rocks and small sediment-covered slabs. From 18 m the bottom begins to shelf more gradually and rocky regions are interspersed with small sand patches. Between 21 and 26 m, small to medium-sized rocks and sand are mixed and at 26 m rocks give way to sand. The shallow area immediately south of the transect site is characterized by slabs and also contains a sandy patch in which submerged macrophytes grow. The area to the north-west is composed of prominent boulders rising out of a bed of medium-sized rocks. A few small slabs are also present.

**Sites B and 1.** In the extreme shallows medium-sized rocks predominate. From 1,5 to 5 m depth the bottom shelves gradually and is dominated by a mixture of small and medium-sized rocks. At about 5 m the incline becomes steeper and rocks are medium-sized. A few slabs and small pockets of sand occur between 3 and 10 m. Sand pockets are interspersed more commonly among the rocks beyond 10 m and at 14 – 16 m the rocky shore terminates. The rocks of the areas flanking the transect site are similar to those within it though several scattered clusters of boulders rise above the rocky floor. Diving station 1 is in a shallow bay in which intermediate habitats predominate.

**Sites C and 2.** At the western-most tip of Thumbi West the

rocks descend steeply to at least 40 m. The topography here is varied. In the extreme shallows a mixture of small and medium-sized rocks predominates, but a few scattered groups of large rocks occur. At 3 m a bed of closely packed small rocks slopes gradually into deeper water. The rocks are larger at 5 m and continue to increase in size as depth increases. By 10 m the bottom slopes steeply downwards and is dominated by large rocks and boulders. Rocks are medium-sized at 15 – 20 m, but large rocks and boulders predominate in deeper water. Diving station 2 is sheltered from winds and wave-action and although it is shallow, sediment accumulates. The intermediate rock-sand bottom shelves gradually from the shore-line, but is traversed by large rocky ridges which run parallel to the axis of the island.

**Site D.** The rocks of the extreme shallows are medium-sized, but from 3 to 40 m where rocks give way to sand, a mixture of slabs, boulders, medium-sized rocks and occasional pockets of small rocks and sand occur.

**Sites E, 3, 4 and 5.** Eastwards from transect station D the rocky shore becomes shallower and is dominated by medium-sized and small rocks. At the transect station the rocky shore shelves gradually giving way to sand at 12 m. The extreme shallows are composed of medium-sized rocks. Small, rounded, closely packed rocks predominate between 3 and 7 m. Thereafter medium-sized, angular rocks continue to the sand-rock interface.

**Table 21** The distribution of Mbuna at Thumbi West and Otter Point indicating those species which were introduced. Present (+), absent (–), if uncertain whether a species was introduced (?). Species believed to be endemic to the area (\*)

Species	Introduced	Thumbi West stations						Otter Point	
		A	B+1	C+2	D	E+3,4,5	F		
1. <i>Pseudotropheus zebra</i>	–	+	+	+	+	+	+	+	
2. <i>P. zebra</i> 'cobalt'	+	+	+	+	+	+	+	–	
3. <i>P. zebra</i> 'fusco'	?	–	–	–	–	+	–	–	
4. <i>P. cf. heteropictus</i> *	–	+	+	+	+	+	+	–	
5. <i>P. aurora</i>	+	+	+	–	–	+	–	+	
6. <i>P. livingstonii</i>	–	+	–	+	–	+	–	+	
7. <i>P. livingstonii</i> 'likoma'	+	–	–	–	–	+	–	–	
8. <i>P. tropheops</i> 'lilac' *	–	+	+	+	+	+	+	+	
9. <i>P. tropheops</i> 'orange chest'	–	+	+	+	+	+	+	+	
10. <i>P. tropheops</i> 'red cheek'	?	–	+	+	+	+	+	+	
11. <i>P. cf. gracilior</i>	–	+	+	+	+	+	+	+	
12. <i>P. tropheops</i> 'intermediate' *	–	+	+	+	+	+	+	–	
13. <i>P. tropheops</i> 'broad mouth'	–	–	–	+	+	–	–	+	
14. <i>P. cf. microstoma</i>	–	–	–	–	–	–	–	+	
15. <i>P. tropheops</i> 'gold otter'	?	–	–	–	–	–	–	+	
16. <i>P. elongatus</i> 'slab'	–	+	+	+	+	+	+	–	
17. <i>P. elongatus</i> 'yellow tail'	–	–	–	+	+	–	–	–	
18. <i>P. elongatus</i> 'aggressive'	–	+	+	+	+	–	+	–	
19. <i>P.</i> 'aggressive brown' *	–	–	–	+	+	+	+	–	
20. <i>P.</i> 'aggressive blue'	–	–	+	+	+	+	–	–	
21. <i>P.</i> 'tiny' *	–	–	+	+	+	+	+	–	
22. <i>P. socolofi</i>	?	–	–	–	–	+	–	+	
23. <i>Melanochromis melanopterus</i>	–	–	–	+	–	+	–	–	
24. <i>M. cf. chipokae</i>	–	+	+	+	+	+	+	–	
25. <i>M. auratus</i>	–	+	+	+	+	+	+	+	
26. <i>M. vermivorus</i>	–	+	+	+	+	+	+	–	
27. <i>M. parallelus</i>	+	–	–	+	–	–	+	–	
28. <i>M.</i> 'red'	+	–	–	–	–	+	+	–	
29. <i>M.</i> 'black-white johanni'	+	–	+	–	–	+	–	+	
30. <i>M. joanjohnsonae</i>	+	+	+	+	+	+	+	–	
31. <i>Petrotilapia tridentiger</i>	–	–	–	–	–	–	–	+	
32. <i>P. genalutea</i>	–	+	+	+	+	+	+	–	
33. <i>P. nigra</i>	–	+	+	+	+	+	+	+	
34. <i>P.</i> 'mumbo blue'	–	+	+	+	+	+	+	–	
35. <i>Labidochromis vellicans</i>	–	+	+	+	+	+	+	+	
36. <i>L. pallidus</i>	?	+	+	+	+	+	+	+	
37. <i>L.</i> 'blue bar'	?	–	–	–	–	–	+	–	
38. <i>L. gigas</i>	+	–	+	–	–	–	+	+	
39. <i>L. strigatus</i>	+	–	–	–	–	+	–	–	
40. <i>L. freibergi</i>	+	–	–	–	–	+	–	–	
41. <i>Cynotilapia afra</i>	+	–	–	–	–	–	+	–	
42. <i>Labeotropheus fuelleborni</i>	–	+	+	+	+	+	+	+	
43. <i>L. fuelleborni</i> 'yellow-flank'	+	–	–	–	–	–	+	–	
44. <i>L. trewavasae</i>	–	+	+	+	+	+	+	+	
45. <i>Cyathochromis obliquidens</i>	–	+	–	+	–	+	–	+	
46. <i>Genyochromis mento</i>	–	+	+	+	+	+	+	+	
Totals	5	12(+), 6(?)	24	27	32	27	35	30	22

**Site F.** This transect was laid westwards from the apex of Mitande Rocks down to the sand base surrounding the rocky outcrop at 25 m depth. The peak of Mitande Rocks

was 1–2 m below the surface during 1979/1980. This area is characterized by slabs, boulders and large rocks, interspersed with areas of broken medium-sized rocks. Small

rocks are rare. Occasional pockets of sand occur below 10 m.

#### The communities

Forty-six species of Mbuna and one introduced colour form (*Labeotropheus fuelleborni* 'yellow flank') were found in this study area; 44 of these species occur at Thumbi West, 22 are at Otter Point and there are 19 species which occur at both localities (Table 21).

*Pseudotropheus cf. microstoma*, *P. tropheops* 'gold otter' and *Petrotilapia tridentiger* are the only species present at Otter Point which are absent from Thumbi West. In addition to the introduced colour form, 18 species are believed to have been introduced into this area (Table 21) during 1972–1974 by an exporter of aquarium fishes. Twenty-four species of this area are undescribed.

Thirty-four species are essentially lithophilous, 10 occur mainly in intermediate habitats and two are sand-dwellers (Figure 43).

The total number of species found at each diving station is given by Table 21. The discrepancy between the number of species found at diving stations and recorded in the transects is accounted for by the fact that the area studied at each diving station is large relative to that covered by the transect. This means that fishes in habitats which were not traversed by the transect could be missed. Similarly, rare

and uncommon species might not be present in the transect during the study period. At Thumbi West, therefore, fishes of the shallow intermediate habitats such as *Cyathochromis obliquidens*, *Pseudotropheus aurora* and *P. tropheops* 'broad mouth' as well as rare or uncommon species, such as some of the introduced species (e.g. *Labidochromis strigatus*, *L. freibergi*, *L. gigas*, *Pseudotropheus livingstonii* 'likoma', *Melanochromis* 'black-white johanni' were either absent from the transects or so poorly represented in them that they were not included in the figures. Similarly, *P. livingstonii* and other endemic species which are rare on the rocky shore were not found in any transect.

The numerical density and the depth distribution of the fishes recorded in the transects are presented in Figures 37–42. The number of Mbuna species and the number of individual cichlids is greatest in the shallows (Table 22). Indeed, at station D, six times as many species were recorded in the shallows as at 40 m. At all stations the number of species and individuals was greatest at 3 m, except at station D where a shoal of non-territorial *P. zebra* entered the transect.

Stations A, C and F supported a significantly ( $P < .001$ ) greater population density in the 1–5 m zone than stations B, D and E. As stations A, C and F are more exposed than the other stations (Figure 36), they are subject to wave action and currents, reduced sediment, clearer water and are

**Table 22** The number of Mbuna species found at the diving stations A–F and the number of individual cichlids of all species counted at different depths in the transects at Thumbi West. Dashes indicate depths at which counts of individuals were not made

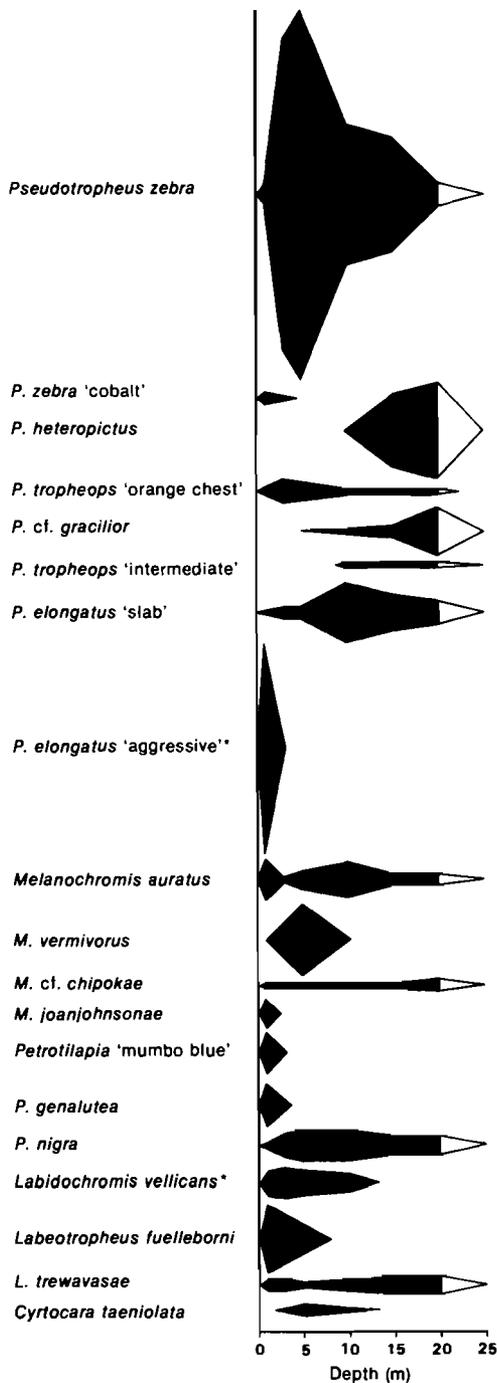
	Depth (m)									
	1	3	5	10	15	20	25	30	35	40
<b>Station A</b>										
No. Mbuna species	20	21	16	14	12	12	11			
No. individuals, all cichlids	467	518	333	251	210	168	–			
No. individuals m <sup>-2</sup>	9,3	10,4	6,7	5,0	4,2	3,4	–			
<b>Station B</b>										
No. Mbuna species	17	23	20	20	9					
No. individuals, all cichlids	290	310	270	120	155					
No. individuals m <sup>-2</sup>	5,8	6,2	5,4	2,4	3,1					
<b>Station C</b>										
No. Mbuna species	22	16	17	14	12	10	10	7	7	5
No. individuals	260	480	253	166	170	230	–	–	–	–
No. individuals m <sup>-2</sup>	5,2	9,6	5,6	3,3	3,4	4,6	–	–	–	–
<b>Station D</b>										
No. Mbuna species	19	25	21	14	11	11	10	8	4	4
No. individuals all cichlids	270	292	288	308	171	158	–	–	–	–
No. individuals m <sup>-2</sup>	5,4	5,8	5,8	6,2	3,4	3,2	–	–	–	–
<b>Station E</b>										
No. Mbuna species	19	23	20	14						
No. individuals all cichlids	367	384	292	201						
No. individuals m <sup>-2</sup>	7,3	7,7	5,8	4,0						
<b>Station F</b>										
No. Mbuna species	27	29	21	18	15	15	8			
No. individuals all cichlids	405	520	434	370	244	220	–			
No. individuals m <sup>-2</sup>	8,1	10,4	8,5	6,4	4,9	4,4	–			

likely to have a more rapid replenishment of current-borne nutrients. These factors are likely to promote primary productivity. We believe that the greater abundance of fishes at those exposed sites reflects a greater primary productivity.

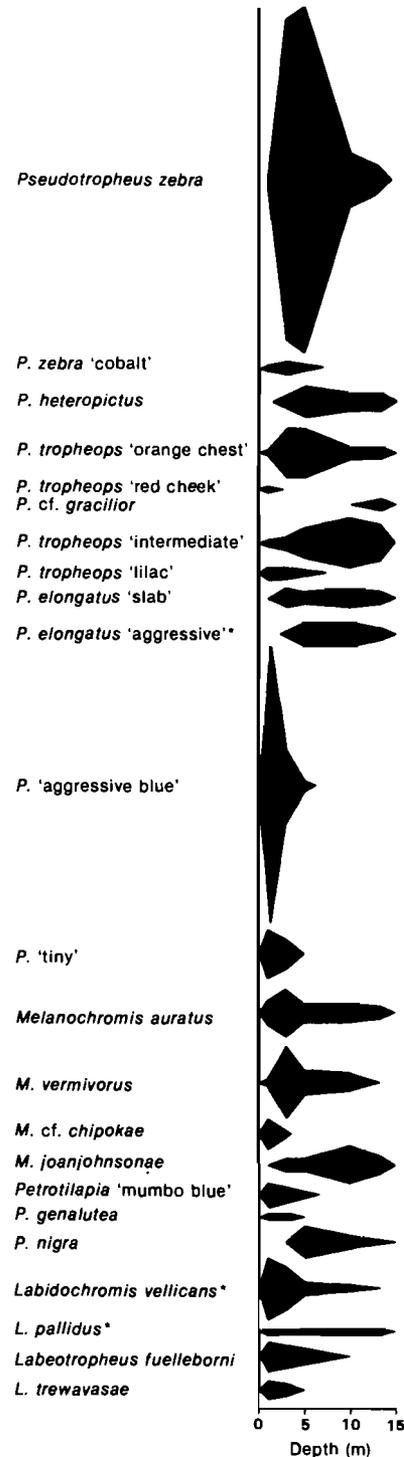
More species of Mbuna occur naturally at Thumbi West than any of the rocky shores closest to it (Table 21), and if the introduced species are included in the list then the species richness at Thumbi West is impressive. Only five of the species at Thumbi West are endemic.

The majority of the species which were introduced to Thumbi West were still restricted to small parts of the island in 1980 despite the four and a half to eight years which had elapsed since they were first released at the island.

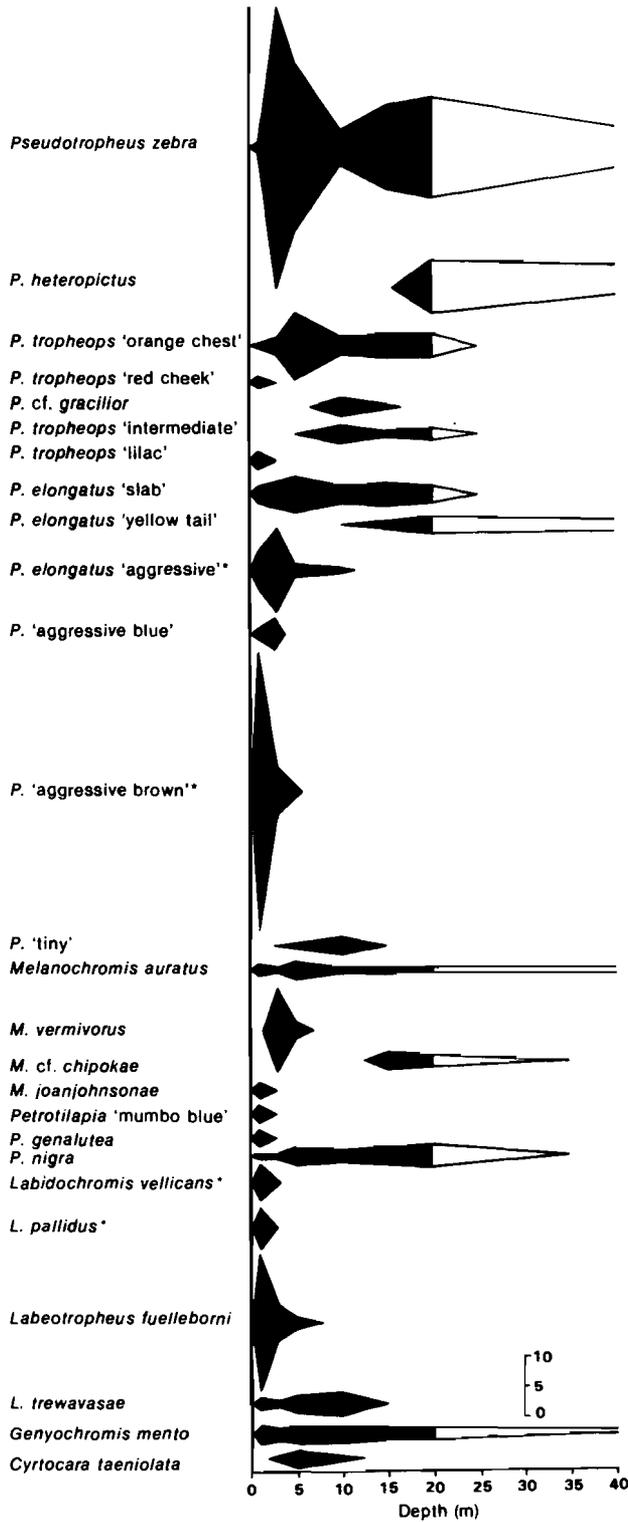
Most *Pseudotropheus zebra* 'cobalt' occur between stations 3 and 5 where they were probably released. This species is relatively poorly represented at other sites (Figures 37 to 42). Similarly *Pseudotropheus livingstonii* 'likoma', *P. socolofi*, *Melanochromis parallelus*, *M.* 'red', *M.* 'black-white johanni', *Labidochromis gigas* *L. strigatus*, *L. freibergeri* and the yellow-flanked form of *Labeotropheus fuelleborni* are all concentrated around sites E and F which is the area in which these species were released. Only *Pseudotropheus aurora* and *Melanochromis joanjohnsonae* are found all round the island. *P. aurora* appears to have



**Figure 37** Transect A at Thumbi West Island, 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<sup>-2</sup>



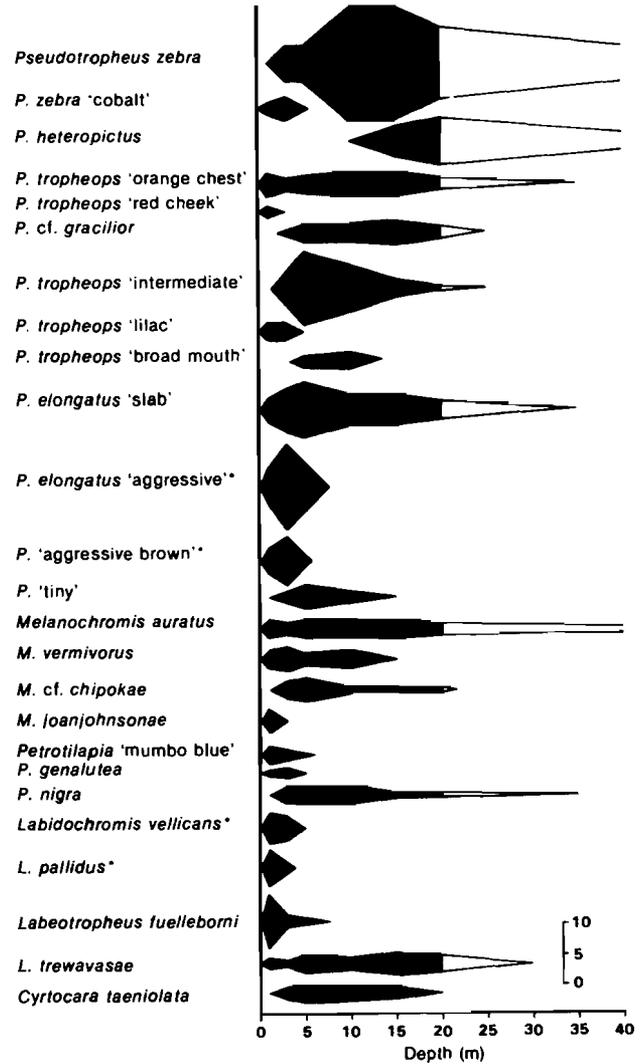
**Figure 38** Transect B at Thumbi West Island, giving the depth distribution and numerical abundance of the Mbuna species. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.



**Figure 39** Transect C at Thumbi West Island, 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<sup>-2</sup>.

followed the sand-rock intermediate zone around Thumbi West though it also occurs in purely rocky regions. *P. aurora* is absent from stations D and F where the habitat appears unsuitable. *M. joanjohnsonae* has spread around the island in the 0–4 m depth zone.

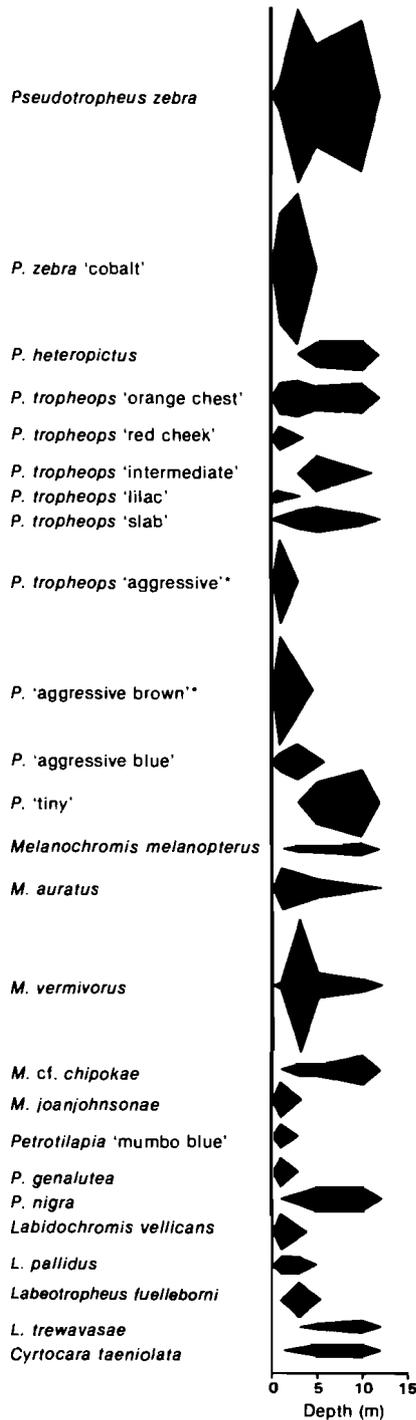
The sedentary nature of Mbuna is also demonstrated by some of the indigenous species. For example, *Labeotropheus trewavasae* is well represented at all rocky



**Figure 40** Transect D at Thumbi West Island, 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<sup>-2</sup>.

shores of Thumbi West but the orange morph which comprises about 25% of the females at Mitande Rocks is rare at stations E and 5 and absent elsewhere. Similarly, the pinkish-yellow morph of *Pseudotropheus zebra*, which is common at Mitande Rocks is absent elsewhere. Males of *P. zebra* at the mainland rocks of Otter Point have different head markings from those of Otter Island, not 50 m away.

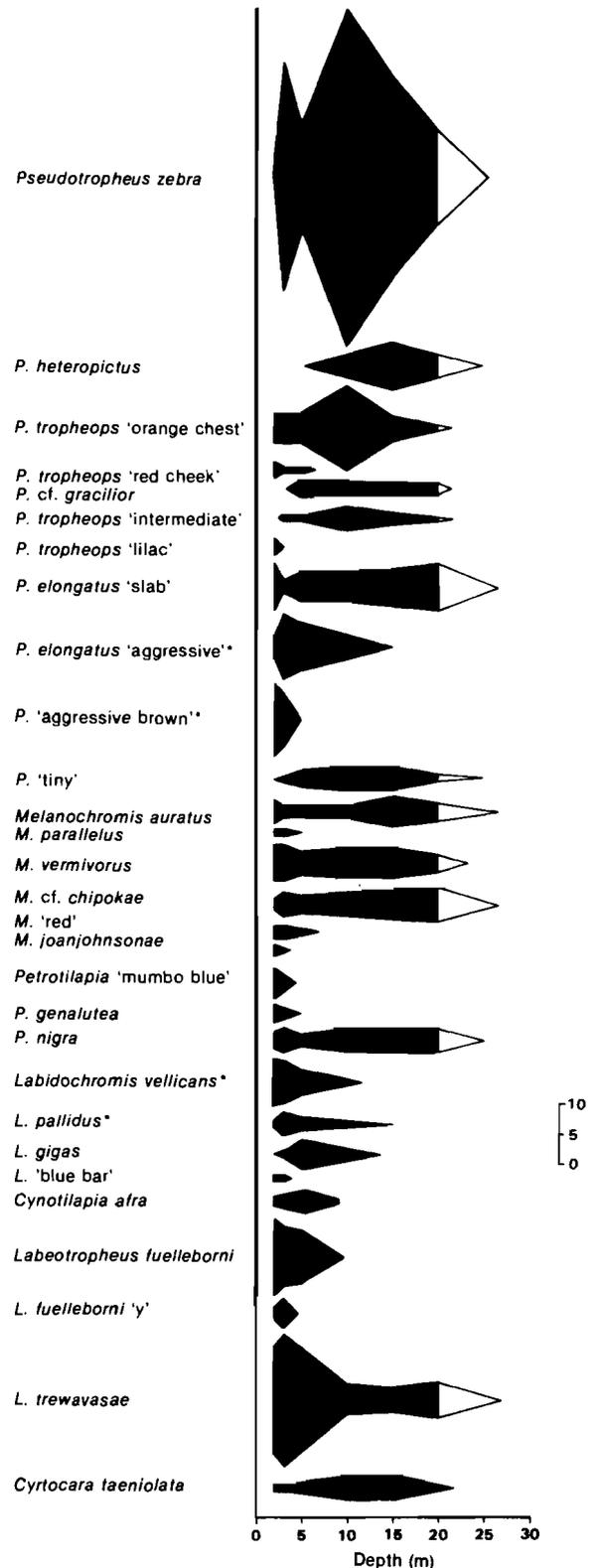
A summary of the depth distribution, habitat preference and degree of territoriality of the Mbuna of Thumbi West is given in Figure 43. Very few species appear to have identical habitat preferences, but since our survey was performed superficially, further studies of the ecological interrelationships are required to establish the extent of resource partitioning among the Mbuna of Thumbi West. The ecological summary and the transect data focus mainly on territorial fishes, but non-territorial individuals are usually more numerous in the community. The non-territorial individuals of most species are solitary or occur in small groups, usually feeding from those rocks which are not guarded by territorial fishes. *Pseudotropheus zebra* and *Melanochromis vermivorus*, however, form large schools which feed upon the plankton in the water column. Both of these species are found at every station around Thumbi West, but *M. ver-*



**Figure 41** Transect E at Thumbi West Island, 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<sup>-2</sup>.

*mivorus* is particularly numerous at Mitande Rocks. *Pseudotropheus elongatus* 'slab' forms feeding schools over the upper surfaces of slabs and boulders and in the extreme shallows the schools may mix with juveniles of *Labeotropheus* spp. and *Pseudotropheus tropheops* 'orange chest'. *Labeotropheus trewasasae* is usually not as numerous as *L. fueleborni* in the shallows, but at Mitande Rocks it is more numerous (Figure 42).

In addition to the Mbuna, many other cichlids inhabit the rocky and intermediate zones of this area. Some of the more common species which feed from the substratum are: *Astatotilapia calliptera*, *Cyrtocara picta*, *C. fenestrata*, *C.*



**Figure 42** Transect F at Thumbi West Island, 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<sup>-2</sup>.

'labrosa', *C. taeniolata*, *C. intermedia*, *C. euchila*, *C. rostrata*, *C. 'pink dorsal'*, *C. kirkii*, *C. johnstonii*, *Hemitilapia oxyrhynchus*, *Trematocranus jacobfreibergi*, *Aulonocara 'yellow collar'*, *A. 'blue collar'*. All of these species are of importance to the aquarium trade, but *Trematocranus jacobfreibergi* is particularly important in this region as almost 90% of individuals caught for export

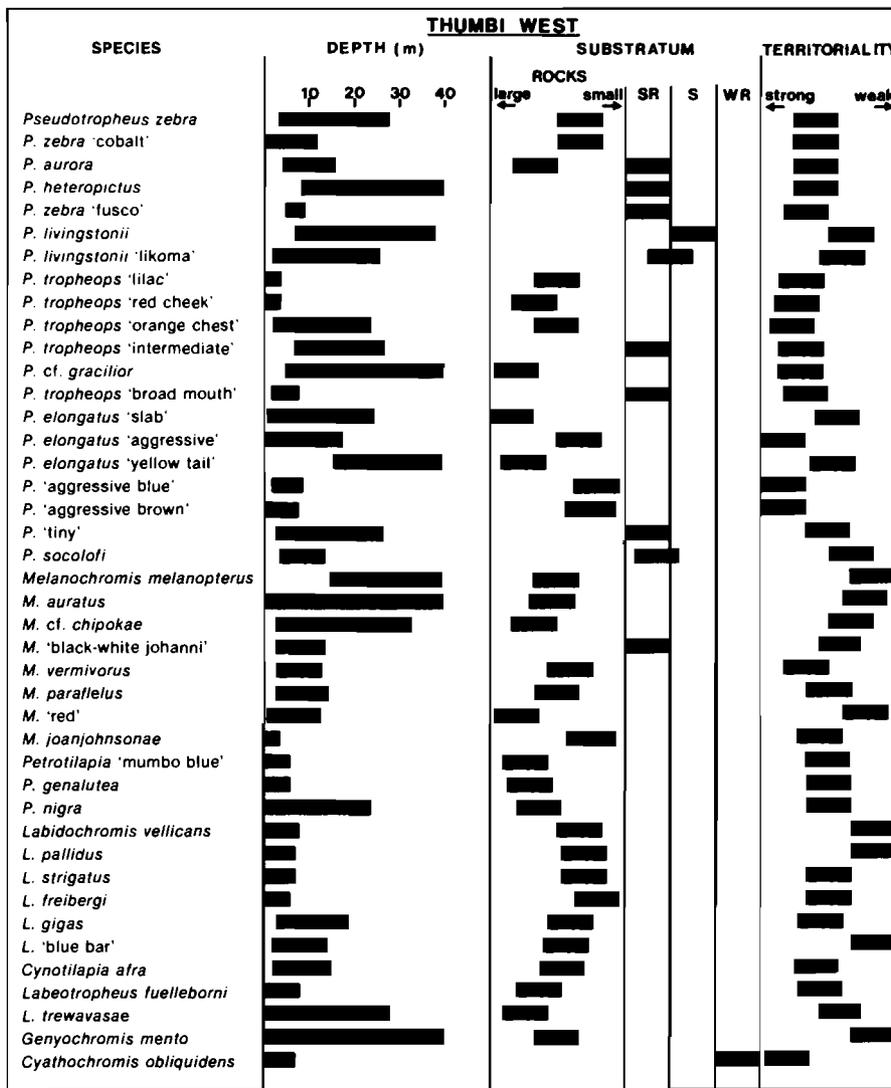


Figure 43 A summary of resource utilization of the Mbuna community at Thumbi West Island. For rest of legend see Figure 28 (p.254).

come from the intermediate habitats of Otter Point. *Cyrtocara* 'pink-dorsal' is common along the sand-rock interface of Thumbi West; it is apparently endemic to the island and is sold in large numbers. The most common non-Mbuna of the rocky shores is *Cyrtocara taeniolata*, the numerical abundance of which is depicted in Figures 36 & 38 – 42.

Piscivorous species found in this study area are *Aristochromis christyi*, *Cyrtocara compressiceps*, *C. fuscotaeniata*, *C. kiwinge*, *C. linni*, *C. livingstonii*, *C. macrostoma*, *C. polystigma*, *C. spilorrhyncha*, *C. woodi*, *Docimodus evelynae*, *Serranochromis robustus* and at least three species of *Rhamphochromis*. *C. linni* and *D. evelynae* are more numerous at Thumbi West than at any other area studied. The most northerly record of *C. fuscotaeniata* is at Otter Point where this species is uncommon.

Several species of Utaka also frequent the rocky shores. Those identified are *Cyrtocara chrysonota*, *C. quadrimaculata* and, at Otter Point, *C. inornata* and *C. eucinostomus*.

Area 5: Mumbo Island

Mumbo Island is a wooded forest reserve within the Lake Malawi National Park. It lies between the Maleri Islands and Thumbi West Island (Figure 44). The water which separates Mumbo Island from other islands is at least 100 m deep. The island itself is little more than 600 m long and

about 400 m wide. Its shore is entirely rocky except for a small beach at the southerly inlet and another in North Bay. Within the shallows of these small bays are beds of *Vallisneria aethiopica*. The rocks are of rough granite which weathers to form a coarse gravel which lies at the sand-rock interface. Large rocks characterize Mumbo Island, though smaller rocks do occur. The shore shelves steeply into deep water except in the vicinity of the beaches.

Diving stations

The fishes at Mumbo Island were studied at four diving stations (sites A – D; Figure 44). Point transects were conducted at stations A and B.

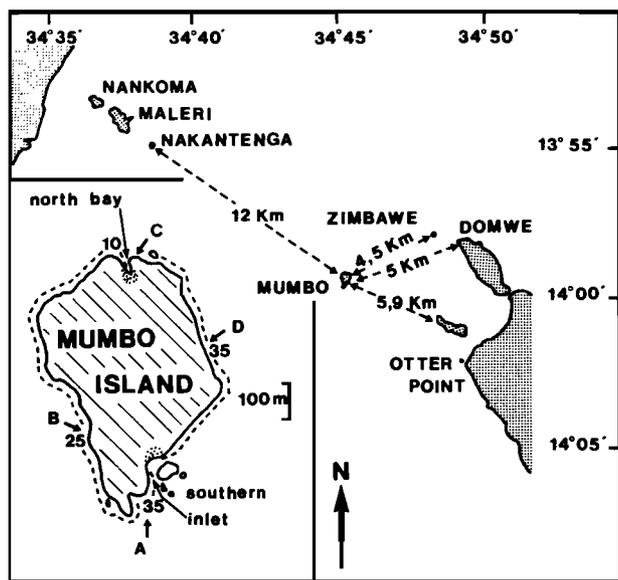
*Station A.* At the mouth of the southerly inlet the rocks shelf very rapidly, sometimes almost vertically, to 35 m. The area is dominated by boulders and slabs, some of which are so large that they form walls of rock many metres in area. A point transect was conducted on the western arm of the inlet.

*Station B.* A second point transect was conducted at site B which shelves gradually to about 5 m and then descends steeply to the sandy plain at 25 m. This site is composed of large rocks and boulders.

*Station C.* At the entrance to the northern bay, boulders

descend steeply to about 12 m. Within the bay, however, the sandy bottom becomes progressively shallower, eventually forming an exposed beach within the inlet.

**Station D.** The shore at this site shelves steeply to 35 m and has a higher proportion of medium-sized rocks than at other sites.



**Figure 44** Mumbo Island and its relation to the nearest rocky shores. In the inset of Mumbo Island the positions of the diving stations A – D are indicated by arrows. The dotted lines indicate the extent of the rocky shore and the numerals within these lines give the depth at which rocks meet the sandy plains. Sandy beaches are stippled.

*The community*

Twenty species of Mbuna occur at Mumbo Island, 16 of which were found at all four diving stations. Four species are endemic to the island (Table 23). Those species which are not endemic differ in coloration from their nearest conspecific neighbours although three species (*Melanochromis auratus*, *M. vermivorus* and *Cyathochromis obliquidens*) have identical coloration to their nearest conspecific neighbours.

A comparison of the fauna of different rocky shores (Table 23) shows that Mumbo Island shares more species of Mbuna with the Thumbi West, Monkey Bay, Domwe Island and Zimbabwe Island region than with the more distant rocky shores of the Maleri Islands. Indeed, all nine species which occur at Zimbabwe also occur at Mumbo Island. All species common to both Mumbo and Maleri Islands are widespread in the southern lake and four of these species (*Labeotropheus fuelleborni*, *L. trewavasae*, *Genyochromis mento* and *Cyathochromis obliquidens*) have an almost lake-wide distribution. Thus the fishes shared by Mumbo and the Maleri Islands are those most likely to be found widely on rocky shores of the southern lake. At Nakantenga Island, which is the closest of the three Maleri Islands to Mumbo Island (Figure 44), and at Mumbo Island

**Table 23** The distribution of Mbuna species at diving stations A – D around Mumbo Island and at neighbour- ing rocky shores. Present (+), absent (–), endemic to Mumbo Island (\*)

Species	Mumbo Island diving stations				Other areas			
	A	B	C	D	Thumbi West I.	Zimbabwe I.	Domwe I. Nankumba	Maleri Islands
1. <i>Pseudotropheus zebra</i>	+	+	+	+	+	+	+	–
2. <i>P. zebra</i> 'mumbo' *	–	+	+	–	–	–	–	–
3. <i>P. tropheops</i> 'lilac mumbo' *	+	+	+	+	–	–	–	–
4. <i>P. elongatus</i> 'aggressive'	+	+	+	+	+	+	+	–
5. <i>P. elongatus</i> 'yellow tail'	+	+	+	+	+	+	+	–
6. <i>P. elongatus</i> 'slab'	+	+	+	+	+	–	–	–
7. <i>Melanochromis melanopterus</i>	+	+	+	+	+	+	+	–
8. <i>M. cf. chipokae</i>	–	+	–	–	+	–	–	–
9. <i>M. vermivorus</i>	+	+	+	+	+	+	+	+
10. <i>M. auratus</i>	+	+	+	+	+	–	+	+
11. <i>M. cf. brevis</i>	+	+	–	–	–	–	+	+
12. <i>Petrotilapia</i> 'mumbo blue'	+	+	+	+	+	–	–	–
13. <i>P.</i> 'mumbo yellow' *	+	+	+	+	–	–	–	–
14. <i>P. genalutea</i>	+	+	+	+	+	–	+	+
15. <i>Labidochromis mylodon</i> *	+	+	+	+	–	–	–	–
16. <i>L. vellicans</i>	+	+	+	+	+	+	+	+
17. <i>Labeotropheus fuelleborni</i>	+	+	+	+	+	+	+	+
18. <i>L. trewavasae</i>	+	+	+	+	+	+	–	+
19. <i>Genyochromis mento</i>	+	+	+	+	+	+	+	+
20. <i>Cyathochromis obliquidens</i>	+	–	+	–	+	–	+	+
Totals	18	19	18	16	15	9	12	8

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the populations of male *Labeotropheus trewavasae* have blue dorsal fins. This could indicate an affinity between the two populations.

The point transects (Figures 45 & 46) show that the greatest number of species inhabit the shallows. They also indicate that the most numerous species are *Pseudotropheus zebra*, *P. tropheops* 'lilac mumbo' and *Melanochromis vermivorus*. All species, however, are common in their preferred habitats with the exception of *Melanochromis cf. chipokae* and *M. cf. brevis* which are rare and uncommon respectively.

There are no important aquarium fishes among the non-Mbuna of Mumbo Island, though the piscivorous species *Cyrtocara kiwinge*, *C. linni*, *C. livingstonii*, *C. macrostoma* and *C. polystigma* are sometimes collected. Other species which occur at Mumbo Island are *Cyrtocara compressiceps*, *C. euchila*, *C. fenestrata*, *C. 'labrosa'*, *C. picta* and several Utaka species. In the beds of *Vallisneria aethiopica*, *Astatotilapia calliptera* is common. Over sand *Lethrinops praeorbitalis* was frequently seen, usually being followed by *Cyrtocara moori* and *C. annectens* which foraged in the feeding excavations made by *L. praeorbitalis*. Several species of *Rhamphochromis* were also seen.

No *Trematocranus* spp. nor *Aulonocara* spp. were recorded from Mumbo Island.

**Area 6: The Maleri Islands**

A cluster of three islands situated in the north-western part of the south-west arm of Lake Malawi are referred to col-

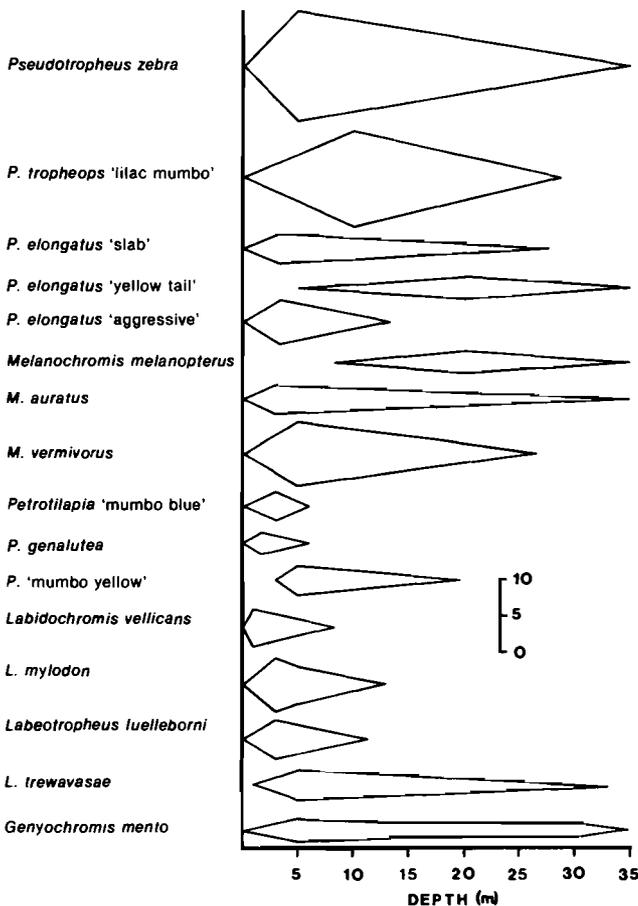
lectively as the Maleri Islands, but only the central, largest island actually bears this name. The island north-west of it is Nankoma and that to the south is Nakantenga (Figure 47). Nankoma is separated from Maleri Island by a channel approximately 520 m wide and no deeper than 18 m. Nakantenga is about 1 820 m from Maleri Island and the water between them is slightly deeper than 60 m.

All three islands are small. Maleri Island is 1 923 m in length and between 780 and 1 300 m wide. Nankoma is 1 090 m by 570 m and Nakantenga is approximately 415 m long and 155 m wide.

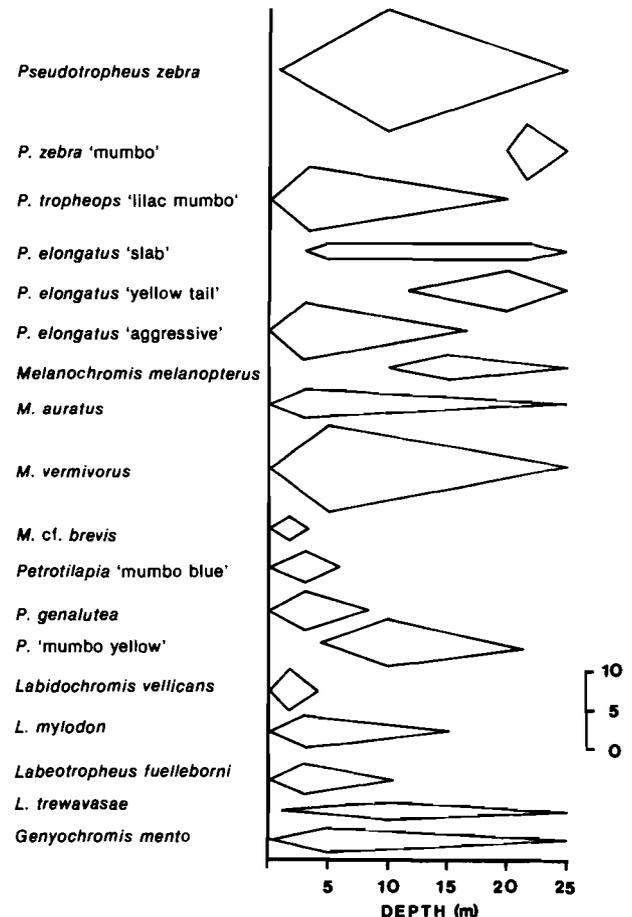
These islands are thickly covered by trees, shrubs and creepers. The vegetation extends to the water's edge and a number of trees and shrubs on the edge of the islands were drowned when the lake reached high levels during the wet seasons in 1978, 1979 and 1980. The rocky shore around the Maleri Islands meets the sandy bottom at depths ranging from 3 to 30 m. Most of the shore shelves steeply. An unusual feature of the Maleri Islands is that rocky areas deeper than 12 m are covered by a thin layer of firm mud on which Aufwuchs grows. When the Linthipe River on the nearby (5,5 km) mainland is in flood the Maleri Islands may be surrounded by muddy water and it is likely that the mud on the rocks comes from this source.

The Maleri Islands are well separated from the other rocky islands of Mumbo, Thumbi West, Zimbabwe and Domwe (Figure 44) as well as from Namalenje Island. Virtually all of the adjacent mainland coastline is sandy with very few, small, scattered rocky regions at Kambiri Point

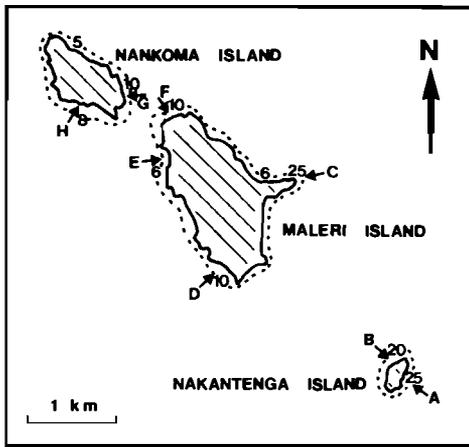
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**Figure 45** The point transect at station A, Mumbo Island, giving the depth distribution and an estimate of numerical abundance of Mbuna species. Estimated numerical abundance is expressed as the number of individual fishes in 50 m<sup>2</sup>.



**Figure 46** The point transect at station B, Mumbo Island, giving the depth distribution and an estimate of numerical abundance of Mbuna species. Estimated numerical abundance is expressed as the number of individual fishes in 50 m<sup>2</sup>.



**Figure 47** Diving stations (A – H) at the three Maleri Islands. The dotted lines indicate the extent of the rocky shore and the numerals within the lines give the depth at which rocks meet the sandy plain. The position of the Maleri Islands relative to other shores is given by Figures 1 and 44.

and Senga Point (Figure 52). Thus, the Maleri Islands are isolated from other rocky shores by large tracts of sand and open water.

#### Diving stations

The fishes of the Maleri Islands were studied at eight stations; two were at Nakantenga (A & B), four were at Maleri (C–F) and two were at Nankoma (G & H; Figure 47). At sites A to D medium-sized and medium-large rocks occur along the water's edge down to a depth of 2–3 m. Below this medium-sized and small rocks predominate, though at sites A & C groups of larger rocks occur between 4 and 8 m. At site B an intermediate zone of small rocks in sand occurs between 8 and 12 m. Stations E to F are in shallow, sheltered, sediment-rich areas. These sites are rocky to about 5 m, then of an intermediate nature until the sandy bottom is reached. The rocks at these stations are mainly small and medium-sized though scattered boulders and slabs are present. An unusual feature at site H is that smooth, rounded light-coloured pebbles cover the bottom of the extreme shallows to a depth of about 2 m. Line transects were laid at sites B, C and D.

#### The communities

There are 35 species of Mbuna at the Maleri Islands of which 34 occur at Maleri Island, 30 at Nankoma Island and 28 at Nakantenga Island (Table 24). Nankoma and Maleri Islands are close to one another and have the same species except that deep-water species such as *Pseudotropheus 'dumpy'*, *Melanochromis crabro* and *Cynotilapia 'maleri'* do not occur at Nankoma where the maximum depth of the rocky shore is 12 m. Seven species present at Maleri and Nankoma Islands are absent from Nakantenga Island which has one species which is not at the other two islands (*P. zebra* 'red dorsal' was probably introduced to Maleri Island see p.162).

Thirteen Mbuna species are endemic to the Maleri Islands (Table 24) and most of the species which also occur in other areas are uniquely coloured at the Maleri Islands. Indeed, even between Maleri Island and Nakantenga Island there are marked colour differences between certain populations. For example, male *Labeotropheus fuelleborni* at Maleri and

Nankoma Islands are powder-blue, but at Nakantenga they have a golden flush on their flanks; male *Labeotropheus trewavasae* are pale blue with orange dorsal fins at Maleri and Nankoma Islands, but they have blue dorsal fins at Nakantenga Island; male *Pseudotropheus zebra* 'black dorsal' have rusty-red cheeks at Maleri and Nankoma Islands, but blue cheeks at Nakantenga Island. Fifteen species recorded at the Maleri Islands also occur naturally at Thumbi West Island, though there is some doubt that *Labidochromis vellicans* of the Maleri Islands is conspecific with the Thumbi West population (Lewis pers. comm.). The Maleri Islands have 14 species in common with Mbenji Island and nine species in common with Mumbo Island. Some of these shared species, however, may not be conspecific as interpopulational differences in colour occur. Eleven species at the Maleri Islands have been described (Table 24).

Twenty-four of the 28 Mbuna species which occur at Nakantenga Island were recorded in the transect (Figure 48). Those species not included in the transect (*Pseudotropheus livingstonii*, *P. 'dumpy'*, *Melanochromis crabro* and *Genyochromis mento*) were uncommon at or absent from the transect site.

Twenty-two Mbuna species are recorded in the transect at station C (Figure 49). Although this is the only site at which we found *Cynotilapia 'maleri'*, this uncommon species was not sufficiently well represented in the transect (only two individuals were seen) to be depicted in the figure.

At station D, 21 Mbuna species are recorded in the transect (Figure 50). Those species not recorded in the transects are either absent from sites (Table 24), or occur in habitats not included in the transects, or they were so uncommon at the time that they were not included in the sample.

Sites E–H are shallow and lack the deep-water species (*Pseudotropheus 'dumpy'* and *Cynotilapia 'maleri'*), but have numerous fishes of the intermediate and sediment-rich habitats, including species such as *Pseudotropheus tropheops* 'broad mouth' and *Cyathochromis obliquidens*.

The majority of species and the greatest number of individuals occur in the shallows, though the extreme shallows have fewer species and individuals than found at 3 m (Table 25).

A summary of the preferred habitats and degree of territoriality is given by Figure 51. Ten species of Mbuna at the Maleri Islands inhabit intermediate or sandy zones, but *P. livingstonii* is the only species consistently found away from the rocks. *P. livingstonii* is also the only species associated with sand and intermediate zones which does not build sand-scrape nests. The summary indicates that, as a consequence of zonation and species-specific habitat preferences, partitioning of resources takes place. None of the sympatric members of the *Pseudotropheus zebra* species-complex have identical habitat requirements, but those of the allopatric *P. zebra* 'red dorsal' and *P. zebra* 'blue' do appear identical.

At the Maleri Islands no single Mbuna species has an overall numerical dominance. However, certain habitats are dominated by particular species: small rocks in the shallows are dominated by members of the *Pseudotropheus* 'aggressive' species-group; medium-sized rocks are dominated by the lithophilous members of the *P. zebra* species-complex and the *P. tropheops* species-complex; medium-large rocks contain numerous members of *Petrotilapia* spp. and

**Table 24** The distribution of Mbuna at the Maleri Islands indicating endemicity (\*) and also those species which the Maleri islands have in common with Mumbo Island, Thumbi West Island and Mbenje Island. Present (+); absent (-); introduced (i); *L. fuelleborni* blue form (b); *L. fuelleborni* yellow-flanked form (y); *L. trewavasae* orange dorsal (od); *L. trewavasae* blue dorsal (bd)

Species	Maleri Islands diving stations								Neighbouring areas				
	Nakantenga		Maleri				Nankoma		Mumbo	Thumbi			
	A	B	C	D	E	F	G	H		West	Mbenji		
1. <i>Pseudotropheus zebra</i> 'blue'	*	-	-	+	+	+	+	+	+	-	-	-	
2. <i>P. zebra</i> 'red dorsal'	*	+	+	-	i	-	-	-	-	-	-	-	
3. <i>P. zebra</i> 'yellow throat'	*	+	+	+	+	+	+	+	+	-	-	-	
4. <i>P. zebra</i> 'black dorsal'	*	+	+	+	+	+	+	+	+	-	-	-	
5. <i>P. zebra</i> 'fusco'		+	+	+	+	+	+	+	+	-	+	+	
6. <i>P. zebra</i> 'patricki'		-	-	-	-	+	+	+	-	-	-	+	
7. <i>P. livingstonii</i>		-	-	-	-	+	+	+	-	-	+	-	
8. <i>P. tropheops</i> 'lilac maleri'	*	+	+	+	+	+	+	+	+	-	-	-	
9. <i>P. tropheops</i> 'maleri blue'	*	+	+	+	-	+	-	+	-	-	-	-	
10. <i>P. tropheops</i> 'maleri yellow'	*	+	+	+	+	+	+	+	+	-	-	-	
11. <i>P. tropheops</i> 'orange chest'		+	+	+	+	+	+	+	+	-	+	-	
12. <i>P. tropheops</i> 'broad mouth'		-	-	-	-	+	+	+	-	-	+	-	
13. <i>P. williamsi</i> 'maleri'	*	+	+	-	+	-	-	-	+	-	-	-	
14. <i>P. elongatus</i> 'slab'		+	+	-	-	-	-	-	-	+	+	-	
15. <i>P. elongatus</i> 'bar'		+	+	+	+	-	-	-	+	-	-	+	
16. <i>P.</i> 'aggressive yellow head'	*	+	+	+	+	+	-	-	+	-	-	-	
17. <i>P.</i> 'aggressive grey head'	*	+	+	+	+	+	-	-	+	-	-	-	
18. <i>P.</i> 'aggressive zebra'		+	+	+	+	+	+	+	+	-	-	+	
19. <i>P.</i> 'aggressive blue'		-	-	-	-	+	-	-	+	-	+	-	
20. <i>P.</i> 'dumpy'	*	-	+	+	-	-	-	-	-	-	-	-	
21. <i>P.</i> 'burrower'	*	+	+	+	+	+	+	+	+	-	-	-	
22. <i>Melanochromis auratus</i>		+	+	+	+	+	+	+	+	+	+	+	
23. <i>M. vermivorus</i>		+	+	+	+	+	+	+	+	+	+	+	
24. <i>M.</i> 'slab'		+	+	+	+	+	+	-	+	-	-	+	
25. <i>M. crabro</i>		+	+	+	-	-	-	-	-	-	-	+	
26. <i>Petrotilapia</i> 'yellow chin'		+	+	+	+	+	-	+	-	-	-	+	
27. <i>P. genalutea</i>		+	+	+	+	+	+	+	-	+	+	+	
28. <i>P.</i> 'fuscous'		+	+	+	+	-	-	+	+	-	-	+	
29. <i>Labidochromis vellicans</i>		+	+	+	+	+	+	+	+	+	+	-	
30. <i>L. pallidus</i>		+	+	+	+	+	+	+	+	-	+	-	
31. <i>Cynotilapia</i> 'maleri'	*	-	-	+	-	-	-	-	-	-	-	-	
32. <i>Labeotropheus fuelleborni</i>		y	y	b	b	b	b	b	b	b	b+y	b	
33. <i>L. trewavasae</i>		bd	bd	od	od	od	od	od	od	bd	od	-	
34. <i>Genyochromis mento</i>		+	+	+	+	+	+	+	+	+	+	+	
35. <i>Cyathochromis obliquidens</i>		-	-	+	+	+	+	+	+	+	+	+	
Totals		13	27	28	28	26	27	22	24	24	9	15	14

*Labeotropheus* spp. and in the intermediate habitats *Pseudotropheus zebra* 'fusco' is extremely numerous, particularly at sites E, F, G and H, and *P.* 'burrower' is common. Members of the *P. elongatus* species-group and of the genus *Melanochromis* are well represented (Figures 48–50).

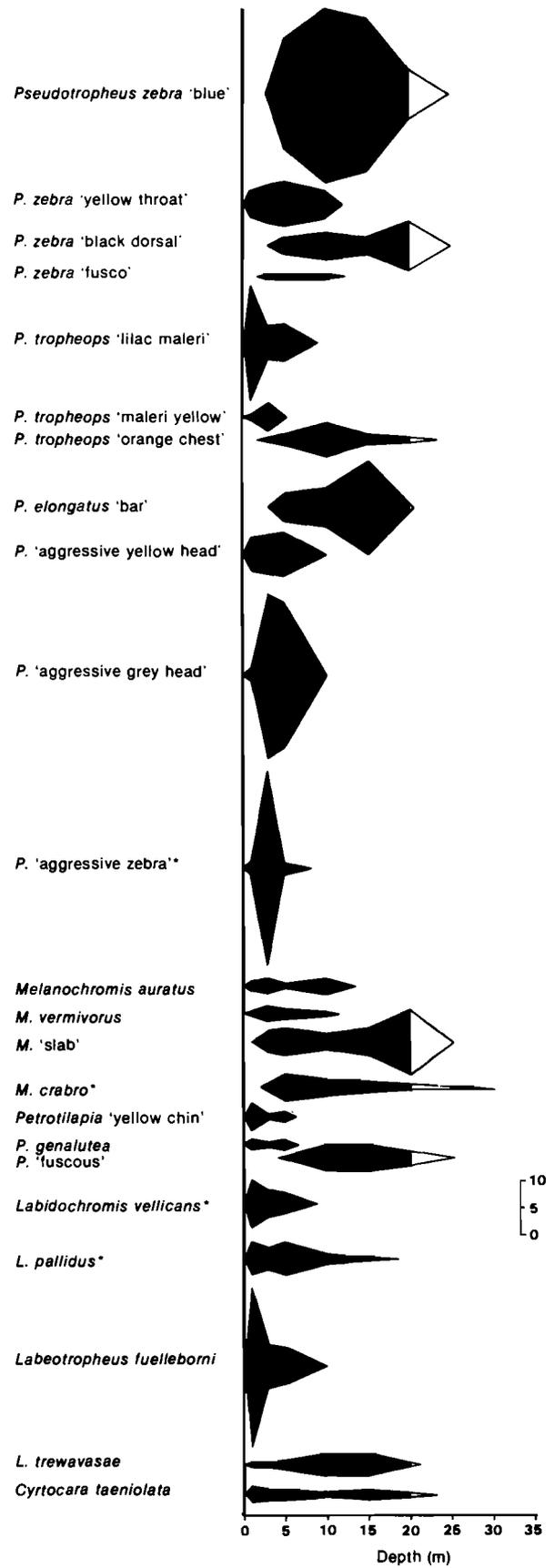
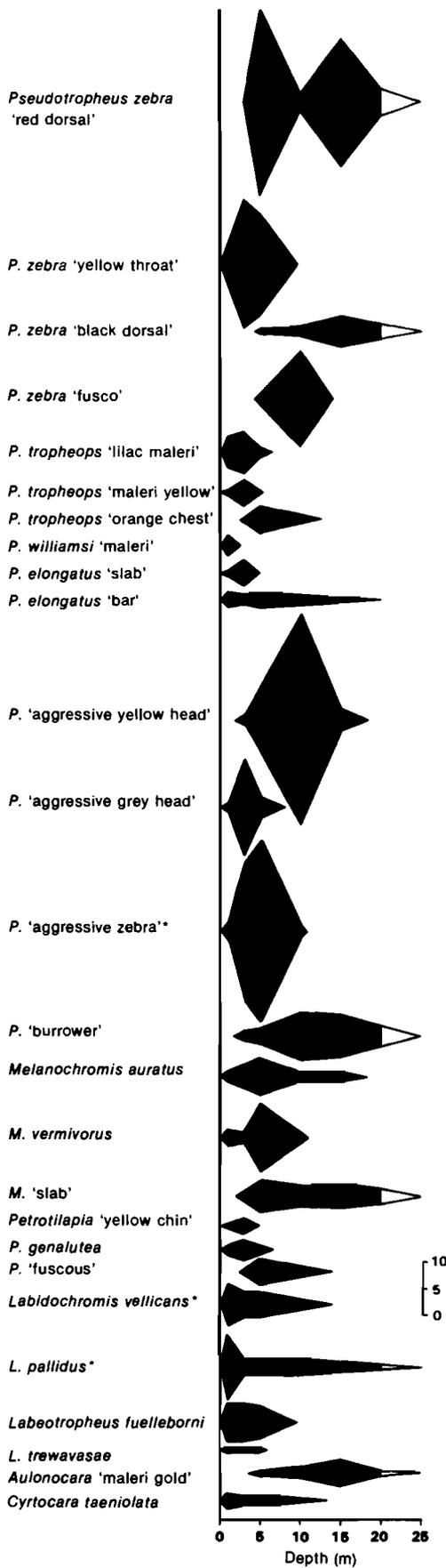
Several of the non-Mbuna which contribute to the cichlid communities of the Maleri Islands are important aquarium fishes particularly *Aulonocara* 'maleri gold' which is common in intermediate habitats in depths of 3–25 m (Figures 48–50). The most numerous non-Mbuna is *Cyrtocara taeniolata* which is included in the transects (Figures

48–50). *C. euchila*, *C. fenestrata*, *C.* 'labrosa', *C.* 'maleri thick lip' and a number of other undescribed species which feed from the rocky and intermediate habitats were also found.

Piscivores are represented by *Aristochromis christyi*, *Cyrtocara kiwinge*, *C. linni*, *C. livingstonii*, *C. polystigma*, *C. macrostoma*, *C. spilorhyncha*, several species of *Rhamphochromis* and by *Serranochromis robustus*.

In addition several species of Utaka were found.

**Area 7: Namalenje Island, Senga Point and Rifu**  
The three rocky regions considered here are in the south-

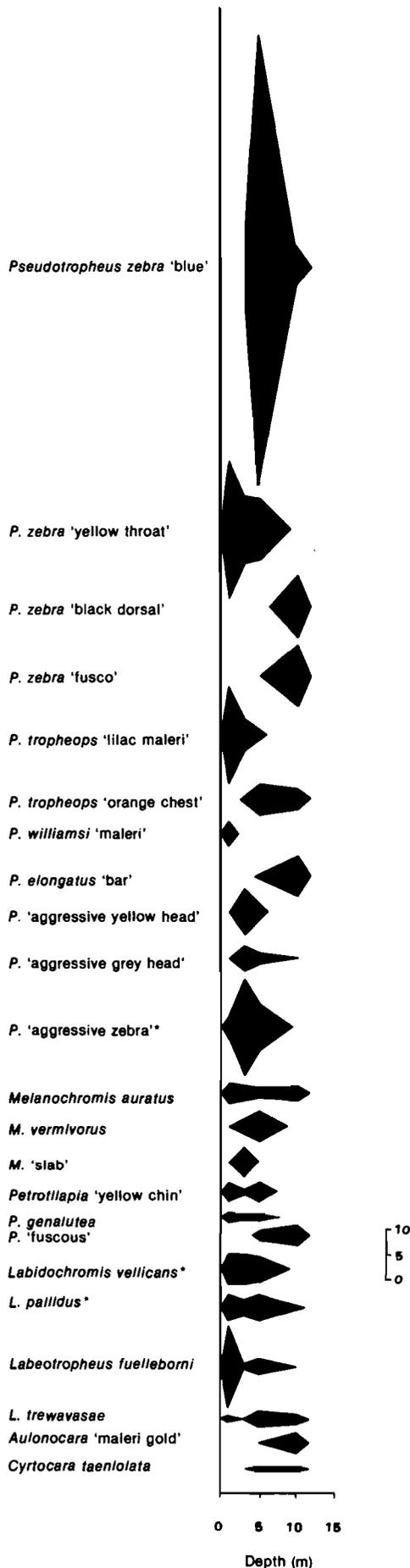


**Figure 48** Transect at station B, Nakantenga Island, giving the depth distribution and numerical abundance of the Mbuna species and of *Aulonocara* 'maleri gold' and *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

**Figure 49** Transect at station C, Maleri Island, giving the depth distribution and numerical abundance of the Mbuna species and *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

western portion of the central lake (Figure 52). The rocks at Senga Point and at Rifu are rounded, medium-large,

shelve steeply and in May 1980 they had a maximum depth of 4 and 6 m respectively. The narrow strip of rocks is about 500 m long at Rifu and approximately 300 m long at Senga



**Figure 50** Transect at station D, Maleri Island, giving the depth distribution and numerical abundance of the Mbuna species and of *Aulonocara* 'maleri gold' and *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

**Table 25** The number of Mbuna species and the number of individual cichlids of all species recorded at different depths in the transects at the Maleri Islands. Dashes indicate the depths at which the number of individuals was not counted

	Depth (m)							
	1	3	5	10	15	20	25	30
<b>Transect B</b>								
No. Mbuna species	17	21	22	19	11	8		
No. individuals all cichlids	340	290	315	180	86	35		
No. individuals m <sup>-2</sup>	6,8	5,8	6,3	3,6	1,7	0,7		
<b>Transect C</b>								
No. Mbuna species	16	21	22	16	11	12	5	
No. individuals all cichlids	305	275	305	170	165	110	-	
No. individuals m <sup>-2</sup>	6,1	5,5	6,1	3,4	3,3	2,2	-	
<b>Transect D</b>								
No. Mbuna species	12	17	19	10				
No. individuals all cichlids	260	580	315	150				
No. individuals m <sup>-2</sup>	5,2	11,6	6,3	3,0				

Point. Both areas are exposed to winds and to waves.

Namalenje is a small island about 200 m long and 100 m wide. It comprises medium-large and large rocks as well as boulders and slabs. The shore shelves steeply to the sandy plain at 6–11 m depth.

At these three diving stations we swam along the rocky shores to establish which fishes were present and to collect specimens.

*The communities*

All 17 species which occur in this study site are found at Namalenje Island, but only four species are found at Senga Point and three species at Rifu (Table 26). Only two species are endemic to the area. The five *Pseudotropheus zebra* 'cobalt' and 14 *P. lombardoi* occurring at Namalenje Island were almost certainly introduced to the island by an exporter of aquarium fishes who has his base at the nearby Kambiri Point.

The ichthyofauna of Namalenje Island has greater affinities with that of the Maleri Islands, with which it shares 11 species, than with Mbenji Island with which it shares seven species, including the introduced *P. lombardoi*. The greater similarity with the Mbuna of the Maleri Islands may be attributed to the fact that these islands are closer (18 km) to Namalenje than is Mbenji Island (41 km).

Both the species richness (Table 26) and the numerical density of Mbuna at Senga Point and Rifu are extremely low. The most common species at both sites are *P. tropheops* 'broad mouth' and *Labeotropheus fuelleborni*; *Petrotilapia* spp. are uncommon and only one *Melanochromis auratus* was seen at each site.

**Area 8: Mbenji Island**

Mbenji Island is a collective name for a number of small islands (Figure 52) which together provide the largest rocky area on the western side of the lake between the Maleri Islands and the north-western shores. Unlike the thickly forested islands occurring elsewhere, Mbenji has been denuded of trees and shrubs by itinerant fishermen who used this vegetation as fuel. The rocks of Mbenji Island are varied, and large, vertical pillars and walls of rock which

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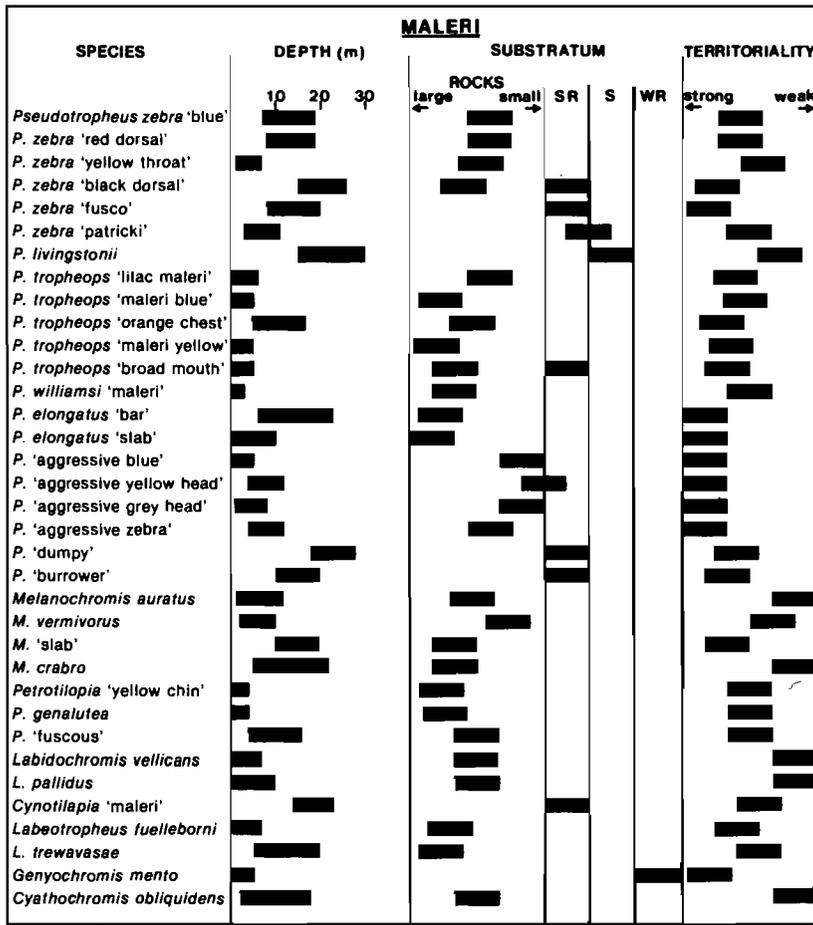


Figure 51 A summary of resource utilization of the Mbuna community at the Maleri Islands. For rest of legend see Figure 28 (p.254).

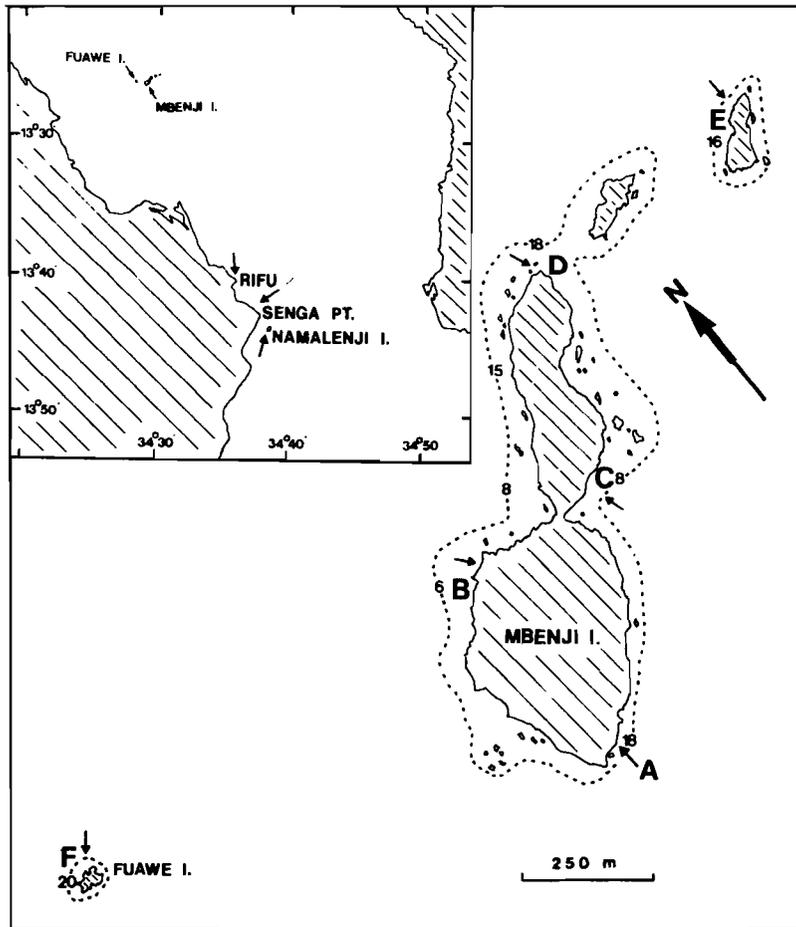


Figure 52 A map of study areas 7 (inset) and 8. The arrows and letters (A – F) show the positions of the diving stations. The dotted lines around the Mbenji Islands indicate the extent of the rocky shore and the numerals within these lines give the depth at which rocks meet the sandy plains. At Rifu, Senga Point and Namalenje Island the rocky shores are in shallow waters (see text: p.272 & 273).

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**Table 26** The Mbuna of Namalenje, Senga Point and Rifu. The species common to Namalenje Island, the Maleri Islands and Mbenji Island are shown. Present (+), absent (–), introduced (i), endemic (\*)

Species	Diving stations			Neighbouring areas	
	Namalenje Island	Senga Point	Rifu	Maleri Islands	Mbenji Island
1. <i>Pseudotropheus zebra</i>	+	–	–	–	–
2. <i>P. lombardoi</i>	i	–	–	–	+
3. <i>P. zebra</i> 'cobalt'	i	–	–	–	–
4. <i>P. zebra</i> 'patricki'	+	–	–	+	+
5. <i>P. tropheops</i> 'lilac maleri'	+	–	–	+	–
6. <i>P. tropheops</i> 'maleri yellow'	+	–	–	+	–
7. <i>P. tropheops</i> 'broad mouth'	+	+	+	+	–
8. <i>P. williamsi</i> 'namalenje' *	+	–	–	–	–
9. <i>P. elongatus</i> 'namalenje' *	+	–	–	–	–
10. <i>Melanochromis auratus</i>	+	+	+	+	+
11. <i>Petrotilapia</i> 'yellow chin'	+	–	–	+	+
12. <i>P. genalutea</i>	+	+	–	+	+
13. <i>Labidochromis</i> 'blue bar'	+	–	–	–	–
14. <i>L. vellicans</i>	+	–	–	+	–
15. <i>Labeotropheus fuelleborni</i>	+	+	+	+	+
16. <i>L. trewasasae</i>	+	–	–	+	–
17. <i>Genyochromis mento</i>	+	–	–	+	+
Totals	17	4	3	11	7

rise from the bottom are a feature of these islands. Beds of small and medium-sized rocks surround the pillars. The rocky shores nearest to Mbenji are those at Rifu which are 28 km away.

#### Diving stations

The fishes were studied at six diving stations A–F (Figure 52).

**Station A.** This site is exposed and comprises medium-sized and large rocks in the extreme shallows, but from 3–18 m small and medium-sized rocks predominate. Sand appears among the rocks from 15 m and at 18 m depth the bottom is sandy. A line transect was laid at this site and in doing so we avoided the massive pillars of rock which rise above the bed of broken rocks.

**Station B.** This is a shallow station where small and medium-sized rocks dominate the shallows to a depth of 4–6 m; thereafter an extensive, gradually shelving intermediate zone continues to 12 m.

**Stations C, D and E.** These stations are composed of rocks of all sizes, but large rocks and boulders predominate with many vertical pillars rising from the lake floor. Site C shelves gradually, but stations D and E descend steeply in a step-wise manner.

**Station F.** The islet of Fuawe, station F, is a pinnacle of large rocks which descends steeply to 20 m. A sand patch occurs at 6 m depth in a valley between two rocky peaks. At the time of our visit the rocks at 9–17 m depth were completely covered by a dense mat of brown slimy alga (unidentified) which could be peeled in strips from the rocks. This alga is not eaten by the fishes and it blocked the gaps

between the rocks preventing access to refuge and spawning sites. Mbuna were almost entirely absent from this algal-covered zone, though they were numerous in shallower and deeper water.

#### The communities

There are 29 Mbuna species at Mbenji Island of which 14 (48%) are endemic (Table 27). Of the other species only *Melanochromis labrosus*, *M. crabro* and the four *Petrotilapia* species appear identical to conspecifics which occur elsewhere. This high degree of endemism and the unique coloration of most of those species which have populations in other regions is probably a consequence of the isolation of the Mbenji Island Mbuna.

Mbenji Island has 13 species in common with the Maleri Islands, six in common with Likoma Island and seven in common with Namalenje Island (Table 27). The closest affinities of the Mbenji community are, therefore, with the Maleri Islands. Eleven species of Mbuna at Mbenji Island have been described.

At diving station A there are 26 Mbuna, 19 of which were recorded in the transect (Figure 53). The discrepancy between the number of species occurring at the station and the number recorded in the transect is accounted for as follows. The two species belonging to the *Pseudotropheus elongatus* species-group did not occur in the transect, probably because they frequent boulders and large rocks which were avoided when the transect lines were laid. *P. zebra* 'patricki', *Melanochromis labrosus*, *M. crabro*, *Petrotilapia* 'fuscous' and *Genyochromis mento* were too sparsely distributed in the transect area to feature in the figure.

Diving station B is a mixture of rocky and intermediate habitats which accommodates all 29 species. Station C is

**Table 27** The Mbuna species at diving stations A – F at Mbenji Island. Mbuna species common to Mbenji, Likoma and Maleri Islands are shown. Present (+), absent (–), endemic to Mbenji Island (\*)

Species	Mbenji diving stations						Maleri Island	Likoma Island
	A	B	C	D	E	F		
1. <i>Pseudotropheus zebra</i> 'mbenji'	*	+	+	+	+	+	–	–
2. <i>P. lombardoi</i>	*	+	+	+	+	+	–	–
3. <i>P. zebra</i> 'fusco'		+	+	+	+	+	+	–
4. <i>P. zebra</i> 'patricki'		+	+	+	–	+	+	–
5. <i>P. tropheops</i> 'mbenji blue'	*	+	+	+	+	+	–	–
6. <i>P. tropheops</i> 'mbenji yellow'	*	+	+	+	+	+	–	–
7. <i>P. williamsi</i> 'mbenji'	*	–	+	–	+	–	–	–
8. <i>P. elongatus</i> 'mbenji blue'	*	+	+	+	+	+	–	–
9. <i>P. elongatus</i> 'mbenji brown'	*	+	+	+	+	+	–	–
10. <i>P.</i> 'aggressive zebra'		+	+	+	+	+	+	+
11. <i>P. tursiops</i> 'mbenji'	*	+	+	+	+	+	–	–
12. <i>P.</i> 'red-dorsal'	*	+	+	+	+	+	–	–
13. <i>P. lucerna</i> 'mbenji'	*	–	+	–	–	–	–	–
14. <i>Melanochromis auratus</i>		+	+	+	+	+	+	–
15. <i>M. vermivorus</i>		+	+	+	+	+	+	–
16. <i>M.</i> 'slab'		+	+	+	+	+	+	–
17. <i>M. labrosus</i>		+	+	–	–	+	–	+
18. <i>M. crabro</i>		+	+	–	+	–	+	+
19. <i>Petrotilapia</i> 'yellow chin'		+	+	+	+	+	+	–
20. <i>P.</i> 'mumbo blue'		+	+	+	+	+	–	–
21. <i>P. genalutea</i>		+	+	+	+	+	+	–
22. <i>P.</i> 'fuscous'		+	+	+	+	+	+	–
23. <i>Labidochromis mbenji</i>	*	+	+	+	+	+	–	–
24. <i>L. ianthinus</i>	*	+	+	+	+	+	–	–
25. <i>Cynotilapia</i> 'yellow dorsal'	*	+	+	+	–	+	–	–
26. <i>C.</i> 'black dorsal'	*	+	+	–	+	+	–	–
27. <i>Labeotropheus fuelleborni</i>		+	+	+	+	+	+	+
28. <i>Genyochromis mento</i>		+	+	+	+	+	+	+
29. <i>Cyathochromis obliquidens</i>		–	+	–	–	–	+	+
Totals	14	26	29	23	26	23	13	6

mainly rocky and does not have several of the fishes which frequent intermediate habitats; it also lacks some of the rarer species such as *Pseudotropheus williamsi* 'mbenji', *Melanochromis labrosus* and *M. crabro* (Table 27). Site D lacks only two fishes of the shallow intermediate habitats (*Pseudotropheus lucerna* 'mbenji' and *Cyathochromis obliquidens*) and the rare *Melanochromis labrosus* (Table 27). Similarly, sites E and F are represented by all but the rare and intermediate zone species.

The majority of Mbuna species and most individuals of the cichlids of rocky shores live at less than 10 m depth (Table 28). The high number of individuals in water less than 5 m depth at station A is due to the numerous resident species and also to schools of *Pseudotropheus* 'red dorsal' and shoals of feeding *Labeotropheus fuelleborni*.

Mbenji Island is the most northerly point in the distribution of *Pseudotropheus zebra* 'fusco', *P. zebra* 'patricki', *Melanochromis auratus*, *M. vermivorus*, *Petrotilapia* 'yellow chin', *P.* 'mumbo blue' and *P.* 'fuscous'. Most of these species are relatively widely distributed in the southern regions of Lake Malawi.

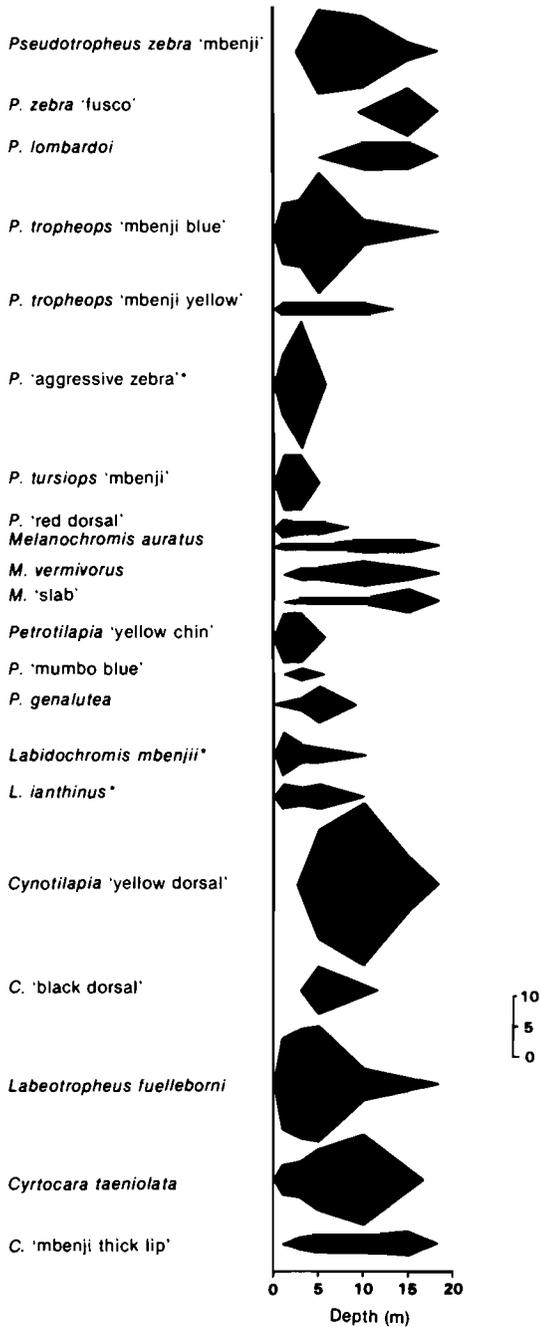
Mbenji Island is the only area of the lake which has four

**Table 28** The number of Mbuna species and the number of individual cichlids of all species counted at different depths in the transect at Mbenji Island

	Depth (m)					
	1	3	5	10	15	18
No. Mbuna species	14	22	24	18	14	9
No. individuals all cichlids	445	382	295	210	260	180
No. individuals m <sup>-2</sup>	8,9	7,6	5,9	4,2	5,2	3,6

species of *Petrotilapia* (*P.* 'yellow chin', *P.* 'mumbo blue', *P. genalutea* and *P.* 'fuscous'); at all other stations fewer species were found. All four species are most numerous on exposed, sediment-free rocky shores where they favour medium-sized and large rocks. At most sites the four species co-exist in the shallows, though a separation with depth occurs in so far as *P.* 'yellow chin' and *P.* 'mumbo blue' are rare beyond 5 m, but *P. genalutea* occurs to 11 m (Figure 53) and *P.* 'fuscous' penetrates to 20 m.

The Mbuna which dominate the rocky shores numerically



**Figure 53** Transect A, Mbenji Island, giving the depth distribution and numerical abundance of the Mbuna and two species of *Cyrtocara*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

are *Pseudotropheus zebra* 'mbenji', *P. tropheops* 'mbenji blue', *Labeotropheus fuelleborni* and *Cynotilapia* 'yellow dorsal' with *Pseudotropheus* 'aggressive zebra' and *P. tursiops* 'mbenji' being numerous among small and medium-sized rocks in shallow water (Figure 53). *Melanochromis* 'slab' is more common among large rocks than it is in the transect area.

The summary of preferred habitats shows that six species inhabit the intermediate zones (Figure 54). Of these, *Pseudotropheus zebra* 'fuscus' and *P. lombardoi* dominate the sand-rock interface in deepish water, though *P. lombardoi* favours the more rocky aspects and *P. zebra* 'fuscus' extends further onto the sand. *P. zebra* 'patricki' is the dominant Mbuna of shallow, intermediate habitats, being particularly common at the extensive intermediate zone at

station B. *Cyathochromis obliquidens* and *Pseudotropheus lucerna* 'mbenji' are uncommon species.

*Cyrtocara taeniolata* is the most common of the non-Mbuna (Figure 53) and appeared more numerous at Mbenji Island than at any other site studied. Other species present which feed from the Aufwuchs mat are *C. fenestrata*, *C. picta* and several species with hypertrophied lips: *C. euchila*, *C. 'labrosa'* and a common species (Figure 53) which is apparently endemic to Mbenji Island, *C. 'mbenji thick lips'* (Plate 12f). *Aulonocara* 'mbenji blue' is an attractive fish (Plate 12d) of the intermediate habitat which is popular with aquarists.

The ambush predators *Cyrtocara livingstonii*, *C. polystigma*, *C. linni* and the pursuit piscivores *C. kiwinge*, *C. macrostoma*, *C. spilorhyncha*, *Aristochromis chrystyi*, *Serranochromis robustus* and several *Rhamphochromis* species were well represented. Particularly common around Mbenji Island are a number of the planktivorous Utaka species which were heavily fished by itinerant fishermen at the time of the survey (May 1980).

**Area 9: The islands of Likoma and Chisumulu**

Likoma and Chisumulu are the biggest islands in Lake Malawi. They are also the only islands which are permanently inhabited, each supporting several thousand people who are largely dependent upon fish for their livelihood. These islands are rich in ornamental fish and together provide a greater variety of species for export than any other area of comparable size in the lake.

Likoma, the larger island, comprises a main island, about 7,4 km at its longest and 3,9 km at its widest, and several islets close to its shore (Figure 55). The rocky shores of Likoma Island are punctuated by a series of beaches which are particularly extensive along the southern half of the island. The continuity of the rocky shores is also broken by two reeded areas: one is at Ngani and the other in the northern inlet of Madimba Bay. All the islets associated with Likoma Island are rocky though there is a shallow sandy patch between the two Mbamba islets. Likoma Island is 4,4 km from the Mozambique coast and 10,4 km from Chisumulu Island (Figures 1 & 4).

Chisumulu Island comprises a main island about 4 km long and 1,8 km wide, two islets and numerous small rocky outcrops and submerged reefs close to its shores (Figure 56). The rocky shores of Chisumulu Island are punctuated by beaches which occur within the bays. The two islets are rocky.

**Diving stations at Likoma Island**

The fishes were studied at 25 diving stations around Likoma and line transects were laid at six (A – F; Figure 55). At most sites the rocks of Likoma Island are small to medium in size, but at Ndumbi Rocks, Ndomo Point and Masimbwe islet, rocks are medium-large and large. Rocky shores in predominantly sandy areas are seldom more than 8 m in depth (e.g. at Ulisa, Khuyu, Mlonga, Ponyemba and White Rock); elsewhere the rocky shores extend into deep water (Figure 55).

**Membe Point.** Transect A was laid at Membe Point where the rocks are predominantly small and medium-sized with a few scattered groups of large rocks. A littoral shelf descends gradually to 8–10 m. The edge of the shelf is marked by medium-large rocks and from this point the bot-

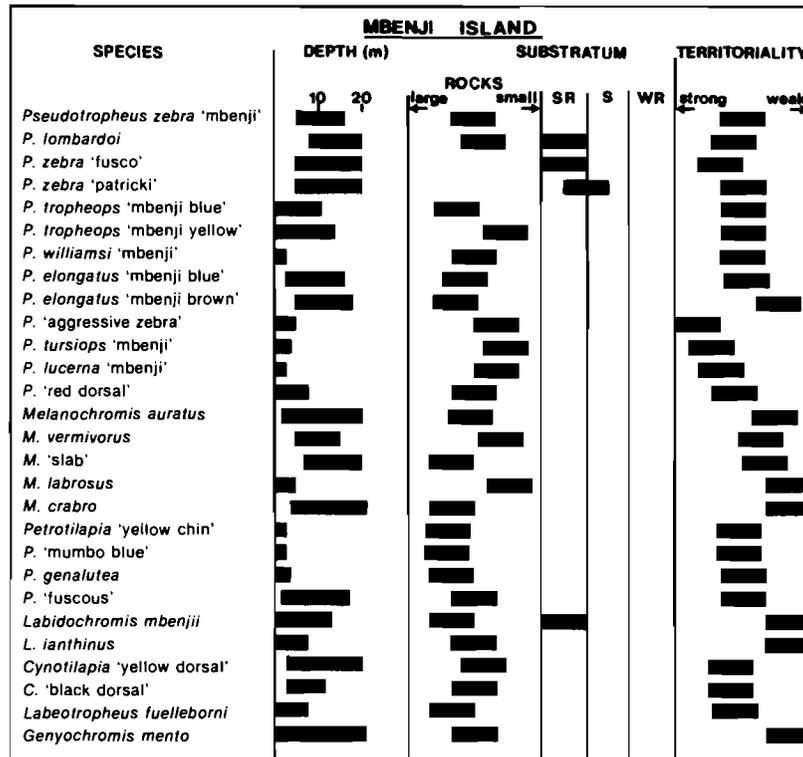


Figure 54 A summary of resource utilization of the Mbuna community at Mbenji Island. For rest of legend see Figure 28 (p.254).

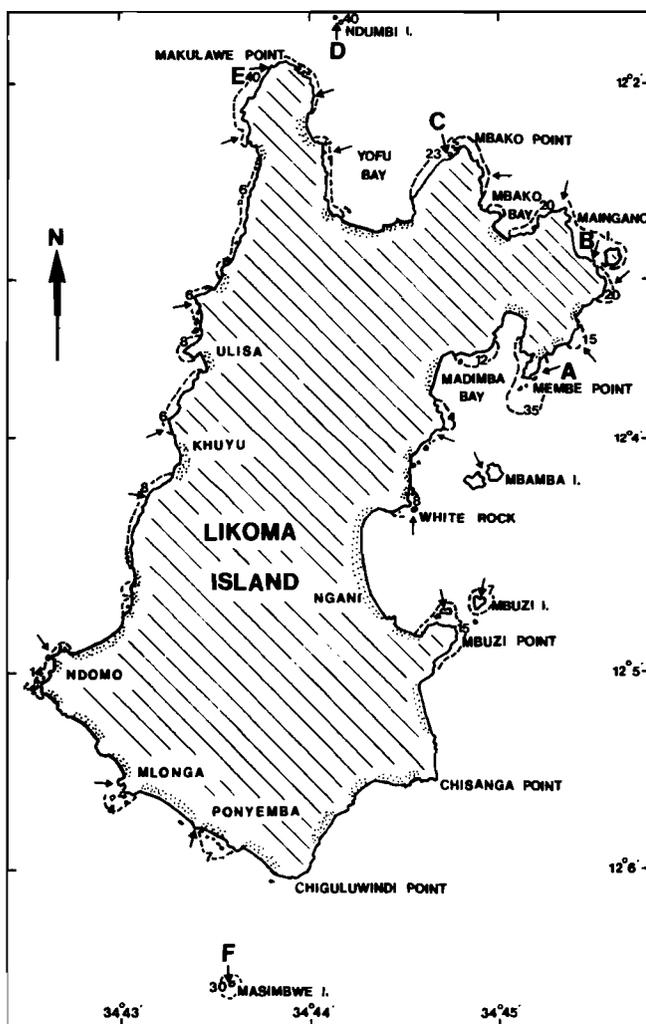


Figure 55 The diving stations at Likoma Island are indicated by arrows. Letters A – F show the position of transect sites. The dotted lines indicate the extent of the rocky shores and the numerals within these lines give the depth at which rocks meet the sandy plain. Sandy beaches are stippled. The position of Likoma Island relative to other shores is given by Figures 1 and 4.

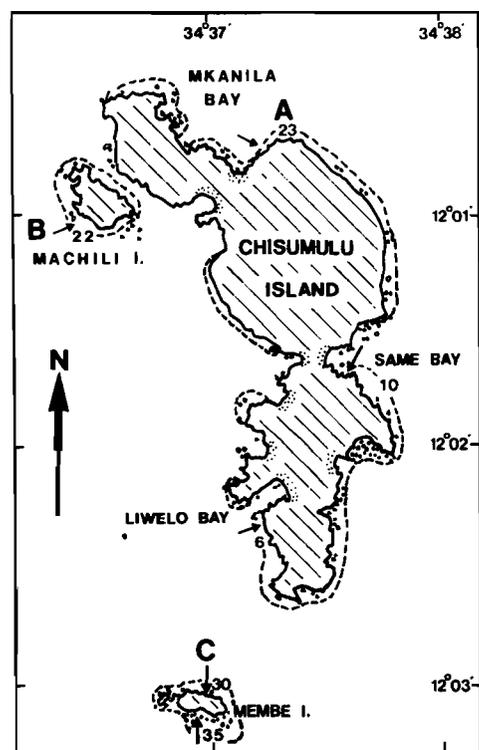


Figure 56 The diving stations at Chisumulu Island are indicated by arrows. Letters A – C show the positions of transect sites. The dotted lines indicate the extent of the rocky shores and the numerals within these lines give the depth at which rocks meet the sandy plain. Sandy beaches are stippled. The position of Chisumulu Island relative to other shores is given by Figures 1 and 4.

tom slopes steeply to 25 m where it then shelves more gradually again. From 25 m to 35 m the bottom becomes intermediate in nature with small rocks set in sand.

*Maingano*. Transect B, at Maingano, was set over small and medium-sized rocks. The bottom in this area shelves very gradually to 10 m, then steeply to sand at 35 m. An unusual

feature of rocks at this site is that many in the 2–8 m depth range are cemented together sometimes forming peculiar shapes. In places the rocky bed is pitted with pot-holes some of which are at least 1 m deep and 1 m in diameter. The rocks comprising the walls of these holes also appear cemented together. A strip of intermediate habitat 5–15 m wide runs from the main island shore past Maingano Islet through the transect station. This strip has the appearance of an ancient stream bed, which it might be.

**Mbako Point.** Transect C was conducted on the Yofu Bay side of Mbako Point where the bottom slopes gradually to a depth of 6 m about 50 m off-shore, then more steeply to sand at 25 m depth. The rocks at this site are predominantly small and medium-sized.

**Ndumbi.** Transect D was laid westwards from the apex of Ndumbi Rocks, a submerged reef situated about 0,8 km north of Makulawe Point. Medium-large and large rocks shelf steeply to at least 40 m depth from about 1 m below the surface (August 1980).

**Makulawe Point.** Makulawe Point (site E) has a bed of small rocks in the shallows which is set among large and medium-sized rocks, but from 3–5 m depth medium-sized and large rocks predominate and descend rapidly to at least 40 m depth.

**Masimbwe Islet.** The islet of Masimbwe (site F) rises from a sandy plain in 30–35 m of water and comprises mainly medium-sized and large rocks. The transect was laid on the northern side of the islet.

#### Diving stations at Chisumulu Island

The fishes were studied at five stations at Chisumulu Island and transects were laid at three (A–C; Figure 56).

**Mkanila Bay.** At site A the bottom comprises mainly rounded, medium-small rocks which descend to sand at 23 m depth, approximately 60 m from the shoreline.

**Machili Islet.** At site B the rocks between 0–5 m depth are medium-sized and medium large, but from 5–18 m the rocks are angular, of variable size ranging from huge boulders and pillars of rock to pebble-sized broken rock. From 18–22 m the bottom comprises small flat rocks on a sandy bottom. The slope is so gradual that the 20 m depth contour is estimated to be more than 200 m from the shoreline.

**Membe Islet.** The northern shore of Membe Islet (site C) comprises small rounded rocks and pebbles in the extreme shallows, but from about 3 m depth angular rocks of variable size, from pebbles to boulders, cover the bottom. Ridges of slab-like rock run east-west along the bottom and may have sandy patches between them. The line transect was laid northwards from this shore, but because of strong northerly winds when we returned to complete the transect, the deep dives were conducted on the southern shore. The rocks of this shore are also variable in size, but are more rounded and close packed.

**Same Bay and Liwelo Bay.** We also dived at Liwelo Bay and Same Bay (Figure 56). The diving station at Liwelo was over a littoral shelf in shallow water which is dominated by small rocks. At Same Bay the bottom is composed of beds of pebbles and small rocks on sand, but flanking these beds are slabs and boulders.

#### The communities

Sixty-two Mbuna taxa were found at Likoma and Chisumulu Islands (Table 29). Forty-nine occur at Likoma Island, 32 occur at Chisumulu Island and there are 19 common to both islands. Forty-seven of these Mbuna taxa were not found anywhere else in the study area, though several might occur on the nearby Mozambique coast. Twenty species have been described. Three species are believed to have been introduced to Likoma Island from Chisumulu and one species from Nkhata Bay.

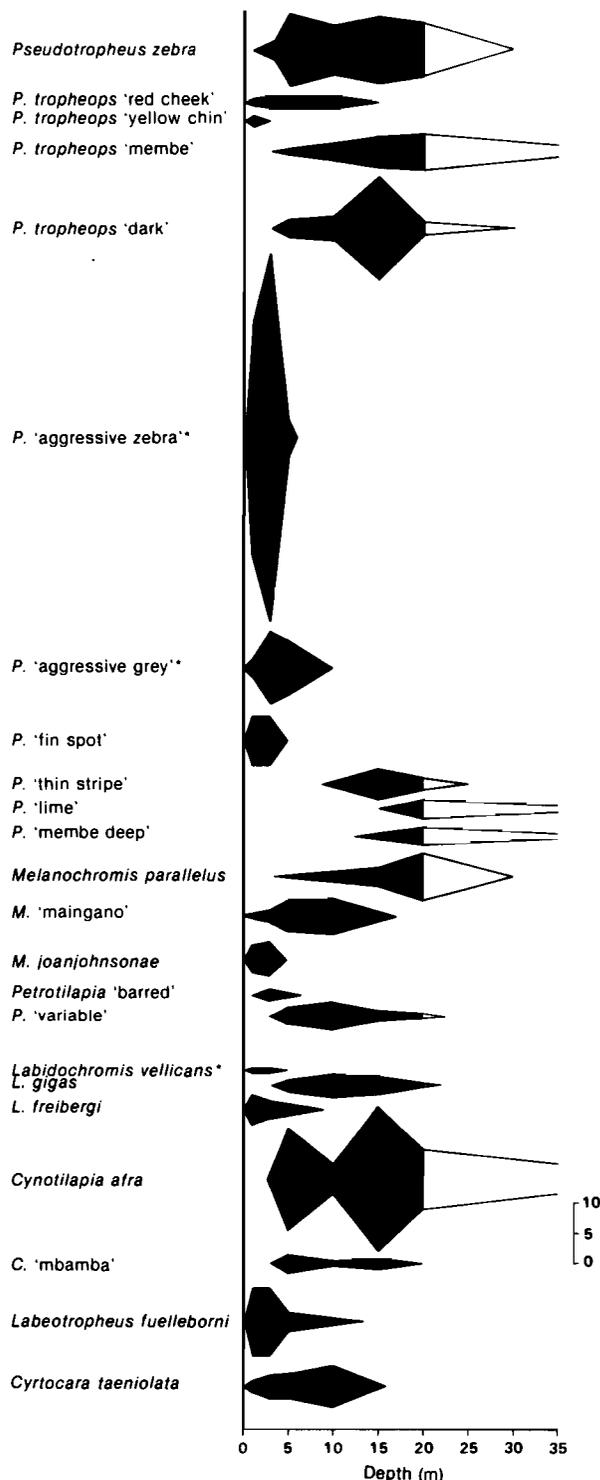
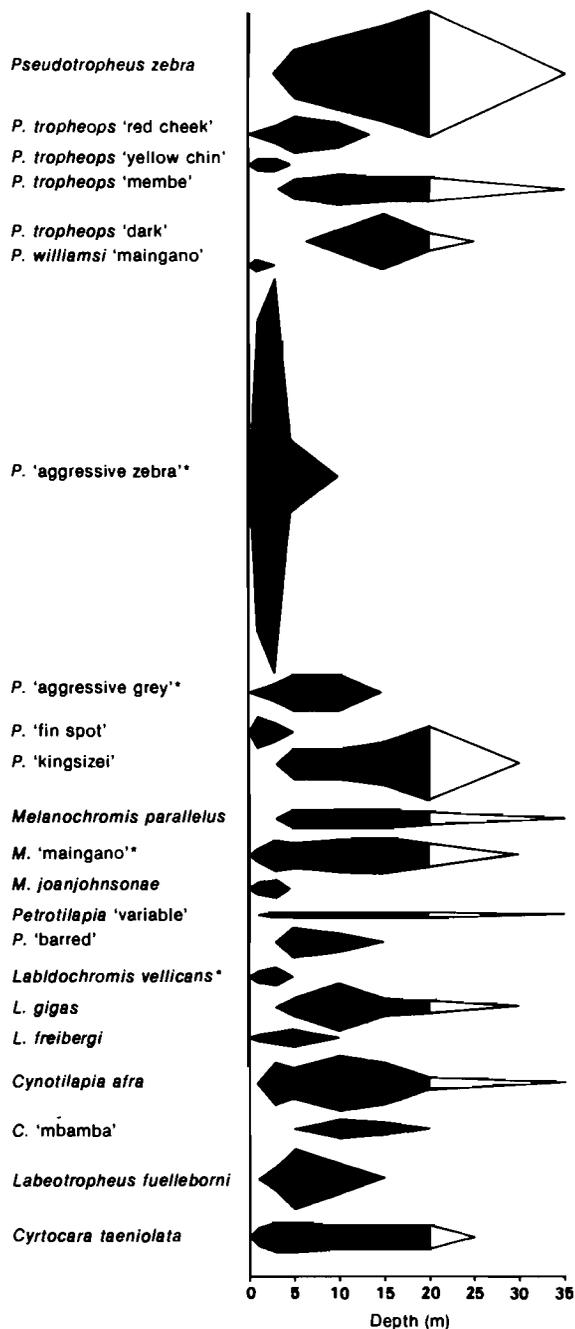


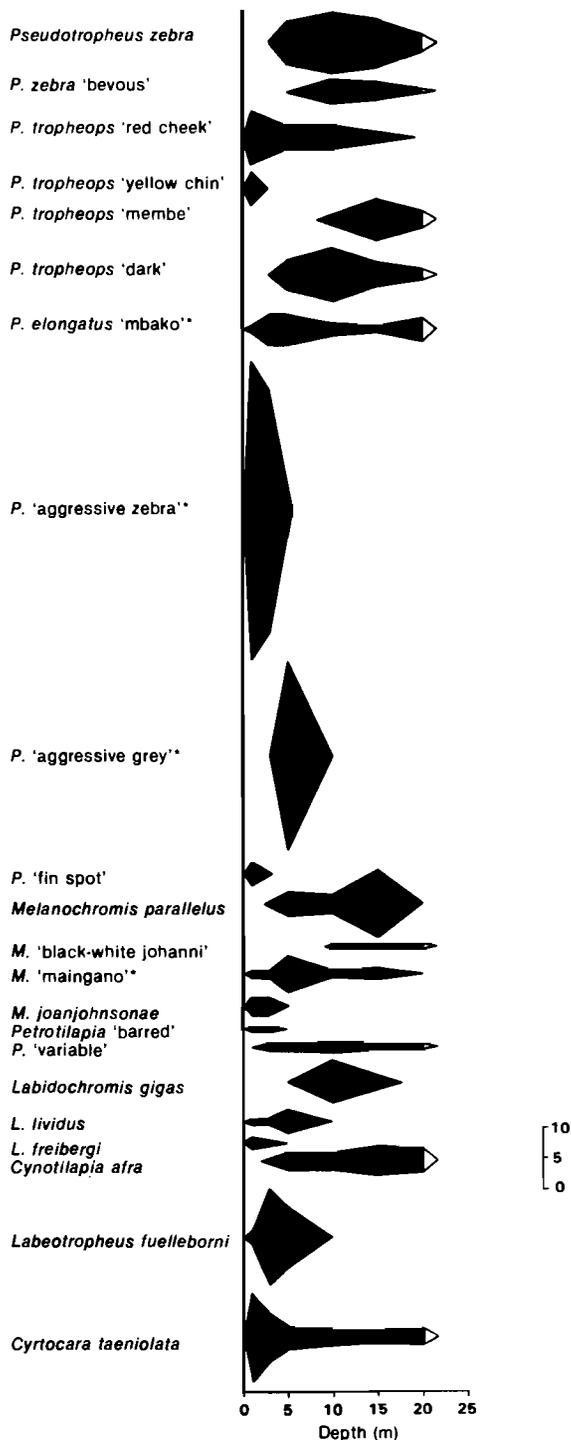
Figure 57 Transect A at Membe Point, Likoma Island, giving the depth distribution and numerical abundance of the Mbuna and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.



**Figure 58** Transect B at Maingano, Likoma Island, giving the depth distribution and numerical abundance of the Mbuna 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<sup>-2</sup>.

A notable feature of the Mbuna of both islands is that many are limited in their distribution to small geographic areas. Consequently, no diving station at Likoma has more than 57% (28 species) of the island's full complement and at Chisumulu Island no station has more than 80% (25 species) of its complement (Table 29). Furthermore, no two diving stations have exactly the same species assemblage (Table 29). The closer stations are to one another and the more similar their habitats, the greater the number of species they have in common. But even species common to two sites may have different abundances being rare at one station and common at a neighbouring site (Figures 57 – 65).

The transect Figures (57 – 65) give the numerical abundance and the depth distribution of the Mbuna at diving stations A – F at Likoma Island. Not all species which occur at the diving stations are included in the transects. The



**Figure 59** Transect C at Mbako Point, Likoma Island, giving the depth distribution and numerical abundance of the Mbuna 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<sup>-2</sup>.

discrepancy is accounted for by the fact that the area studied at each diving station is larger than the area sampled by the transect and so fishes in microhabitats not traversed by the transects would have been omitted. Similarly, rare and uncommon species may not have been represented in the transect during the study period or, if they were present, they may have been too scarce to feature in the transect figures. Fishes which are generally rare or uncommon at Likoma Island, and therefore occurred in few transects are *Melanochromis melanopterus*, *M. 'blue'*, *M. labrosus*, *M. crabro*, *Cynotilapia 'ndumbi'* and *Genyochromis mento*,

**Table 29** The Mbuna at the principal diving stations of Likoma and Chisumulu Islands. Present (+); absent (-); uncertain (?); introduced (i); found at Likoma and/or Chisumulu Islands only (\*)

Species	Likoma Island stations													Chisumulu stations						
	Membe	Maingano	Mbako	Makulawe	Ndumbi	Ulisa	Khuyu	Ndomo	Mlonga	Ponyemba	Masimbwe I.	Mbuzi	White Rock	Madimba	Mbamba	Membe I.	Liwelo	Machili I.	Mkanila	Same
1. <i>Pseudotropheus zebra</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2. <i>P. zebra</i> 'cobalt'	-	-	-	-	-	-	-	-	-	-	-	i	i	i	-	-	-	-	-	-
3. <i>P. zebra</i> 'bevous'	*	-	+	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-
4. <i>P. aurora</i>	*	-	-	-	-	+	+	+	+	+	-	+	+	-	-	-	-	-	-	-
5. <i>P. livingstonii</i> 'likoma'	*	-	-	-	-	+	+	+	+	+	-	+	+	-	-	-	-	-	-	-
6. <i>P. zebra</i> 'greberi'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	+
7. <i>P. tropheops</i> 'red cheek'	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
8. <i>P. tropheops</i> 'yellow chin'	*	+	+	+	+	-	+	+	+	+	-	+	+	+	+	+	+	+	+	+
9. <i>P. tropheops</i> 'membe'	*	+	+	+	+	-	-	+	-	-	+	+	+	+	+	-	-	-	-	-
10. <i>P. tropheops</i> 'dark'	*	+	+	+	+	-	-	+	-	-	+	+	+	+	+	-	-	-	-	-
11. <i>P. tropheops</i> 'gold'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
12. <i>P. williamsi</i> 'maingano'	*	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13. <i>P. williamsi</i> 'khuyu'	*	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
14. <i>P. williamsi</i> 'chisumulu'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+
15. <i>P. elongatus</i> 'mbako'	*	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16. <i>P. elongatus</i> 'ndumbi'	*	-	-	-	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-
17. <i>P. elongatus</i> 'ornatus'	*	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18. <i>P. elongatus</i> 'gold bar'	*	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-
19. <i>P. elongatus</i> 'chisumulu'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
20. <i>P.</i> 'aggressive zebra'	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
21. <i>P.</i> 'aggressive grey'	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
22. <i>P. tursiops</i>	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
23. <i>P.</i> 'aggressive yellow fin'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
24. <i>P.</i> 'yellow tail'	*	-	-	-	+	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-
25. <i>P.</i> 'ndumbi gold'	*	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26. <i>P.</i> 'fin spot'	*	+	+	+	-	-	+	+	+	-	-	+	+	+	-	-	-	-	-	-
27. <i>P.</i> 'cobalt'	*	-	-	-	-	-	+	+	+	-	-	-	-	-	-	+	-	-	+	+
28. <i>P.</i> 'lime'	*	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29. <i>P.</i> 'membe deep'	*	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30. <i>P.</i> 'kingsize'	*	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31. <i>P.</i> 'thin stripe'	*	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32. <i>P.</i> 'jacksoni'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
33. <i>P.</i> 'newsi'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	+
34. <i>Melanochromis melanopterus</i>	+	+	+	+	+	-	-	-	-	-	+	-	-	-	+	+	+	+	+	+
35. <i>M. parallelus</i>	+	+	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+
36. <i>M.</i> 'maingano'	*	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37. <i>M.</i> 'black-white johanni'	*	+	-	+	-	-	+	+	+	+	+	+	+	+	+	-	-	-	-	-
38. <i>M.</i> 'blue'	+	-	+	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-
39. <i>M.</i> 'red'	*	-	-	-	-	-	-	-	-	-	-	i	-	i	-	+	+	+	-	-
40. <i>M.</i> 'blotch'	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
41. <i>M. joanjohnsonae</i>	*	+	+	+	+	-	+	+	+	-	-	+	+	+	+	-	-	-	-	-
42. <i>M. labrosus</i>	+	+	+	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	-	-
43. <i>M. crabro</i>	-	-	-	-	-	-	+	+	-	+	-	+	-	-	-	-	-	+	+	+
44. <i>Petrotilapia</i> 'likoma variable'	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
45. <i>P.</i> 'likoma barred'	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
46. <i>P.</i> 'orange pelvic'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
47. <i>P.</i> 'retrognathus'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
48. <i>P.</i> 'yellow ventral'	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	-
49. <i>Labidochromis gigas</i>	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
50. <i>L. freibergi</i>	*	+	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-
51. <i>L. lividus</i>	*	-	-	+	+	-	+	+	-	-	?	-	-	-	-	-	-	-	-	-
52. <i>L. vellicans</i>	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
53. <i>L. zebroides</i>	*	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
54. <i>L. strigatus</i>	*	-	-	-	-	-	-	-	-	-	-	-	i	i	-	+	+	+	+	+
55. <i>L. flavigulus</i>	*	-	-	-	-	-	-	-	-	-	-	-	i	i	-	+	+	+	+	+
56. <i>L. chisumulae</i>	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+

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Table 29 continued

Species	Likoma Island stations															Chisumulu stations					
	Membe	Maingano	Mbako	Makulawe	Ndumbi	Ulisa	Khuyu	Ndomo	Mlonga	Ponyemba	Masimbwe I.	Mbuzi	White Rock	Madimba	M b a m b a	Membe I.	Liwelo	Machili I.	Mkanila	Same	
57. <i>Cynotilapia afra</i>	+	+	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	
58. <i>C. 'mbamba'</i>	+	+	+	+	+	-	-	+	-	-	+	-	-	-	+	+	-	+	+	-	
59. <i>C. 'ndumbi'</i>	*	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
60. <i>Labeotropheus fuelleborni</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
61. <i>Genyochromis mento</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	
62. <i>Cyathochromis obliquidens</i>	-	-	-	-	-	+	+	+	-	-	-	-	+	+	-	-	-	-	-	-	
Totals	47	28	28	27	23	19	21	25	26	13	13	20	21	28	25	17	25	19	24	25	24

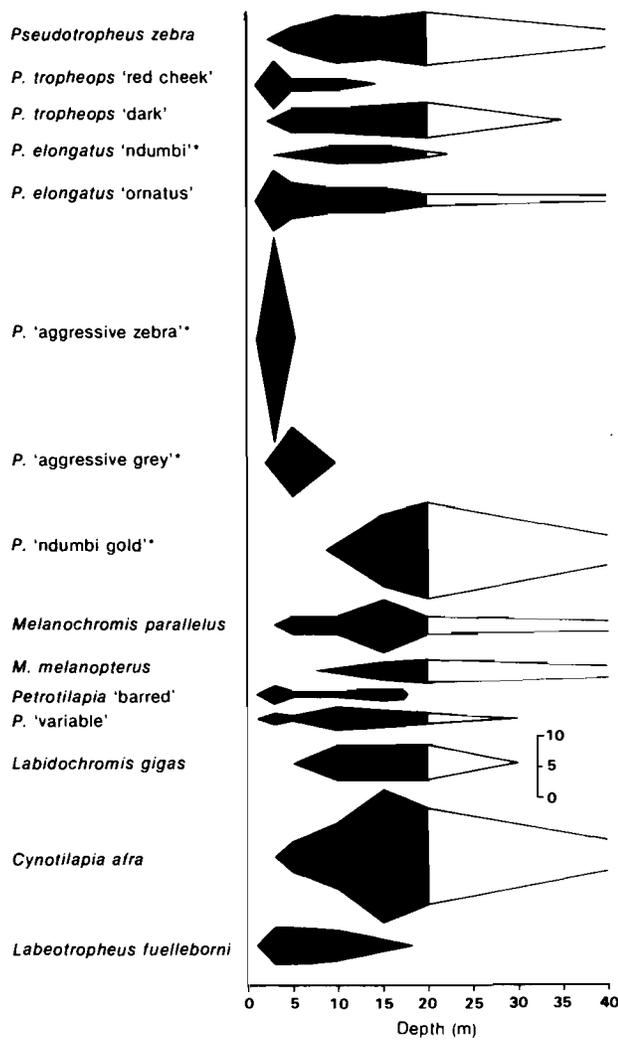


Figure 60 Transect D at Ndumbi Rocks, Likoma Island, giving the depth distribution and numerical abundance of the Mbuna and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

though *G. mento* was well represented at Masimbwe Islet (Figure 62).

Ten species found at Likoma Island did not occur in any transect. Six of these (*Pseudotropheus aurora*, *P. livingstonii* 'likoma', *P. williamsi* 'khuyu', *P. elongatus* 'gold bar', *P.*

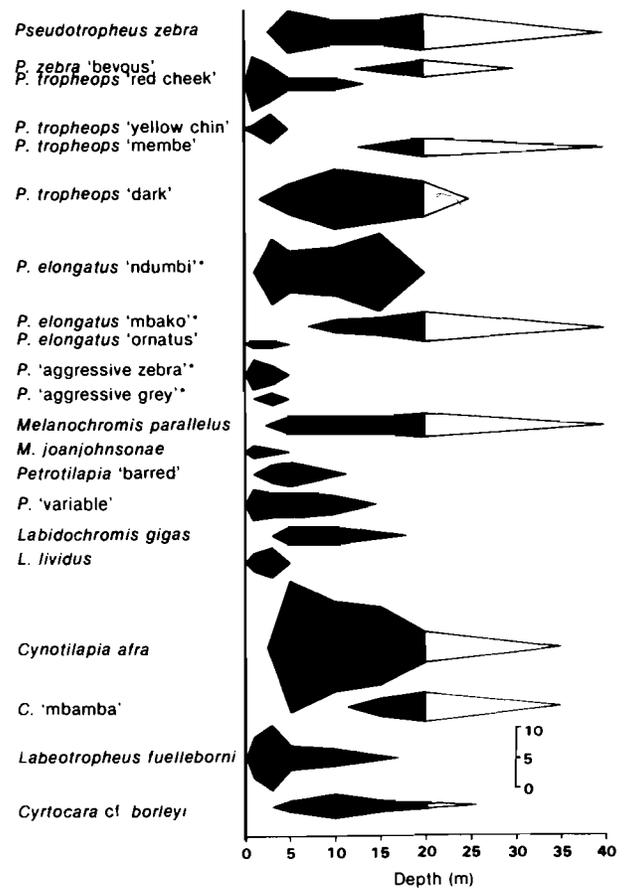
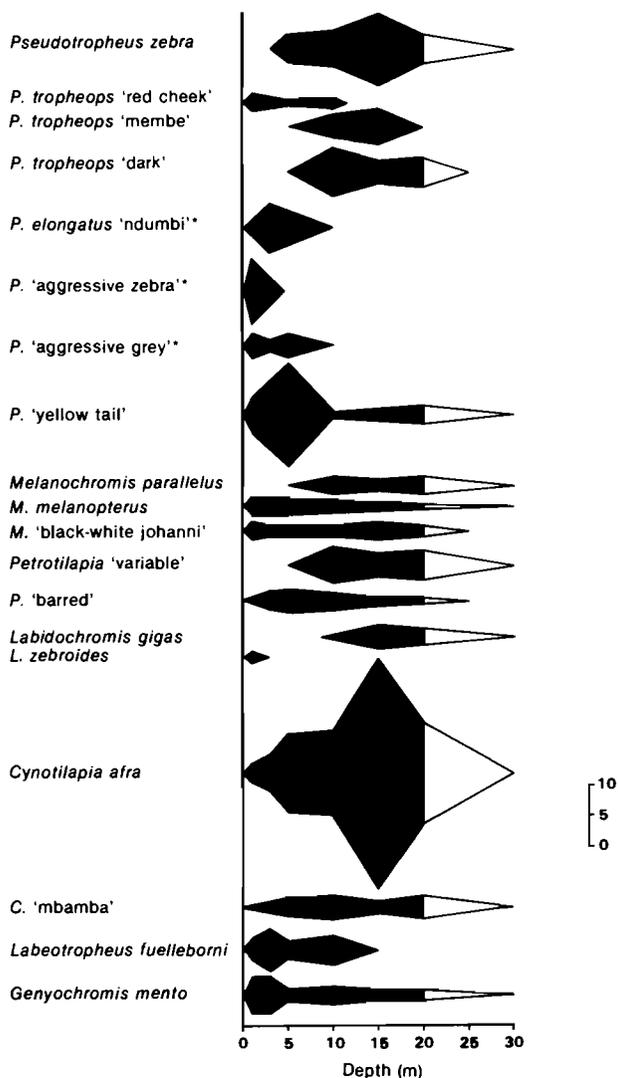


Figure 61 Transect E at Makulawe Point, Likoma Island, giving the depth distribution and numerical abundance of the Mbuna and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

'cobalt' and *Cyathochromis obliquidens*) live in shallow intermediate or in sandy habitats, principally around the southern half of the island, where transects were not laid. The four introduced species *Pseudotropheus zebra* 'cobalt', *Melanochromis* 'red', *Labidochromis strigatus* and *L. flavigulus* all live in the shallows of Madimba Bay, White Rock and Mbuzi where transects were not laid.

Figures 63 – 65 give the numerical abundance and depth distribution of the Mbuna at diving stations A – C at Chisumulu Island. The two yellow-chinned species of

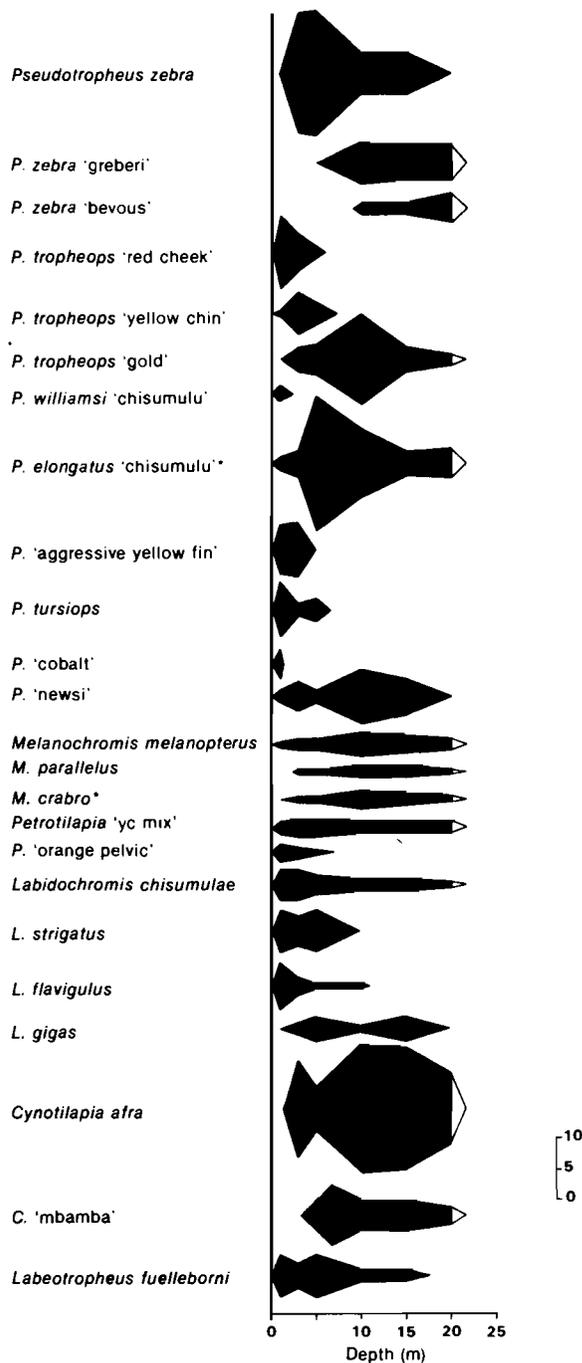


**Figure 62** Transect F at Masimbwe Islet, Likoma Island, giving the depth distribution and numerical abundance of the Mbuna and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

*Petrotilapia*, *P. retrognathous* and *P. yellow ventral*, were not recognized as being distinct until after the completion of the transects and so both species are recorded together as *P. 'yc, mix'* in the figures. The shallow-water species is *P. retrognathous* which normally does not venture beyond 10 m depth, and the deeper water species is *P. yellow ventral* which has a depth range extending to at least 33 m. The bidomal distribution of *P. 'yc, mix'* suggests that the two species do not overlap much in their depth distribution.

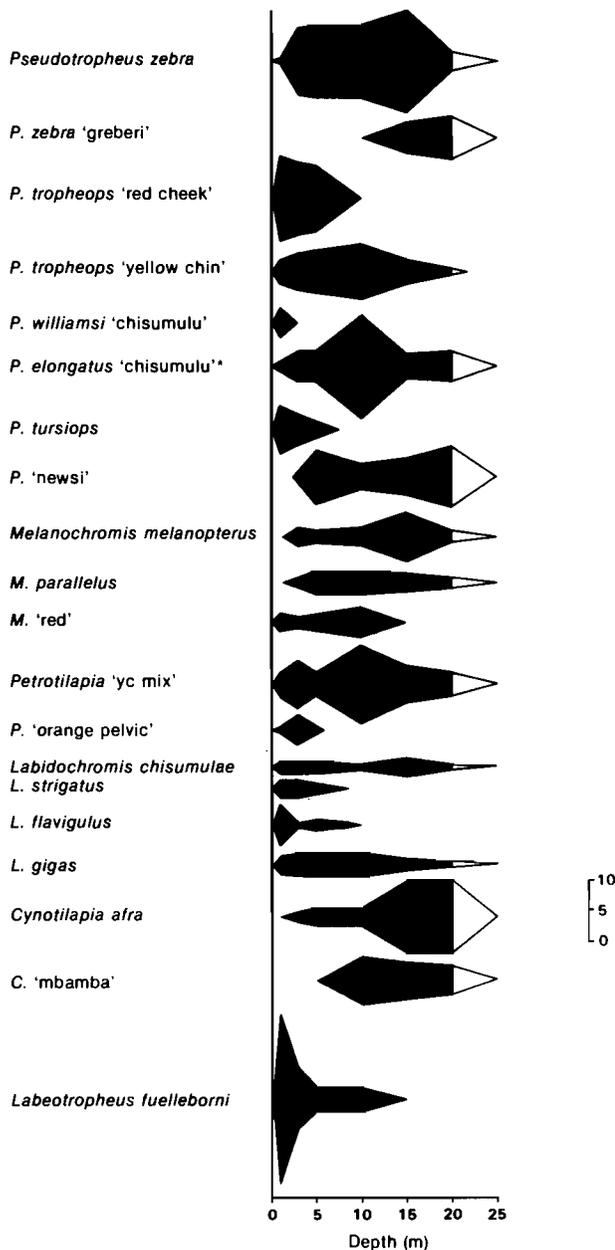
*Pseudotropheus elongatus* 'gold bar' and *P. jacksoni* do not feature in any transect as they live in Liwelo Bay and Same Bay, respectively, where transects were not laid. The rarity of *P. aggressive yellow fin*' at Machili Islet, site B, and its consequent absence from the transect is probably due to the presence of medium-sized and medium-large rocks in the shallows. Rocks of this size appear unsuitable to this species which normally lives among small rocks. In contrast, territorial and particularly non-territorial adult and juvenile *P. tropheops* 'red cheek', *P. tropheops* 'yellow chin' and *Labeotropheus fuelleborni* are more numerous at this site than at any other station.

In general, the greatest species richness was found at



**Figure 63** Transect A at Mkanila Bay, Chisumulu Island, giving the depth distribution and numerical abundance of the Mbuna 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<sup>-2</sup>.

3 – 10 m and the greatest number of individual cichlids occurred in the shallows at both Likoma and Chisumulu Islands (Table 30–31). *Labeotropheus fuelleborni* and *Pseudotropheus tropheops* species-complex subadults feed in large numbers in the extreme shallows and this accounts, in part, for the high numerical abundance of cichlids at these depths at all transect stations. The only exception is the submerged reef, Ndumbi Rocks (site D) Likoma Island. The reasons for the relatively low numbers of fishes in the shallows of the reef are that (i) the apex at which the transect was laid was submerged to a depth of 1–2 m and (ii) it consists of medium-large rocks with few refuge sites. From 5–15 m depth schools of non-territorial *Cynotilapia afra* and *Pseudotropheus zebra* contributed to the high numbers

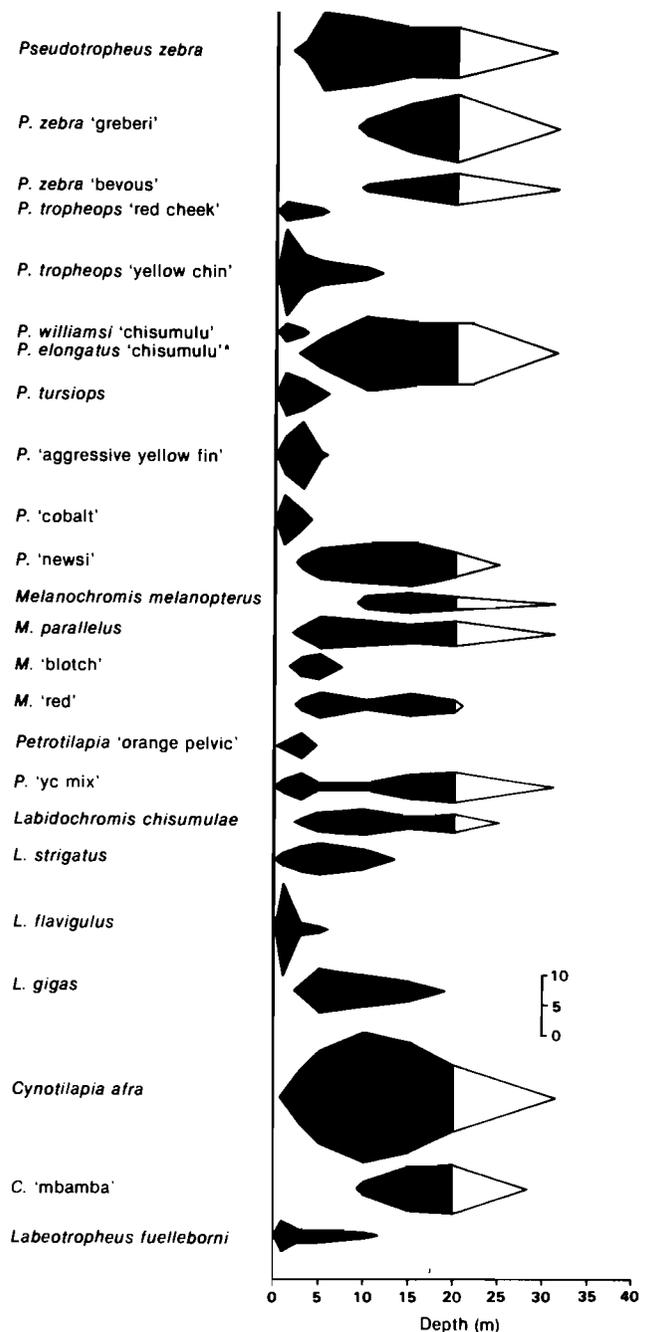


**Figure 64** Transect B at Machili Islet, Chisumulu Island, giving the depth distribution and numerical abundance of the Mbuna and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes  $50 \text{ m}^{-2}$ .

of cichlids within the transect.

Figures 66 and 67 summarize the preferences for particular depth zones and microhabitats of Mbuna of Likoma and Chisumulu, giving a general indication of how these resources are partitioned. It should be noted that several species with apparently identical requirements occur allopatrically (Table 29).

Within the littoral rocky environments of Likoma Island the areas of large rocks are dominated numerically by the *Petrotilapia* spp. and by territorial and particularly non-territorial *Labeotropheus fuelleborni*, *Pseudotropheus tropheops* 'red cheek' and *P. tropheops* 'dark'. At Ndumbi Rocks schools of *P. elongatus* 'ornatus' are common over large rocks and boulders. Territorial *P. elongatus* 'ndumbi' are also common in these areas at Ndumbi Rocks and Makulawe Point. At Chisumulu Island areas of large rocks are dominated by *Petrotilapia* spp., *Labeotropheus*



**Figure 65** Transect C at Membe Islet, Chisumulu Island, giving the depth distribution and numerical abundance of the Mbuna and of *Cyrtocara taeniolata*. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes  $50 \text{ m}^{-2}$ .

*fuelleborni* and members of the *Pseudotropheus tropheops* species-complex. Upper surfaces of slabs and boulders are frequented by schools of *Melanochromis* 'red', while *Pseudotropheus elongatus* 'chisumulu' is common on vertical rock faces.

At both islands, *Cynotilapia afra* and *Pseudotropheus zebra* are the most numerous fishes in habitats of medium-sized and small rocks. However, in the shallows of Likoma Island these habitats, particularly those where small rocks predominate, are inhabited by many *Pseudotropheus* 'aggressive zebra' and *P. 'aggressive grey'* (Figures 57–62). These species are absent from Chisumulu Island where *P. 'aggressive yellow fin'* and *P. tursiops* occupy similar ecological niches. All species of *Labidochromis* are com-

**Table 30** The number of Mbuna species and the number of individual cichlids of all species counted at different depths in transects A – F at Likoma Island. A = Membe Point, B = Maingano, C = Mbako Point, D = Ndumbi Rocks, E = Makulawe Point, F = Masimbwe. Dashes indicate that individual fishes were not counted below 20 m depth

	Depth (m)									
	1	3	5	10	15	20	25	30	35	40
<b>Transect A</b>										
No. Mbuna species	14	18	22	15	13	11	9	8	4	
No. individuals all cichlids	430	382	305	290	285	170	–	–	–	
No. individuals m <sup>-2</sup>	8,6	7,6	6,1	5,8	5,7	3,4	–	–	–	
<b>Transect B</b>										
No. Mbuna species	15	19	19	18	16	11	10	9	6	
No. individuals all cichlids	256	239	241	332	293	180	–	–	–	
No. individuals m <sup>-2</sup>	5,1	4,8	4,8	6,6	5,9	3,6	–	–	–	
<b>Transect C</b>										
No. Mbuna species	13	17	17	14	13	10				
No. individuals all cichlids	310	280	250	240	210	155				
No. individuals m <sup>-2</sup>	6,2	5,6	5,0	4,8	4,2	3,1				
<b>Transect D</b>										
No. Mbuna species	8	12	15	14	13	13	10	8	7	7
No. individuals all cichlids	215	320	290	295	280	275	–	–	–	–
No. individuals m <sup>-2</sup>	4,3	6,4	5,8	5,9	5,6	5,5	–	–	–	–
<b>Transect E</b>										
No. Mbuna species	12	17	16	13	13	11	10	9	7	
No. individuals all cichlids	442	263	324	231	173	233	–	–	–	
No. individuals m <sup>-2</sup>	8,8	5,3	6,5	4,6	3,5	4,7	–	–	–	
<b>Transect F</b>										
No. Mbuna species	13	15	16	15	14	13	10	9		
No. individuals all cichlids	440	400	370	252	234	155	–	–		
No. individuals m <sup>-2</sup>	8,8	8,0	7,4	5,0	4,7	3,1	–	–		

**Table 31** The number of Mbuna species and the number of individual cichlids of all species counted at different depths in transects A – C at Chisumulu Island. A = Mkanila Bay, B = Machili Islet, C = Membe Islet. Dashes indicate that individual fishes were not counted below 20 m depth

	Depth (m)							
	1	3	5	10	15	20	25	30
<b>Transect A</b>								
No. Mbuna species	18	19	21	18	16	13	–	–
No. individuals all cichlids	305	270	260	183	192	174		
No. individuals m <sup>-2</sup>	6,1	5,4	5,2	3,7	3,8	3,5		
<b>Transect B</b>								
No. Mbuna species	17	19	17	16	14	13	12	
No. individuals all cichlids	285	345	280	290	150	200	–	
No. individuals m <sup>-2</sup>	5,7	6,9	5,6	5,8	3,0	4,0	–	
<b>Transect C</b>								
No. Mbuna species	14	21	18	17	14	13	11	9
No. individuals all cichlids	430	325	315	315	140	210	–	–
No. individuals m <sup>-2</sup>	8,6	6,5	6,3	6,3	2,8	4,2	–	–

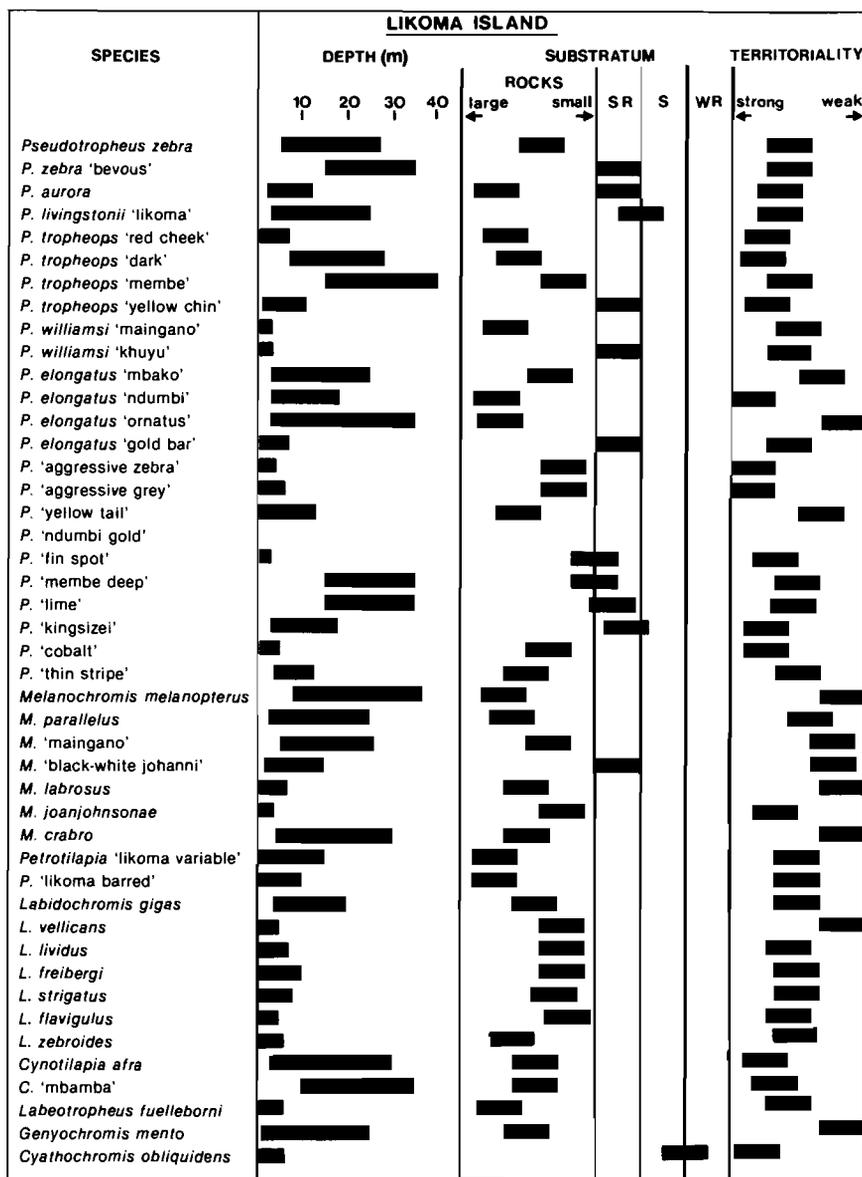


Figure 66 A summary of resource utilization of the Mbuna community at Likoma Island. For rest of legend see Figure 28 (p.254).

mon among small-medium and medium-sized rocks at both islands, and at Likoma Island *Melanochromis joanjohnsonae* is a common inhabitant of these zones in the shallow water.

There are 14 species which inhabit the intermediate zones at Likoma, though only *Pseudotropheus livingstonii* 'likoma' is common over sand (Figure 66). At Chisumulu there are five species which frequent the intermediate zones (Figure 67), but none of these ventures far from rocks. The *Melanochromis* species of these two islands are weakly territorial, the only exception is *M. joanjohnsonae* which is comparatively aggressive (Figure 66).

A behavioural characteristic of *Labidochromis* species occurring elsewhere in the lake is that they are not territorial; but of the eight species found at Likoma and Chisumulu all but *L. chisumulae* and *L. vellicans* are territorial (Figures 66 & 67). An intriguing, but unanswered question is whether the territoriality of *Labidochromis* species found at these islands is related to the fact that there are so many members of the genus at these islands.

In addition to Mbuna, a great variety of other fishes occur at Likoma and Chisumulu. Many species (e.g. Utaka species) are numerically abundant and are harvested for

food to support local fisheries (Iles 1960; Fryer & Iles 1972). Several of these fishes are also of value to the ornamental fish trade, including Utaka species such as *Cyrtocara chrysonota* and a bottom-dwelling species which builds sand-scrape nests at the sand-rock interface from 8–35 m depth. This species is sold as *Cyrtocara mloto*, but is black with contrasting light markings and does not resemble the species described as *C. mloto* by Iles (1960).

Also exploited for export to aquarists are *Aristochromis christyi*, *Cyrtocara euchila* (which is more common at Liwelo Bay, Chisumulu, than at any other site visited in Lake Malawi), *C. rostrata*, *C. moori*, *C. linni*, *C. polystigma*, *C. livingstonii*, *C. annectens* and a fish tentatively identified as *Lethrinops macrophthalmus* which builds turret nests on most of the beaches around Likoma Island. A popular aquarium fish, *Cyrtocara electra* Burgess, 1979 occurs along the rock-sand interface from 5 to at least 35 m depth. Both *Aulonocara* 'yellow collar' and *A.* 'blue collar', of the sand-rock interface, are caught for export.

#### Area 10: The north-western shores

The first comprehensive study of Mbuna ecology was conducted by Fryer (1959a) at Nkhata Bay on the western shores

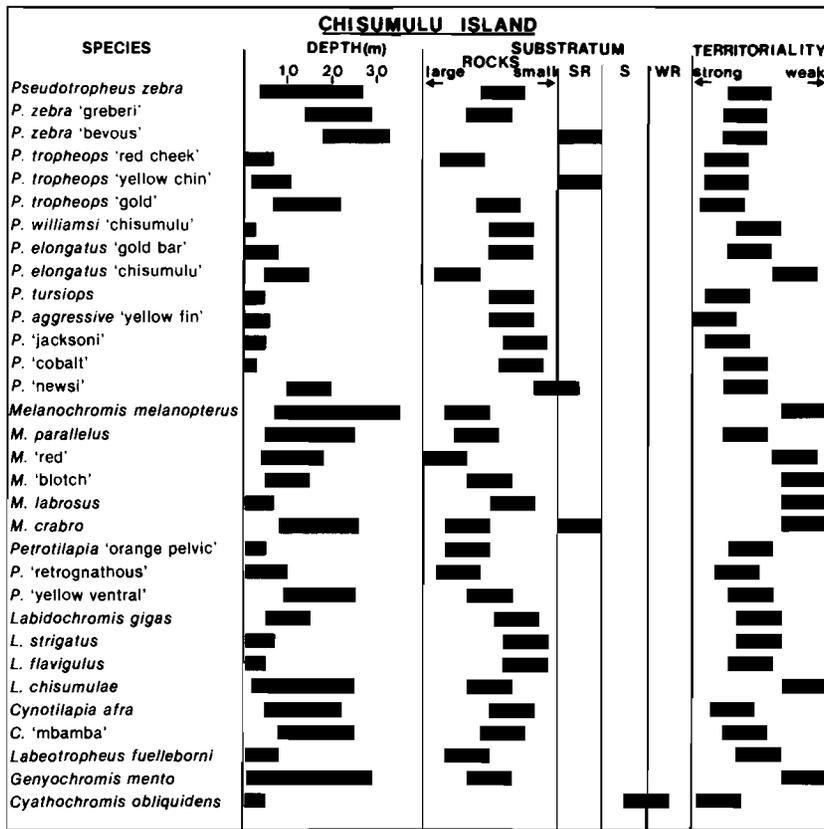


Figure 67 A summary of resource utilization of the Mbuna community at Chisumulu Island. For rest of legend see Figure 28 (p.254).

of Lake Malawi. This work was followed by an eco-behavioural programme which concentrated on the *Pseudotropheus zebra* species-complex of the same region (Holzberg 1978). Both of these studies provided an invaluable foundation for our survey of the north-western shores which extended northwards from Chirombo Point to include stations at Nkhata Bay, Lion's Cove, Mara Rocks, Dankanya Bay, Mpandi Point, Ruarwe and Chilumba (Figure 68).

The shores of this region are a little more than 150 km in length and are predominantly rocky though sandy beaches occur in most bays. A major division of the rocky shores occurs at Dankanya Bay and at Usisya Bay where long beaches (7 and 14,8 km respectively) occur on both sides of Mpandi Point (Figure 68). Sandy shores dominate the mainland coast of Chirombo Point to the Nankumba Peninsula, but a rocky zone occurs at Bandawe Point and at Bandakusha Island.

**The diving stations**

The fishes were studied at nine stations between Chirombo Point and the sandy beach at Dankanya Bay (area 10a, Figure 4), at Mpandi Point, Mara Rocks and the northernmost point in Usisya Bay (area 10b, Figure 4) and at Ruarwe and Chilumba (area 10c, Figure 4). In addition, a brief visit was made to Bandawe Point, south of Chirombo Point.

**Bandawe Point.** Bandakusha Island off Bandawe Point is a rocky outcrop in 6–8 m depth. A single 2-h visit was made to Bandawe Point and Bandakusha Island. The species found there are recorded in Table 32. A fish very like *Petrotilapia genalutea* occurs there but its coloration is not identical and the affinities are obscure at present. The uncertainty regarding the identification of this species is in-

dicated in Table 32.

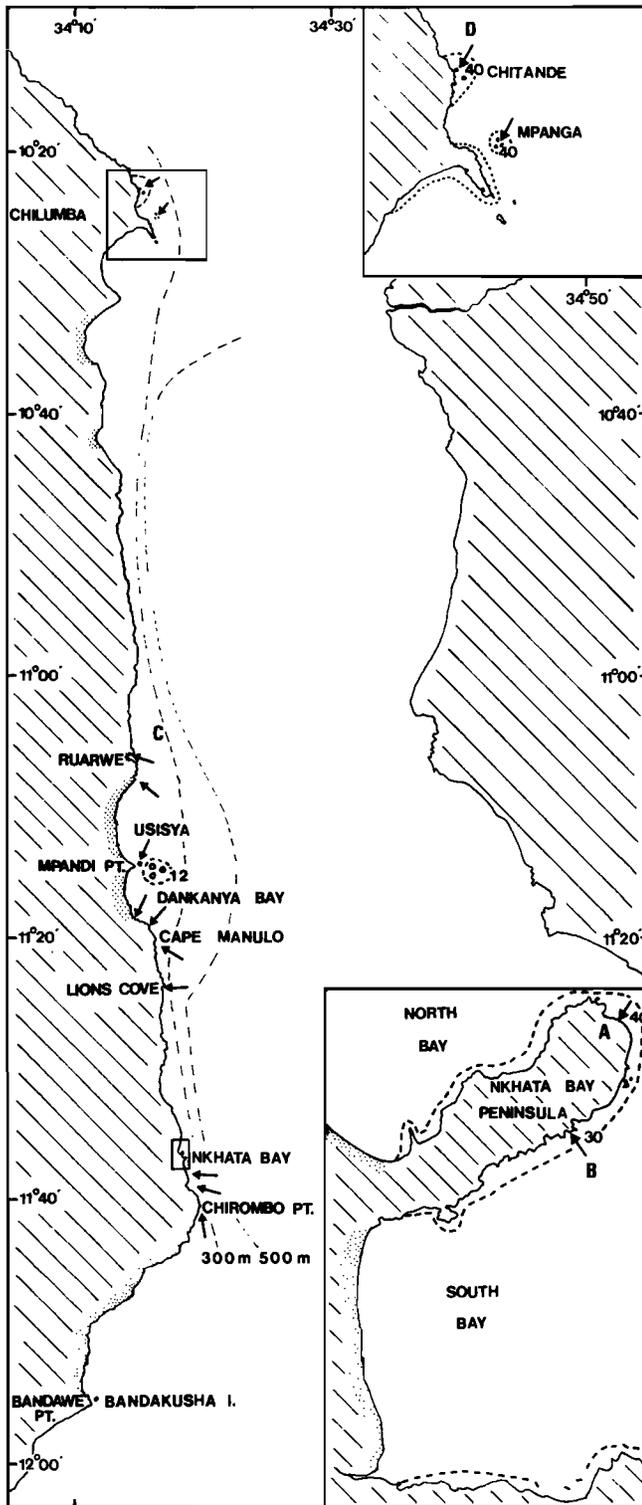
**Chirombo Point to Nkhata Bay.** The rocky shores between Chirombo Point and Nkhata Bay are dominated by large, steeply shelving rocks. Only one small sandy bay (about 100 m wide) breaks this rocky shore.

**Nkhata Bay.** At Nkhata Bay (Figure 68) two transects were conducted: (A) at the point of the peninsula which divides Nkhata Bay and (B) on the southern shore of the same peninsula (Figure 68). The rocky shore of this peninsula was described in detail by Fryer (1959a) and also by Holzberg (1978). It comprises small and medium-sized rocks on the littoral shelf, with large rocks, boulders and slabs dominating the steeply shelving region at the edge of the shelf where the rocky shore plunges steeply into deep water. At the point of the peninsula (site A) the littoral shelf extends about 110 m from the shore, where it reaches a depth of 8–10 m, and then descends rapidly to a depth in excess of 40 m. Several sandy patches occur among the rocks of the littoral shelf. On the southern shore, at site B, the littoral shelf reaches a depth of 6–9 m about 50 m from the shoreline. The bottom then descends steeply to the sandy plain at 30 m.

**Lion's Cove.** This is a small bay about 20 km north of Nkhata Bay (Figure 68). It has a sandy beach, flanked by rocky shores that shelf very steeply into deep water. The majority of rocks at Lion's Cove are medium-sized.

**Dankanya Bay and Usisya Bay.** The five stations visited in this area are:

- (i) Cape Manulo, where medium-sized and large rocks descend rapidly to 30 m.
- (ii) The southern shore of Dankanya Bay, where a gradual-



**Figure 68** The diving stations along the north-western coast of Lake Malawi are indicated by arrows. Insets show the positions of transect stations A and B on the Nkhata Bay Peninsula, and transect D at Chitande. The position of the Ruarwe transect is indicated by the letter C. The dotted lines within the insets indicate the extent of the rocky shores and the numerals within these lines give the depth at which rocks meet the sandy bottom. The shores shelf steeply, as indicated by the inshore positions of the 300 m and 500 m depth contours. Sandy beaches are stippled.

ly shelving shore of medium-sized and small rocks meets the sandy plain at 7 m.

- (iii) Mpandi Point, a small rocky outcrop on the end of a sandy peninsula between the two bays. It comprises large rocks in 3–5 m of water.
- (iv) Usisya Bay which is mainly sandy, but fishes were

studied at the site on its northern shore where small rocks predominated though scattered groups of medium-sized and large rocks rose above the general level of the bottom.

- (v) Mara Rocks, a group of rocks off Usisya which rise from the bottom at 15–25 m of water. These rocks are mainly medium-sized and large, and subject to wave action; at the time we dived a strong southerly current was prevalent.

*Ruarwe.* A transect was laid at Ruarwe on the northern arm of the bay where medium-sized rocks shelf gradually to 12 m depth and then more steeply to at least 40 m. From 30 to 40 m depth sand patches appeared among the rocks.

*Chilumba.* Two sites were studied at Chilumba; Mpanga Rocks and Chitande Point (Figure 68). Mpanga Rocks form part of a rocky reef that runs out from the mainland and comprises huge boulders and large rocks. Isolated patches of small and medium-sized rocks were found between the boulders and at one site a little sand had gathered in a rocky valley. At the diving station the rocks descended to at least 40 m. A transect was laid on the north-easterly shore of Chitande Point where medium-sized rocks descended gradually to 11 m and then more steeply to 40 m. At the time of the survey (Oct. 1980) Chitande Point was cut off from the mainland by a 10 m stretch of water which was no more than 1,5 m deep.

#### *The communities*

There are at least 54 Mbuna species along the rocky shores of the north-western regions (Table 32). The species assemblage at each diving station is unique and the differences between the assemblages become progressively greater as the distance between stations increases. Thirty-seven species of Mbuna occur along the southern rocky shore from Chirombo Point to Dankanya Bay, 17 occur in the central region, including Mara Rocks and Mpandi Point and 35 were found in the northern region from Usisya to Chitande. The northern and southern regions have 19 species in common, but there are 30 species which do not occur in both regions; 16 of these occur in the southern region only and 14 are confined to the northern region. Of the 17 species found in the central region one is endemic, two are shared with the northern region and 14 occur in both the northern and southern regions. These differences in the species assemblages along this coast may be attributed to the sedentary nature of Mbuna (see p.301), the considerable distance between stations and, as most Mbuna have a reluctance to cross sandy areas (Fryer 1959a), it is likely that the various beaches, particularly those at Dankanya Bay and Usisya Bay, constitute major physical barriers to the distribution of at least some species.

Forty of the species occurring along the north-western shores were found nowhere else in the lake and several species are apparently restricted in their distribution to small parts of the coast. The number of previously described species in the area is 20 (Table 32).

This study area has more members of the *Pseudotropheus zebra* species-complex, the *P. tropheops* species-complex, the *P. elongatus* species-group, and more species in the genera *Petrotilapia* and *Cynotilapia* than any other area. In contrast, the *Pseudotropheus* 'aggressive' species-group and the *P.* 'miscellaneous' species-group are poorly represented, each having only three members (Table 32).

**Table 32** The Mbuna at the principal diving stations of the north-western shores of Lake Malawi. Present (+); absent (-); uncertain (?); present but identification uncertain (+ ?); found at sites along the north-western shores only (\*)

Species	Diving stations of north-western shores										
	Southern				Central		Northern				
	Bandawe	Nkhata Bay	Lion's Cove	Dankanya Bay	Mara Rocks	Mpandi Point	Usisya	Ruarwe	Mpanga Rocks	Chitande	
1. <i>Pseudotropheus zebra</i>	-	+	+	+	-	-	-	-	-	-	
2. <i>P. zebra</i> 'cobalt'	*	-	+	+	+	-	-	-	-	-	
3. <i>P. zebra</i> 'gold'	*	-	+	+	+	-	-	+	-	-	
4. <i>P. zebra</i> 'ruarwe'	*	-	-	-	-	-	-	+	-	-	
5. <i>P. zebra</i> 'chilumba'	*	-	-	-	-	+	+	+	+	+	
6. <i>P. zebra</i> 'mpanga'	*	-	-	-	-	-	-	+	-	-	
7. <i>P. zebra</i> 'pearly'	*	-	-	-	-	-	-	+	+	-	
8. <i>P. zebra</i> 'ianth'	*	-	-	-	-	-	-	-	+	-	
9. <i>P. zebra</i> 'chitande'	*	-	-	-	-	-	-	-	-	+	
10. <i>P. tropheops</i> 'mauve'	*	+	+	+	+	+	+	+	+	+	
11. <i>P. tropheops</i> 'olive'	*	-	+	+	+	+	+	+	+	+	
12. <i>P. tropheops</i> 'black'	*	+	+	+	+	+	+	+	+	+	
13. <i>P. tropheops</i> 'rust'	*	+ ?	+	+	-	-	-	-	-	-	
14. <i>P. tropheops</i> 'deep'	*	-	+	-	-	-	-	-	-	-	
15. <i>P. tropheops</i> 'band'	*	-	+	-	-	-	-	-	-	-	
16. <i>P. tropheops</i> 'no band'	*	-	+	-	-	-	-	-	-	-	
17. <i>P. tropheops</i> 'red fin'	*	-	-	-	-	?	-	-	+	+	
18. <i>P. tropheops</i> 'weed'	*	-	-	+	+	-	+	-	?	-	
19. <i>P. tropheops</i> 'chitande yellow'	*	-	-	-	-	-	-	-	-	+	
20. <i>P. williamsi</i> 'nkudzi'	*	-	+ ?	-	-	-	-	-	-	-	
21. <i>P. elongatus</i>	*	+ ?	+	-	-	-	-	-	-	-	
22. <i>P. elongatus</i> 'nkhata brown'	*	-	+	-	-	-	-	-	-	-	
23. <i>P. elongatus</i> 'mara'	*	-	-	-	-	+	-	-	-	-	
24. <i>P. elongatus</i> 'ruarwe'	*	-	-	-	-	-	-	+	-	-	
25. <i>P. elongatus</i> 'bee'	*	-	-	-	-	+	-	-	-	+	
26. <i>P. elongatus</i> 'mpanga'	*	-	-	-	-	-	-	-	+	-	
27. <i>P. fuscus</i>	*	+	+	+	-	-	-	-	-	-	
28. <i>P. fuscoides</i>	*	-	+	+	-	-	-	-	-	-	
29. <i>P. cf. M. perspicex</i>	*	-	-	-	-	-	-	+	-	+	
30. <i>P. lucerna</i>	*	+	+	+	-	-	+	+	-	-	
31. <i>P. minutus</i>	*	-	+	+	-	-	-	+	-	+	
32. <i>P. 'polit'</i>	*	-	-	+	-	-	-	-	-	-	
33. <i>Melanochromis melanopterus</i>	*	-	+	+	-	+	-	-	+	+	
34. <i>M. parallelus</i>	*	-	+	+	+	+	-	-	+	+	
35. <i>M. 'blue'</i>	*	-	+	-	-	-	-	+	+	+	
36. <i>M. crabro</i>	*	-	+	-	-	-	-	-	-	-	
37. <i>Petrotilapia tridentiger</i>	*	-	+	+	+	+	+	+	+	+	
38. <i>P. genalutea</i>	*	+ ?	+	+	+	-	+	+	-	-	
39. <i>P. 'small blue'</i>	*	-	+	+	+	-	-	-	-	-	
40. <i>P. 'ruarwe'</i>	*	-	-	-	-	-	-	+	-	+	
41. <i>P. 'chitande'</i>	*	-	-	-	-	-	-	+	+	+	
42. <i>P. 'black flank'</i>	*	-	-	-	-	-	-	-	+	-	
43. <i>Labidochromis maculicauda</i>	*	-	+	+	+	+	+	+	+	+	
44. <i>L. caeruleus</i>	*	-	+	+	-	-	-	+	?	?	
45. <i>Cynotilapia afra</i>	*	-	+	+	+	+	+	+	+	+	
46. <i>C. axelrodi</i>	*	-	+	+	-	-	-	-	-	-	
47. <i>C. 'mbamba'</i>	*	-	+	+	+	-	-	+	+	+	
48. <i>C. 'lion'</i>	*	-	-	+	-	-	-	-	-	-	
49. <i>C. 'mpanga'</i>	*	-	-	-	-	-	-	-	+	-	
50. <i>Labeotropheus fuelleborni</i>	*	+	+	+	+	+	+	+	+	+	
51. <i>L. trewavasae</i>	*	-	+	+	+	+	+	+	+	+	
52. <i>Gephyrochromis lawsi</i>	*	-	+	+	-	-	-	-	-	-	
53. <i>Genyochromis mento</i>	*	+	+	+	+	+	+	+	+	+	
54. <i>Cyathochromis obliquidens</i>	*	-	+	+	-	-	+	?	-	+	
Totals	40	9	34	29	17	14	13	12	26	22	24

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Similarly, the genus *Melanochromis* is poorly represented, having only four species of which three are uncommon or rare.

Figures 69 – 72 give the numerical abundance and depth distribution of the more common Mbuna at the two diving stations at Nkhata Bay and at the stations at Ruarwe and Chitande. Twenty-seven of the 34 Mbuna of Nkhata Bay were recorded in the transects (Figures 69 – 70). Four of those not recorded (*Pseudotropheus williamsi* 'nkudzi', *Melanochromis* 'blue', *Melanochromis crabro* and *Gephyrochromis lawsi*) are rare or uncommon. *Cyathochromis obliquidens* did not occur in either transect as it inhabits intermediate, weeded areas. *Genyochromis mento* which occurs sparsely over all rocky areas is also not included.

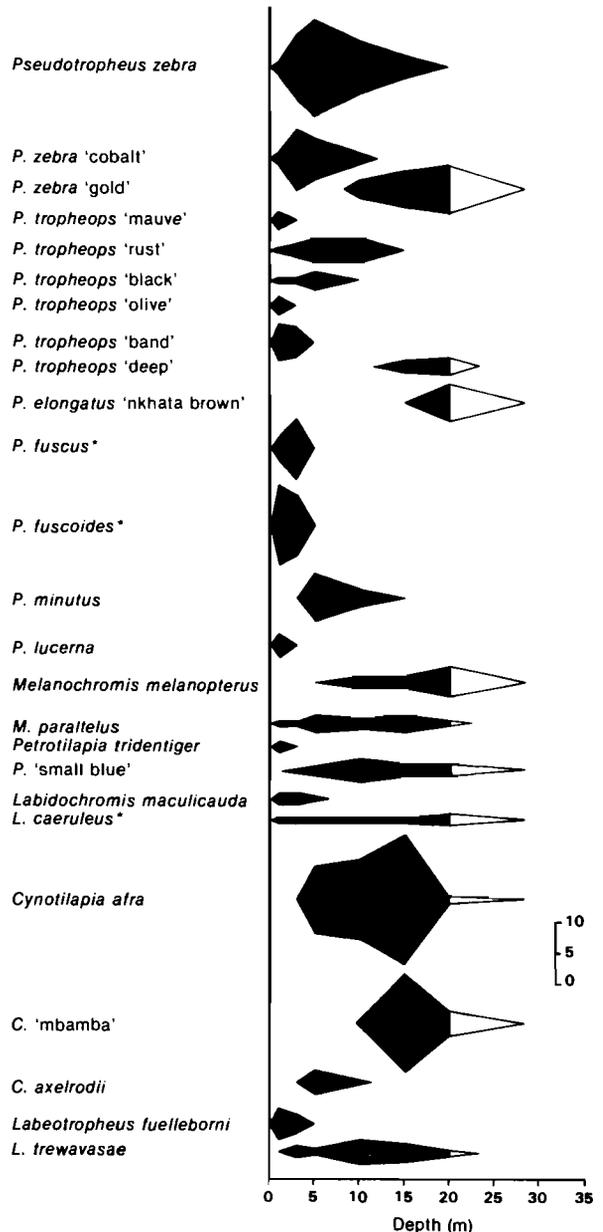
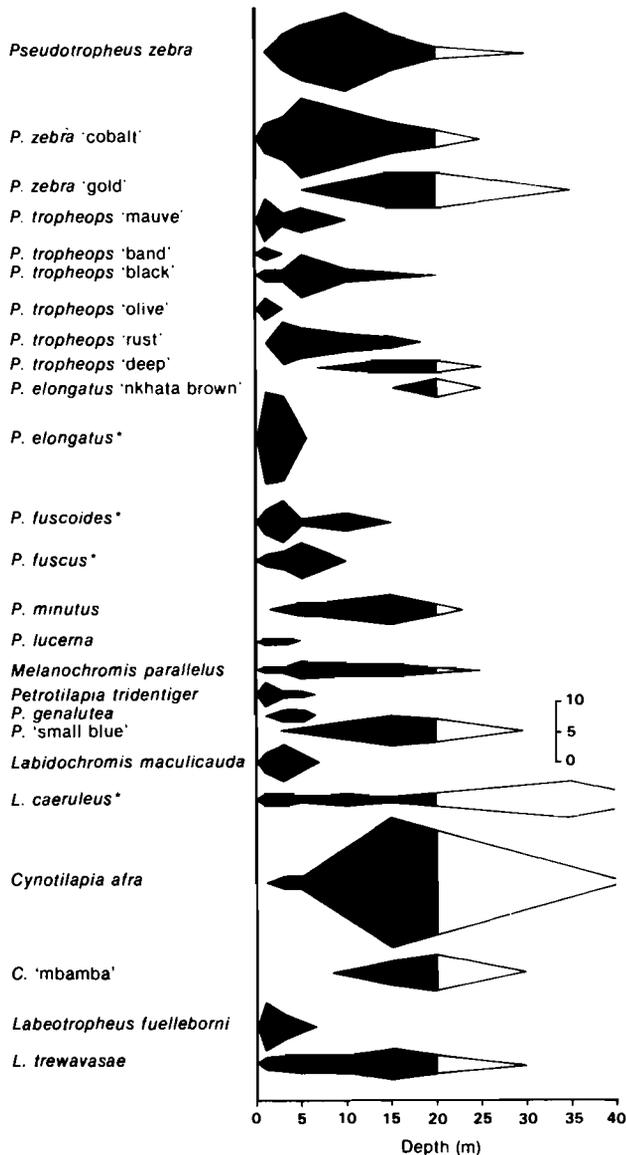
At the time the transects were laid we did not recognize the differences between *Pseudotropheus tropheops* 'band' and *P. tropheops* 'no band' and so these two fishes are recorded together as *P. tropheops* 'band' (Figures 69 & 70).

At Ruarwe, *Pseudotropheus lucerna*, *Melanochromis melanopterus*, *Petrotilapia genalutea*, *Labidochromis*

*caeruleus*, *Cynotilapia axelrodi* and *Genyochromis mento* were too sparsely distributed to be recorded in the transect.

Eighteen of the 23 species occurring at Chitande were recorded in the transect; those not recorded are the inhabitants of the intermediate zone (*Pseudotropheus tropheops* 'weed', *P. elongatus* 'bee', *P. cf. Melanochromis perspicax*, *Cyathochromis obliquidens*) and *Genyochromis mento*.

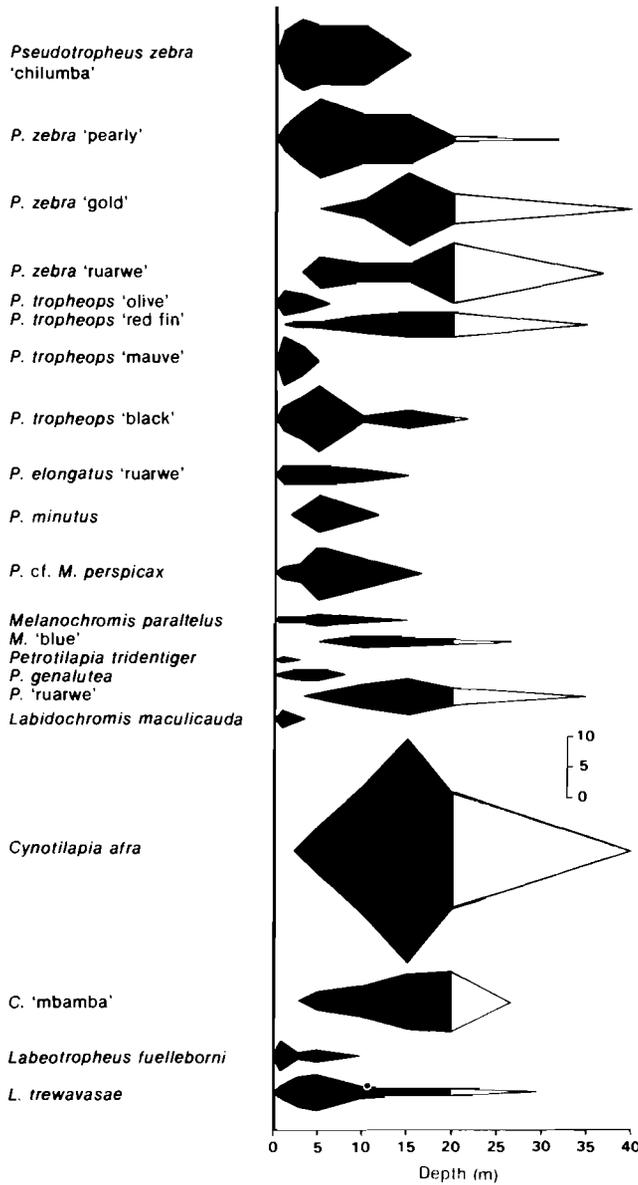
At all sites members of the genus *Cynotilapia*, particularly *C. afra*, and of the *Pseudotropheus zebra* species-complex dominate the rocky shores numerically (Figures 69 – 72). These habitats also teem with numerous individuals, especially non-territorial individuals, of a variety of species of the *Pseudotropheus tropheops* species-complex. Furthermore, the *Petrotilapia* spp. and the *Labeotropheus* spp. are well represented among medium-large and large rocks. The areas of small rock at Nkhata Bay are dominated by *Pseudotropheus fuscus*, *P. fuscooides* and *P. minutus*. Similar habitats at Ruarwe and Chilumba are dominated



**Figure 69** Transect A, Nkhata Bay, 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<sup>-2</sup>.

**Figure 70** Transect B, Nkhata Bay, 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<sup>-2</sup>.

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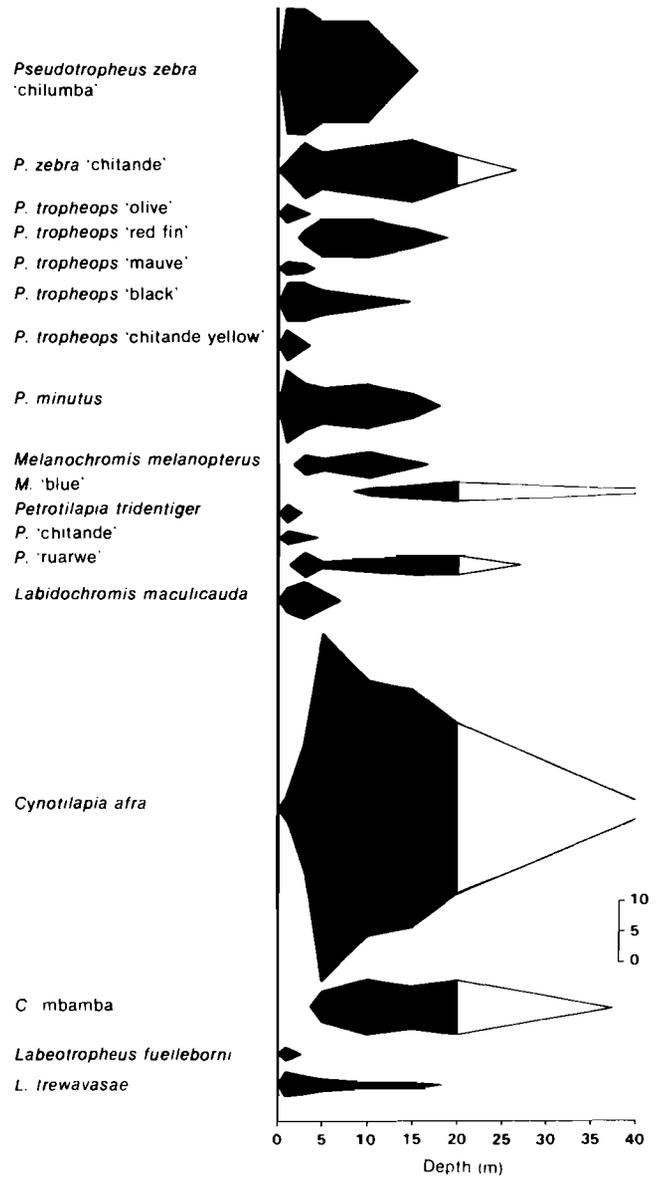
**Figure 71** Transect C at Ruarwe, giving the depth distribution and numerical abundance of the Mbuna species. Territorial males of each species were counted except for those species marked (\*) where both sexes were counted. Numerical abundance = fishes 50 m<sup>-2</sup>.

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<sup>-2</sup>.

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

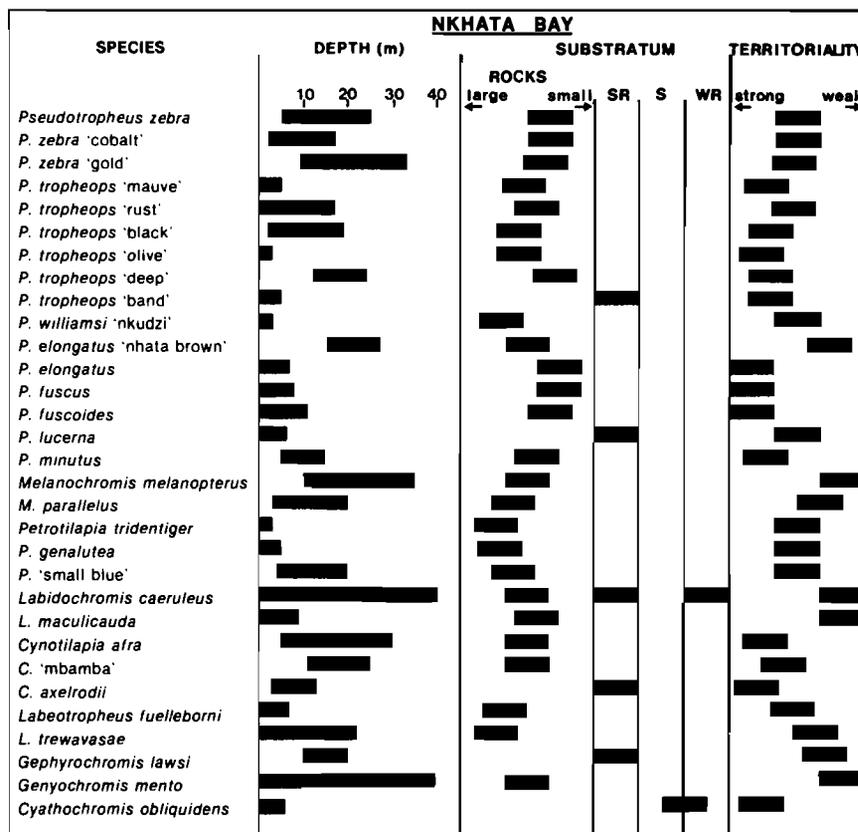
**DISCUSSION**  
**Aquarium fish resource**

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

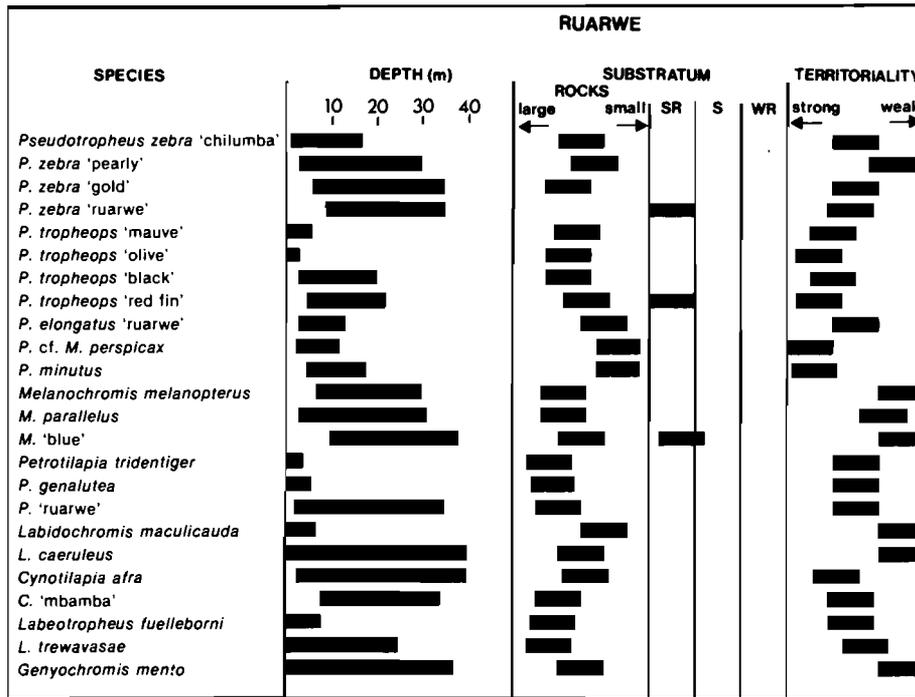


Figure 74 A summary of resource utilization of the Mbuna community at Ruarwe. For rest of legend see Figure 28 (p.254).

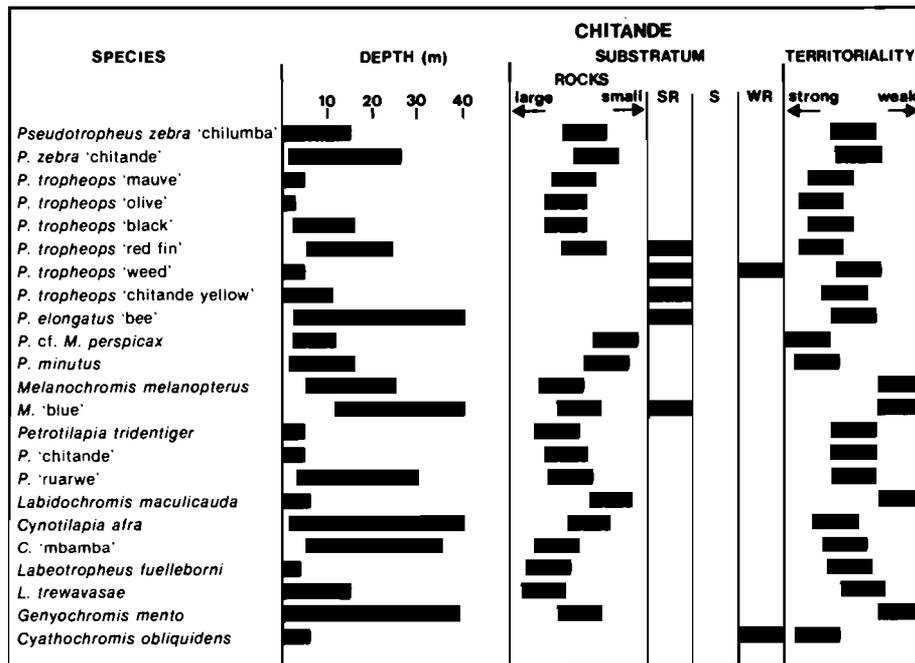


Figure 75 A summary of resource utilization of the Mbuna community at Chitande. For rest of legend see Figure 28 (p.254).

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 in 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. freibergi*, *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. 'burrer'*, *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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# South African Journal of Zoology

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