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

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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 preferenda, 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.

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Die meeste van die akwariumvisse wat vanaf die Malawimeer uitgevoer word, is sikliede 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 akwariumvisbron berus hoofsaaklik op sy spesierykdom. 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 mikrohabitatte 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 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^2 (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^{-1} (Eccles 1974) and sometimes blowing at 60 – 70 km h^{-1} (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 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.

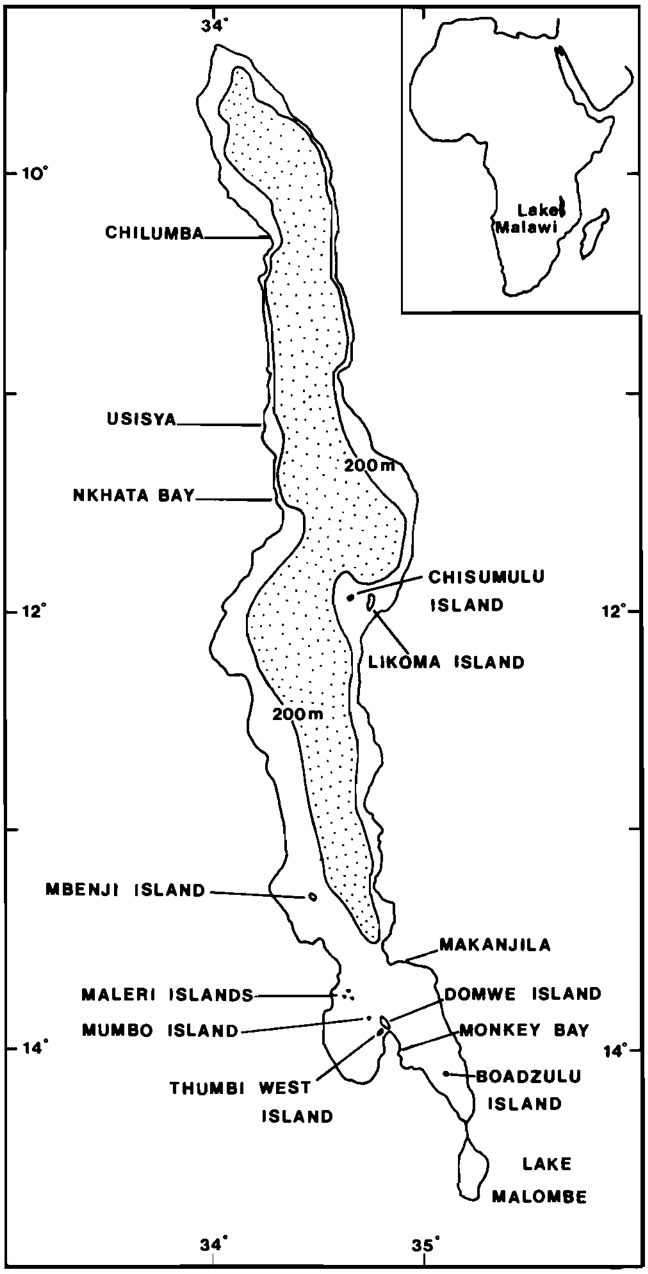

Figure 1 A map of Lake Malawi with an insert of Africa showing the location of the lake. The position of some of the more important study sites and of the 200 m depth contour are indicated.

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 taxonomic 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 fluviatile, 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^2 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 overestimate 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 within some of the areas studied was confirmed by rotenone poisoning and night dives (unpublished data).

Figure 2 Divers retrieving a line transect.

The 50 m^2 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^2 are based on considerable experience of

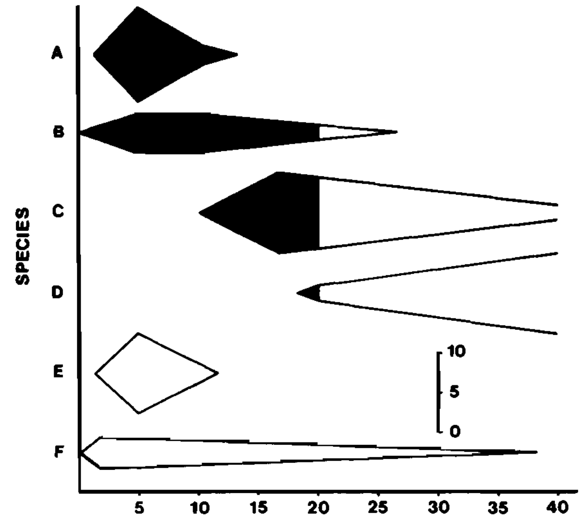

Figure 3 The convention used to show numerical abundance of different species with depth. Solid black sections are line transects in which the individuals were counted. Open sections are point transects in which fish numbers were estimated, as for species E and F. All individuals of species A occur in 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^2 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

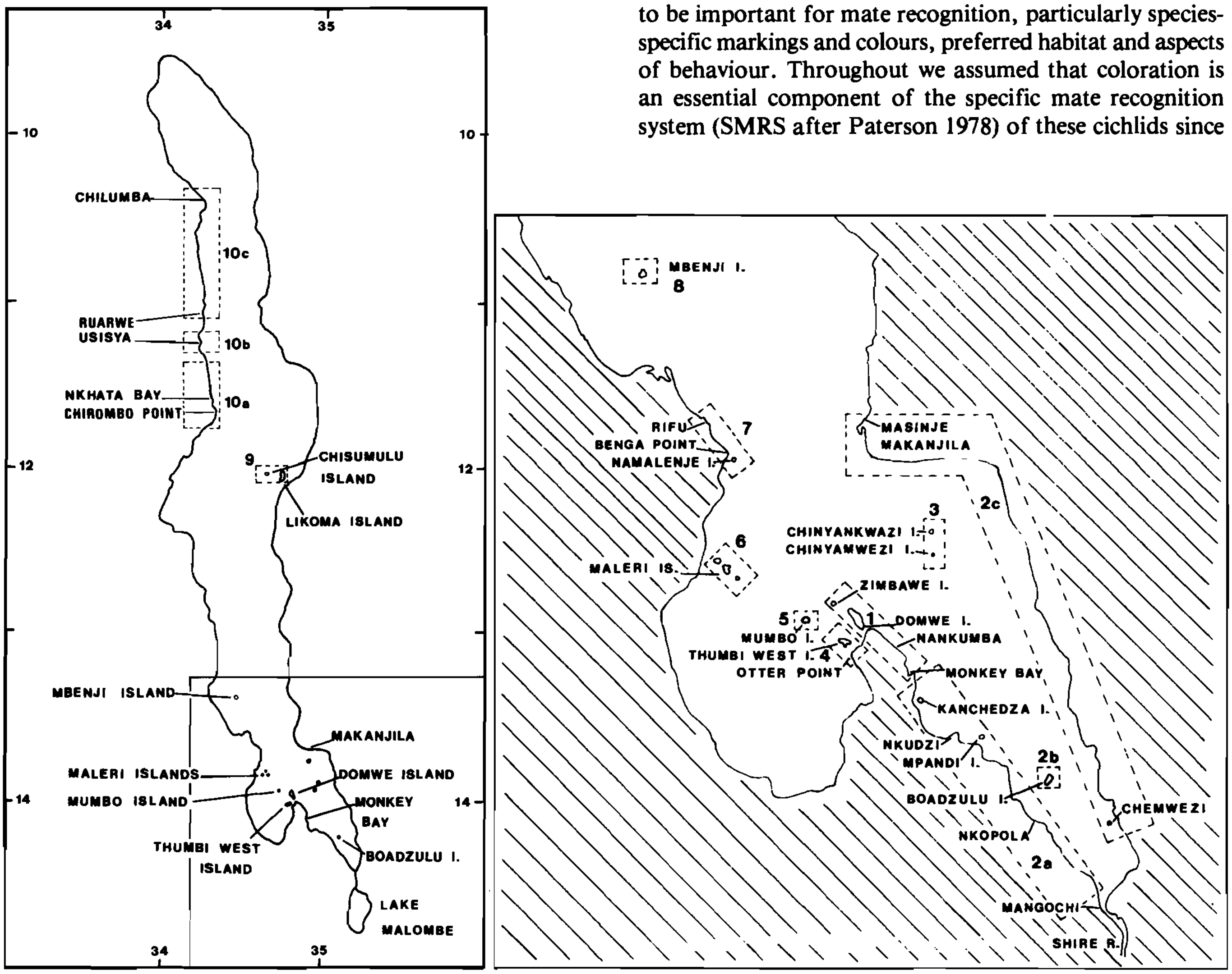

Figure 4 The 14 major study areas in Lake Malawi are indicated by the dotted blocks and are numbered 1 – 10c.

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 popuations 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, superspecies, 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 trinominals 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 popuations 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 preferenda 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 preferenda 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

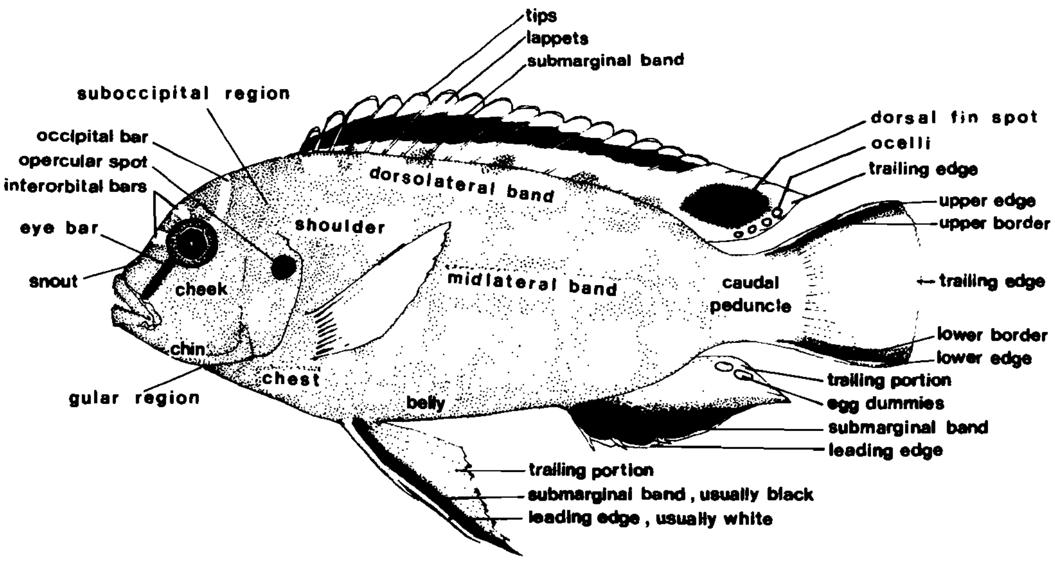

Figure 5 An illustration of the markings and the terminology used to describe them.

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.