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The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation

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Abstract

Mbuna, the dominant fishes on the rocky shores of Lake Malawi, have become a major 'model system' for the study of rapid speciation and adaptive radiation. At least 295 putative species are known, of which more than 200 remain undescribed. There is no good evidence for monophyly in the mbuna, rather mitochondrial DNA phylogenies indicate that they are polyphlyetic with respect to benthic feeding cichlids of the genera *Aulonocara*, *Alticorpus* and some species of *Lethrinops*. Male mbuna hold territories for 18 months or more and breed year-round. All species are maternal mouthbrooders, but females do not guard free-swimming young. Mbuna are polygamous (both sexes). There is sexual dimorphism in size, colour and fin length, and many species show within-population colour polymorphism. Mbuna genera are largely differentiated on the basis of head, jaw and tooth morphology, but congeneric species are generally distinguished by male colour. Many morphologically specialized forms have broad diets and often feed on common easily obtainable resources. While it is likely that dietary and habitat niche partitioning contributes to species coexistence, this has never clearly been demonstrated under experimental conditions. Populations on spatially separated habitat patches are often genetically differentiated, probably because most species are specialized for life on rocky shores, and lack a dispersal phase in their life histories. Males seem to disperse more than females, but are able to home several kilometres back to their territories. Some closely related ecologically equivalent allopatric populations are differentiated in male colour. Those tested have been shown to mate at least partially assortatively. Sexual selection acting on male colour seems the most plausible mechanism for initial species divergence. The same colour forms seem to have arisen several times, suggesting frequent parallel evolution. The main conservation threat to mbuna at present seems to be translocation of species within the lake as a result of the aquarium trade. However, deleterious effects on indigenous populations are not documented. In the long run, sedimentation, pollution, introduction of alien species and the development of targeted food fisheries could be more serious threats.

Keywords adaptive radiation, cichlid fish, conservation, Lake Malawi, mbuna, speciation

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Introduction

The cichlid fishes of the Great Lakes of Africa have become internationally renowned for their rapid speciation and adaptive radiation. It is estimated that the three largest African lakes may contain between them as many as 1500 cichlid species (Genner *et al.* 2004a). Approximately 450–535 species are endemic to Lake Victoria (Genner *et al.* 2004a), which is believed to have largely or wholly dried up as recently as 14 500 years ago (Johnson *et al.* 1996). Although there is debate over how much of the species richness and adaptive diversity persisted in refuges during this period (Seehausen 2002; Verheyen *et al.* 2003), it is likely that the rate of diversification of these fishes is remarkably high. Lake Tanganyika contains around 160–185 endemic cichlid species (Genner *et al.* 2004a). These are representatives of several ancient distinct lineages (Salzburger *et al.* 2002) and are well known for their remarkable diversity of reproductive habits, as well as in morphological and ecological variation (Rossiter 1995). Lake Tanganyika is thought to be at least 5–6, or perhaps even 20 million years old, and it has proved feasible to elucidate the phylogenetic relationships of the major groups within the lake using mitochondrial DNA sequences (Salzburger *et al.* 2002). Lake Malawi contains 450–600 species of cichlid fishes (Genner *et al.* 2004a), of which five species are members of the tilapiine tribe (Turner 1996), and the rest are haplochromines of which only two are not endemic to the Lake Malawi Basin (Turner 1996). The endemic haplochromines are found in all surveyed habitats, and show great morphological diversity. They include the mbuna which dominate the rocky shores of Lake Malawi (Fig. 1). The mbuna are arguably the best-studied cichlid fishes from the African Great Lakes, and are developing as a model system for the study of explosive speciation and rapid adaptive radiation. There is now a substantial body of literature describing their systematics, ecology, behaviour and life-history strategies. A recent field guide to the Malawi cichlids listed 295 candidate mbuna species (Konings 2001), of which only 89 have been formally described within 10 to 12 recognized

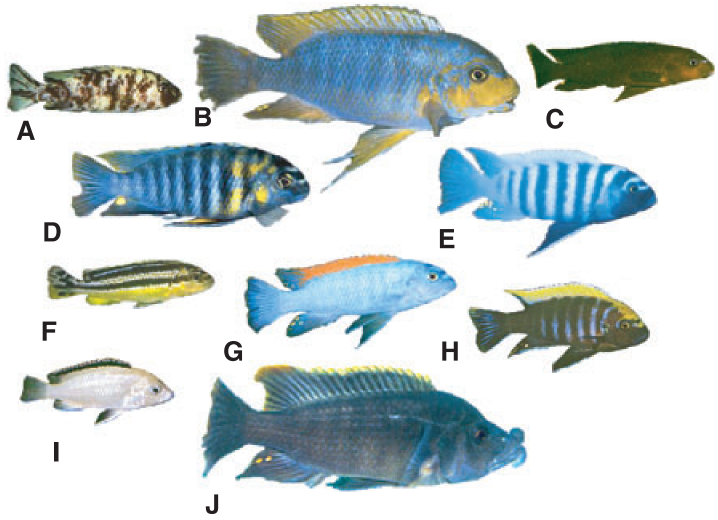

Figure 1 Representative mbuna body shapes and colour patterns: A, *Genyochromis mento* feeds mainly on fish scales, OB-morph female; B, *Petrotilapia* sp. 'retrognathus' combs edible material from between strands of filamentous algae, male; C, *Pseudotropheus ater*, a member of the 'elongatus' group, is a cryptic species living in caves among rocks, male; D, *Pseudotropheus* (*Tropheops*) sp. 'red cheek' feeds with its body at about 45°, scraping algae close to the rock surface, male; E, *Pseudotropheus* (*Maylandia*) *zebra* is an abundant generalist feeder on rocky shores, BB-morph male of a blue-dorsal race; F, *Melanochromis auratus* is a roaming opportunist that feeds within the territories of other species, female; G, *Labeotropheus trewavasae* has an underslung mouth allowing it to feed close to rock surfaces while holding its body almost parallel to the substract, BB-morph male of a red-dorsal race; H, *Cynotilapia* sp. 'mbamba' – like many other zooplanktivores, males have a bright 'blaze' on the dorsal fin and upper surface of the head, probably to attract females down from the water column, male; I, *Labidochromis caeruleus* uses its narrow mouth to feed on tiny invertebrates among rocks, male of white race; J, *Melanochromis labrosus* feeds on small animals which it suck from cracks between rocks, probably using its thickened lips to help seal the crack, male. Edited from photographs by Ad Konings.

genera. Given the apparent high species richness, diverse functional morphology and the geologically short timescale over which these have arisen, research over recent years has focussed on the evolutionary and ecological processes responsible for generating and maintaining diversity. Although mbuna figure prominently in other reviews of African cichlid biology, we aim to provide the first comprehensive review devoted entirely to this important group. We summarize current knowledge on the many aspects of mbuna diversity ranging from genetic to ecological variation, and review the empirical evidence for possible mechanisms of speciation and coexistence. Finally, we reflect on the conservation biology of these fishes.

What are mbuna?

The term 'mbuna' comes from the Chitumbuka language spoken in northern Malawi (A. Konings pers. comm.). The term has no formal taxonomic validity and the diagnosis of mbuna as a group is not clear-cut. To our knowledge, they have no morphological characters or behavioural traits that are not also shared with other groups of haplochromine cichlids. Trewavas (1935) mentions that mbuna have small scales on the cheek and nape, but recognizes that some do not differ from the majority of haplochromines in this respect. Fryer (1959a) describes mbuna showing a 'rather abrupt change in scale size from the chest to flank.' This trait is found in other rocky shore cichlids, including the Lake Victoria mbipi (Seehausen 1996), as well as some riverine forms, such as the Congolese-Nilotic genus *Thoracochromis* (Eccles and Trewavas 1989). It has been stated that a distinctive trait is that female mbuna generally have a clear asymmetry in ovary size, with the left being somewhat smaller than the right (Stauffer *et al.* 1997), but this character is also found in the Malawian pelagic *Diplotaxodon* (Turner and Stauffer 1998) and *Rhamphochromis* (G.F. Turner, pers. obs.), as well as in Lake Victoria mbipi (O. Seehausen pers. comm.). When considering diagnostic features of mbuna, Trewavas (1935) also emphasized coloration that is rarely encountered elsewhere, including broad black submarginal bands on the dorsal fin (also noted in *Simochromis babaulti* from Lake Tanganyika by Eccles and Trewavas 1989), and the posterior position and bright intensity of the one or more spots on the male anal fin. Eccles and Trewavas (1989) described these as 'true ocelli', in other words non-overlapping spots that have a dark or translucent ring around the bright yellow spot. However other taxa possess such well-defined patterning on the anal fin, including *Astatotilapia calliptera* (see illustration in Konings 2001), although the spots of *A. calliptera* are arranged in a long row, while those of the mbuna are irregularly distributed on the posterior part of the anal fin (Eccles and Trewavas 1989), a trait shared with the Lake Victoria mbipi (Seehausen 1996).

While mbuna populations are largely restricted to the rocky shore habitats (Figs 2 and 3), this also cannot be considered to be a diagnostic trait of the group. Many other non-mbuna are found in this habitat and many species of mbuna are found away from rocky habitats (Figs 2 and 3). For example, *Pseudotropheus livingstonii*, *P. elegans* and *P. lanisticola* are associated with empty snail shells on a sandy or muddy bottom, often kilometres away from the nearest rocky habitat, while adult *P. pursus* do not seem to require even such a minimal amount of hard substrate (Stauffer 1991). The same appears to be true of *Gephyrochromis lawsi* and *Cyathochromis obliquidens*, two species that are present in the only major outflow from the lake, the Upper Shire River, and in Lake Malombe, a rather shallow muddy satellite lake joined to the main basin by the Upper Shire (Turner 1996).

Nonetheless, despite the absence of a convincing diagnosis, most researchers, experienced aquarists and African fishermen and fish collectors seem to have little trouble in assigning most species to the mbuna or non-mbuna group, with the exception, perhaps, of *Melanochromis labrosus*.

Systematics

The first taxonomic descriptions of mbuna were made by Günther and Boulenger of the British Museum of Natural History (BMNH) from the

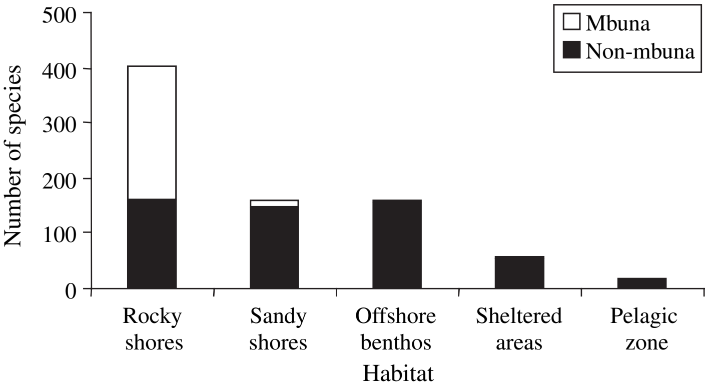

Figure 2 The broad habitat distribution of Lake Malawi cichlid species. Data obtained from Konings (1995); Spreinat (1995) and Turner (1996). 'Sheltered areas' refers to sheltered inshore bays, lagoons, river mouths, the Shire River and Lake Malombe.

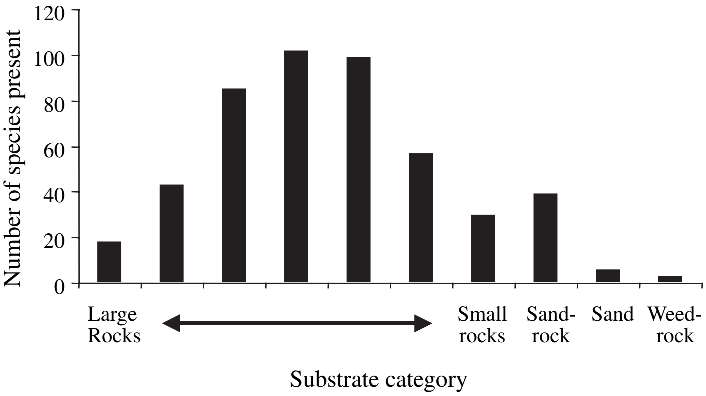

Figure 3 The habitat preferences of mbuna species on the rocky shores of Lake Malawi. Data derived from Ribbink *et al.* (1983). Note species are usually present within more than one habitat category. Rock-size category units are not presented on the original charts from where data are taken.

collections of Kirk, the physician-naturalist with Livingstone's second (1858–1864) expedition to the Zambezi region (e.g. Günther 1864; Boulenger 1915). Following this, a series of descriptions were made by Regan (1922) and Trewavas (1935), both also working at the BMNH. Subsequent mbuna descriptions have been made by a series of professional and amateur researchers. More recent large-scale taxonomic reviews include those of *Labidochromis* (Lewis 1982), part of *Pseudotropheus* (*Maylandia*) (Stauffer *et al.* 1997), and part of *Melanochromis* (Bowers and Stauffer 1997). The first large-scale biogeographic survey of mbuna was conducted by Ribbink and colleagues in the late 1970s and early 1980s. They recognized 196 mbuna taxa from the Malawian shores of the lake, of which a mere 49 were previously described as species (Ribbink *et al.* 1983). They initiated a nomenclature system, intended as temporary, of providing taxa with mixed Latin/English names, such as *Pseudotropheus* 'zebra gold', *Cynotilapia* 'mbamba' or *Pseudotropheus* 'tiny'. However, their system has proved remarkably stable. For example, all three of the preceding names were still in use 18 years after the Ribbink group's paper (e.g. Konings 2001). A number of species, most of which had already been identified by Ribbink *et al.*, have been formally named since then, but the majority remain undescribed. The attraction of Ribbink *et al.*'s system has been to provide a means of rapid, efficient and clear communication without the need to carry out laborious and repetitive formal descriptions. The key features of the Ribbink *et al.* identification guide were the clarity of the colour description, often backed by underwater colour photographs, and the accuracy of the location information. This has enabled most subsequent workers to identify mbuna species readily, indeed often more readily than on the basis of a formal description with an anatomically accurate black and white drawing that often fails to capture the subtle nuances of the body shape which are a useful aid to identification. By providing many more colour underwater illustrations, the ability of field workers to identify mbuna species has been greatly enhanced by the excellent field guides of Konings (1989, 1990, 1995, 2001) and Spreinat (1995), who have revised some of Ribbink *et al.*'s classification on the basis of field observations, and have expanded the geographical coverage to other locations in Malawi, as well as to the Mozambican and Tanzanian shores. Consequently, it seems likely that the great majority of mbuna taxa are now known, and can readily be identified. However, their status as biological species is often contentious.

Diagnosis of sympatric species

For many years, cichlid systematists tried to define species on the basis of morphological traits apparent on preserved material, particularly skull form, jaw shape and positioning, morphology and arrangement of teeth in the oral and pharyngeal jaws, and the thickness and shape of the lips (Barel *et al.* 1977; Ribbink 1994). Fryer (1959a) speculated that anatomical differences were perhaps not essential for delimiting species, proposing that instead colour differences may act as significant barriers to interbreeding. Fryer suggested that the *P. zebra* complex might be a good place to start such investigations. Holzberg (1978) examined the courtship behaviour of what was then considered to be a single colour-polymorphic species, *Pseudotropheus zebra* at Nkhata Bay. He found that males with plain blue courtship coloration, now known as *P. callainos*, courted only blue or white females, while males with blue-black striped courtship coloration, *P. zebra*, courted only brown, orange or orange-blotch females. Thus, these taxa appeared to represent two sympatric, yet assortatively mating populations of anatomically indistinguishable individuals. Enzyme electrophoresis (McKaye *et al.* 1984) and microsatellite DNA allele frequency analysis (Van Oppen *et al.* 1998) later confirmed the genetic isolation of these taxa. Similar results have been found with groups of sympatric colour forms of *Petrotilapia* (McKaye *et al.* 1982) and *Pseudotropheus* (*Tropheops*) species (Van Oppen *et al.* 1998), as well as a third *P. zebra* species at Nkhata Bay, known as *P.* 'zebra gold' (Van Oppen *et al.* 1998).

Allopatric species and colour races

Estimates of total species counts for the mbuna and component genera are heavily influenced by the allocation of species status to allopatric populations (Turner *et al.* 2001; Genner *et al.* 2004a). While field sampling can be used to delimit sympatric taxa with considerable accuracy, the status of allopatric colour races is more contentious.

It seems that there are no clear-cut morphological forms of mbuna that are geographically restricted within the lake (Turner 1994a). Stauffer *et al.*

(1997) used a combination of colour and multivariate shape differences to diagnose species. The use of shape seems problematic. There is as yet no evidence that subtle differences in body shapes have anything to do with reproductive isolation. While we know of sympatric species with very similar body shapes that differ in colour and do not interbreed, we do not know of any sympatric species with the same colour, but subtly different body shapes that behave as biological species, although it could be argued that it would not be easy to detect such species. Second, it would appear that subtle anatomical differentiation can arise very quickly among allopatric populations of the same species. For example, Stauffer and Hert (1992) found considerable differences between the morphology of a native population of *Pseudotropheus callainos* and one founded from individuals translocated to another location in the lake around 20 years earlier. Such allopatric divergence may have a genetic basis or it could be a consequence of the phenotypic plasticity that has frequently been demonstrated in African lake haplochromines (e.g. Witte *et al.* 1997). In any case, because such rapidly acquired allopatric differences can be of the scale that has been used to delimit species, the use of morphometrics alone to resolve species differences among mbuna might be unwise.

To delimit putative species found in allopatry, Ribbink *et al.* (1983) applied the concept that differences in (usually male) colour are a consequence of the evolution of divergent mate recognition systems that would maintain species distinctness should currently allopatric taxa later find themselves in sympatry. However, where there was clearly a recognizably similar form found in other locations, but never alongside a similar morphotype, they allowed some populations, however different in male colour, to be considered conspecific geographic races. Ecological differences and microhabitat preferences were also employed as part of the species diagnosis. Sometimes the application of this appears somewhat arbitrary. For example, Ribbink *et al.* identified eight allopatric species within the *Pseudotropheus williamsi* complex. In contrast, they recognized only two species of *Labeotropheus* found throughout the lake in sympatry, although male coloration in each species of this genus varies considerably more than in the *P. williamsi* complex (see photographs in Konings 1995, 2001).

Perhaps the most conservative method for determining species status is to find out if closely-related taxa ever occur in sympatry, and if not to allocate them to the same species (Genner *et al.* 2004a). Alternatively, if reasonable molecular phylogenetic estimates are available, the criterion of genetic similarity or clade monophyly could be used to group together populations of allopatric forms into species (e.g. Rico *et al.* 2003). However, this level of phylogenetic resolution is only just becoming possible with mbuna (see below) and presently, little information is available.

Finally, species status could be tested in the laboratory. This has been carried out for many organisms where species do not interbreed because the hybrids are sterile or fail to survive or where mating cannot take place because of physical or behavioural incompatibilities. Studies of mbuna and other haplochromine cichlids have shown that often even quite distantly related species can interbreed to produce viable fertile hybrids (Crapon de Caprona and Fritzsch 1984; Knight *et al.* 1998). However, Turner *et al.* (2001) argue that laboratory studies of assortative mating under conditions where mate choice is possible can give an insight into species status of allopatric populations. Using laboratory mate choice trials, Knight and Turner (2004) demonstrated partial assortative mating among all bar one combination of five geographically isolated races of the *P. zebra* complex. In all of these races, the commonest male colour form was blue with dark vertical bars and races differed in traits such as dorsal fin colour (blue, orange, blue with black band), throat colour (blue, yellow) and intensity of dark bars. Populations of *P. zebra* from Nkhata Bay and Chisumulu Island, where males differed only in the presence or absence of a dark stripe between the eyes, mated randomly with each other. This demonstrates that it may be appropriate to use fairly subtle differences in male courtship colour to designate allopatric species or subspecies.

Genera

Ten genera are commonly recognized to comprise the mbuna (Table 1). An eleventh genus, *Microchromis*, was erected by Johnson (1975) and is listed as valid by Eschmeyer (2004), but the sole described species of the genus, *M. zebroides*, has yet to be positively identified from the field since description, and the genus is considered of dubious validity (Ribbink *et al.* 1983), and is probably a junior synonym of *Cynotilapia* (Oliver 2004). The most species rich genus is *Pseudotropheus*, which Ribbink

Table 1 Estimated species richness of genera and subgenera of mbuna (data from Konings 2001).

Genus/Subgenus	Valid described species	Junior synonyms	Undescribed taxa	Estimated valid species
Cyathochromis Trewavas	1	0	0	1
Cynotilapia Regan	2	1[1]	8	10
Genyochromis Trewavas	1	0	0	1
Gephyrochromis Boulenger	2	0	1	3
Iodotropheus Oliver and Loiselle	2	1	0	2
Labeotropheus Ahl	2	1[2]	1	3
Labidochromis Trewavas	17	2[3]	21	38
Melanochromis Trewavas	17	7	5	22
Petrotilapia Trewavas	4	0	17	21
Pseudotropheus Günther				
P. (*Maylandia*)	17	7	27	44
P. (*Pseudotropheus*)	19[4]	1	81	99
P. (*Tropheops*)	7	0	44	51
Total	90	20	205	295

[1–3]Species not mentioned by Konings (2001), as names have not recently been used for live fish: [1]*Microchromis zebroides* Johnson; [2]*Labeotropheus curvirostris* Ahl; [3]*Labidochromis mathotho* Burgess and Axelrod. [4]Konings' undescribed *Pseudotropheus* 'red dorsal' has been described as *Pseudotropheus galanos* by Stauffer and Kellogg (2002).

et al. (1983) subdivided into six species-complexes on the basis of morphology and behaviour (*P. elongatus*, *P. tropheops*, *P. williamsi*, *P. zebra*, *Pseudotropheus* aggressive and *Pseudotropheus* miscellaneous). Subsequently Meyer and Foerster (1984) proposed the subgenus *Pseudotropheus* (*Maylandia*) for members of the *P. zebra* complex and Trewavas (1984) established the subgenus *Pseudotropheus* (*Tropheops*) for members of the *P. tropheops* complex. Following this, Stauffer *et al.* (1997) constructed a new genus, *Metriaclima*, to contain most members of the *Maylandia* subgenus, claiming *Maylandia* was a *nomen nudum*. Condé and Géry (1999) considered that *Maylandia* was a senior synonym of *Metriaclima*, but their arguments have been disputed by Geerts (2002). There is also an argument for raising *Pseudotropheus* (*Tropheops*) to generic level (e.g. Konings 2001). While these issues are unresolved, we retain subgeneric status for *Maylandia* and *Tropheops*. We feel that the distinction between *Maylandia* and the other *Pseudotropheus* species is not as clear as the delineation of some of the previous mbuna genera.

Mbuna genera were originally diagnosed on the basis of the morphology of head structures, such as jaws and teeth, but as has been true of species, this classification has proved difficult to sustain, and colour traits have also been used. The genus *Melanochromis* provides a good case study. Trewavas (1935) originally diagnosed *Melanochromis* on the basis that individuals of the constituent species that had larger and fewer pharyngeal teeth than those of *Pseudotropheus*. The species included were *M. melanopterus*, *M. vermivorus*, *M. brevis*, *M. perspicax* and *M. labrosus*. Ribbink *et al.* (1983) later split *Melanochromis* into two informal groups. The *M. melanopterus* group comprised 15 species of slender fish with horizontal bands and weakly developed territorial behaviour. The *Melanochromis* 'heterogeneous' group was a 'dustbin' for five species with apparently little in common, including *M. labrosus* and *M.* cf. *brevis*. Ribbink *et al.* were not sure they had identified the latter correctly in the field. Nor were Ribbink *et al.* sure they had properly identified *M. perspicax*, but in any case, they called it *Pseudotropheus* cf. *M. perspicax*, and placed it in the *Pseudotropheus* 'aggressive' group on the basis of its behaviour and lack of horizontal bands. Trewavas (1984) then amended her definition of *Melanochromis*, focussing on the presence of horizontal bands rather than on dentition. She did not give a list of included species, although the discussion of her paper mentions that *Melanochromis crabro* should be considered a member of *Pseudotropheus* on the basis of its colour. Konings (2001) included several species in *Melanochromis* which do not have clear-cut horizontal bands. *Melanochromis brevis* is one, although some populations do indeed have both horizontal and vertical bands. However, the same is true of *Pseudotropheus* 'msobo', a species that, like many *Melanochromis*, also has bright yellow females. *Melanochromis joanjohnsonae* is also included, although it was originally described as a *Labidochromis*. This species looks and behaves superficially like several *Labidochromis* species (e.g. *L. textilis* and *L. maculicauda*), but specimens usually have bicuspid teeth in the outer series of the oral jaws, instead of the unicuspid teeth characteristic of *Labidochromis.* This prompted Lewis (1982) to exclude it from his *Labidochromis* revision. *Melanochromis labrosus* is also still kept in the genus. Konings (2001) considers that his observation of an orange-morph female suggests that this species must be an mbuna, yet there are no other known examples of intraspecific polymorphisms in *Melanochromis*. Other genera, subgenera and species complexes give a similar picture to *Melanochromis*: there is a core group of species that obviously show strong similarities in morphology, colour and behaviour, along with a group of other taxa that share various traits with members of other complexes. This pattern could be consistent with relatively superficial taxonomic investigation, the rapid evolution of these fishes, frequent parallel and convergent evolution of functional traits and reticulate evolution. All of these explanations are plausible.

Tests of mbuna relationships

To investigate the processes that have led to the evolution of the mbuna, an estimate of their phylogenetic history would be helpful (Kornfield and Smith 2000; Turner *et al.* 2001). Attempts have been made to employ characters from morphology, allozymes, mitochondrial and nuclear DNA to examine mbuna phylogeny (Table 2). Morphological taxonomic studies have made relatively little progress in resolving their interrelationships. This is probably because of the lack of suitable traits to work with. Although there is much variation in structures associated with adaptations to aspects of ecological niches, there is a lot of good evidence for convergent evolution in these traits, most clearly in the similarities between unrelated species from Lakes Malawi and Tanganyika (e.g. Kocher *et al.* 1993). If such distantly related species can independently develop similar structures in different lakes, the potential for convergent evolution among more closely related species sharing the same lake would appear to be even greater. Colour also seems to be prone to parallel evolution, both within and between lakes (Seehausen *et al.* 1999b; Allender *et al.* 2003). A few detailed studies of bones and muscles have been attempted. Some have proved useful in confirming interrelationships among taxa from different lakes (e.g. Stiassny 1981), but there has been little resolution of relationships within Lakes Malawi. Stauffer *et al.* (1997) used the shape and angle of the ethmovomerine process (part of the skull) to help define their genus *Metriaclima* (=*Maylandia*). However, the character states of this trait seem to be largely

Table 2 Molecular tests of mbuna monophyly. Note that most of these studies were not designed explicitly to test this question.

Method	Status of mbuna	Comments	References
mtDNA sequences	Monophyletic	19 Malawi haplochromine species	Meyer *et al.* 1990
mtDNA RFLP	Paraphyletic	40 Malawi haplochromines: mbuna clustered with *Aulonocara*, *Alticorpus* and *Lethrinops*	Moran *et al.* 1994
mtDNA sequences	Monophyletic	One species each of three mbuna and three non-mbuna endemic genera	Kocher *et al.* 1993
Nuclear MHC genes	Unresolved	Mbuna taxa mixed up with forms generally considered distantly related, such as *Pelvicachromis*	Klein *et al.* 1993
Scale morphology	Polyphyletic	Moderate taxonomic coverage (24 species), but similar mbuna genera clustered with very different non-mbuna	Kuusipalo 1998
Nuclear AFLP	Monophyletic	Only one non-mbuna included, so unable to test Moran *et al*'s findings	Albertson *et al.* 1999
mtDNA sequences	Untestable	Only one mbuna included, but cluster with non-mbuna *Aulonocara*, *Alticorpus* and some *Lethrinops*	Shaw *et al.* 2000
Allozymes	Polyphyletic	Similar mbuna clustered with very different non-mbuna	Kuusipalo 2000
Nuclear SINES	Unresolved	Based on six mbuna and eight non-mbuna Malawi endemics	Takahashi *et al.* 2001
Nuclear LWS Opsin	Non-monophyletic	Based on three mbuna and three non-mbuna Malawi endemics	Terai *et al.* 2002

correlated with externally apparent changes in snout proportions and mouth positioning associated with changes in feeding habits, and as such might be expected to be equally prone to selection-driven convergent evolution. Kuusipalo (1998) examined the morphology of scales surrounding the upper lateral lines in 24 Malawi cichlid species, based on the premise that scale and squamation characters may be less likely to undergo morphological convergence than anatomical traits associated with food handling and processing (Lippitsch 1997). However, the conclusions of this study were at variance with both traditional taxonomy and molecular evidence, and the method does not seem to have been widely used since.

Mitochondrial DNA sequences have been found useful for estimating fine-scale relationships among animals because of the typically rapid evolution of the mitochondrial genome (Kocher *et al.* 1989). Resolving relationships within the mbuna using mtDNA has proven to be difficult. It has been found that sequence variation between species is often small, and variation within populations is often of comparable magnitude. Bowers *et al.* (1994) studied two species of *Melanochromis* from populations in the south of the lake and found exceptionally small amounts of sequence divergence both within and between species that rendered it impossible to reliably delimit species on the basis of mtDNA alone. Using the highly variable 445-bp first part of the control region, only six haplotypes were found in each of the species. These species were sampled thoroughly: 68 individuals of *M. auratus* were collected from eight locations, along with 32 individuals of *M. heterochromis* from six locations. Mean sequence divergence of haplotype pairs within a species (*M. auratus*: 0.45%; *M. heterochromis*: 1.13%), was very similar to that between species (1.1%). The difference between genera was greater: in a comparison of sequence divergence between *Melanochromis* and *Pseudotropheus* (*Maylandia*), the mean difference between haplotype pairs was 2.52%. Reinthal and Meyer (1997) also found very small levels of interspecific differentiation of mtDNA sequences between populations of the *Pseudotropheus* (*Tropheops*) complex. Twenty-nine individuals belonging to 10 putative species were found to have a total of 10 variable sites in 427 base pairs of the control region, and other neighbouring regions. Moran and Kornfield (1993) found that many morphologically distinct species had identical mtDNA haplotypes, and populations of single species contained individuals from different major mtDNA lineages that had on average 1.8% sequence divergence. Thus it would appear possible for what are considered relatively distantly related cichlid species to share mitochondrial haplotypes (Moran and Kornfield 1993; Kornfield and Parker 1997). This 'incomplete lineage sorting' could result if mtDNA variants do not have time to become fixed within a species prior to the next speciation event (Moran and Kornfield 1993; Takahashi *et al.* 2001). In a rapidly radiating group like the mbuna, the interval between speciation events may be too short to allow fixation of different mtDNA variants in sister species. Lack of fixation of mtDNA is more likely if the species has a large population size, even through speciation events, as would be expected if speciation followed a sympatric, parapatric or vicariant mode. Another possibility is that polymorphisms result from reticulate evolution – introgressive hybridization among non-sister taxa (Turner 2002; Seehausen *et al.* 2003). Thus, the results of phylogeny estimation based on mtDNA need to be interpreted with caution (Parker and Kornfield 1997). With a small effective population size, mtDNA can be susceptible to drift, and its non-recombinant nature means that it behaves as a single locus, and after fixation all traces of former interrelationships are erased. However, mtDNA may still reveal important insights at a population level, particularly if analyses are based on large samples per species or population, making use of methods such as Nested Clade Analysis (Templeton 2004).

Allozyme polymorphisms are ultimately based on variation in the sequences of protein-coding nuclear DNA sequences, but the level of variation revealed by this method has not proved adequate to give much insight into mbuna relationships (see attempts by Verheyen and van Rompaey 1986; Kuusipalo 2000). Direct sequencing of nuclear DNA regions has been successfully used for investigating deeper phylogenetic relationships of cichlids whose gene pools have been separated for millions of years (Sültmann *et al.* 1995). These methods have so far proved of limited use for studies for recently diverged taxa: for example the Internal Transcribed Spacer 1 (ITS1) region is among the most variable regions in the nuclear genome, but minimal sequence divergence was found among the endemic haplochromines from Lake Victoria (Booton *et al.* 1999). Ono *et al.* (1993) sequenced major histocompatibility complex (MHC) genes of two species of mbuna, *P. zebra* and *Melanochromis auratus.* They found that while the two species did not share MHC alleles, sequences from the same species did not cluster together and thus were not phylogenetically informative. This may be because individuals have several different MHC loci, which were not distinguished, nevertheless, MHC may in future be helpful in identifying cases of hybridization and in the study of intraspecific evolutionary processes once the MHC loci in mbuna are fully characterized. Short Interspersed Repetitive Nuclear Elements (SINEs) are inserts (retroposons) that are dispersed throughout the genome and apparently show no preference for sites of insertion. Thus, the presence or absence of these markers in a particular part of nuclear genome appears to be a reliable homologous molecular character. At present the technique has been used to show the distinction of members of the Lake Malawi haplochromines from outgroups (Takahashi *et al.* 2001), but whether the technique can realistically be used to distinguish finer-level phylogenetic relationships within mbuna is unclear at present. Microsatellites are simple sequence repeats distributed throughout the nuclear genome, and are highly variable in cichlid fishes. Because of their high mutation rate, they have been extensively used to examine fine-scale population structuring (Markert *et al.* 2001) and they may also be useful in constructing phylogenetic relationships of very closely related populations (Smith and Kornfield 2002; Rico *et al.* 2003). However, phylogenetic estimation with microsatellites is arduous. About 50 individuals per population screened at 10 or more loci appears to be required to obtain even limited phylogenetic resolution.

Amplified fragment length polymorphisms (AFLPs) are studied by selectively isolating fragments of DNA from throughout the (mainly nuclear) genome and then comparing fragments among taxa. The most closely related species are assumed to share more fragments. The technique has been found to be useful for examining intraspecific and fine-level interspecific differentiation (Albertson *et al.* 1999; Markert *et al.* 2001; Allender *et al.* 2003), as well as deeper relationships (Seehausen *et al.* 2003). However AFLP data suffer from a lack of repeatability among laboratories because of, for example, contrasting band resolution on different DNA sequencers. The search for informative nuclear sequences continues, although at present, AFLP seems to hold the most immediate prospect of utility in phylogenetic studies of mbuna. However, the potential of mtDNA studies in phylogeographic analysis remains untested. Comparison of mitochondrial and well-resolved nuclear phylogenies has the potential to generate insights into evolutionary processes such as hybridization (Seehausen 2004).

Evolutionary history

Published nuclear and mitochondrial phylogenies indicate that all bar two of the haplochromine species found in the Lake Malawi catchment form a monophyletic clade (Meyer *et al.* 1990; Shaw *et al.* 2000; Seehausen *et al.* 2003; Turner *et al.* 2004). The exceptions are *Serranochromis robustus* and *Pseudocrenilabrus philander*, which seem not to have given rise to any endemic forms in the Malawi catchment.

We have little idea how old the mbuna are as a group. Meyer *et al.* (1990) estimated it would have taken the Malawi haplochromines approximately 700 000 years to evolve the observed level of sequence differentiation from a single common ancestor, which is consistent with geological estimates of the age of the lake of some 1–2 million years. However, the molecular clock used was derived from mammalian cytochrome *b* sequence divergence rate estimates, and based on a relatively simple model of sequence evolution. Further work on this estimate is probably required using clock estimates calibrated for cichlids or related fish. However, it is clear that many mbuna species pairs show very low levels of sequence divergence and few fixed differences, suggesting that much of the radiation has been very recent, and is probably still in progress.

It was originally thought that mbuna represented one of two major subclades of Malawian haplochromines (e.g. Meyer *et al.* 1990), but later results of mitochondrial DNA analysis suggest there there are six major subclades (Moran *et al.* 1994; Shaw *et al.* 2000; Turner *et al.* 2004). The subclade containing the mbuna also contains species that would not be placed in the mbuna on the basis of morphology, colour or habitat preference. None of the studies which have sampled all six subclades have indicated that the subclade containing the mbuna occupies a basal position within the radiation of Malawian endemic haplochromines; that position is taken by one of the midwater feeding groups: *Rhamphochromis* (Moran *et al.* 1994); *Rhamphochromis* plus the *Diplotaxodon-Pallidochromis* clade (Shaw *et al.* 2000) or the *Copadichromis virginalis* complex perhaps in combination with *Rhamphochromis* (Seehausen *et al.* 2003).

Rather surprisingly, phylogenetic estimates based on mitochondrial DNA indicate that the 'mbuna clade' contains members of the genera *Aulonocara*, *Alticorpus* and some species of *Lethrinops* (Moran *et al.* 1994; Shaw *et al.* 2000; Turner *et al.* 2004). Another member of the mbuna clade appears to be *Placidochromis milomo*, a species with hypertrophied lips which lives on rocky shores (D. Joyce *et al.* unpubl. data). On the basis of morphology, behaviour and habitat preferences, no close relationship between these forms and the mbuna had previously been suggested. To date, there is no clear indication of phylogenetic structure distinguishing the morphological mbuna from the other forms. Furthermore, from mitochondrial sequences, the mbuna *Labidochromis caeruleus* is placed as a member of the clade dominated by benthic non-mbuna (shown without comment in a table in Sturmbauer *et al.* 2001, but confirmed by later analyses of new material by D. Joyce *et al.*, unpubl. data). Thus, molecular phylogenetic studies to date do not provide any support for regarding the mbuna as a clade, and indeed suggest parallel evolution of the mbuna morphotype.

Life history and territoriality

Those mbuna species that have been studied intensively seem to breed throughout the year, but there appears to be some seasonality in the intensity of reproductive actively which may be linked to food availability. Marsh *et al.* (1986) identified peaks in mbuna gonadosomatic indices from August to October when upwelling of nutrient rich water promotes plankton blooms in the south of the lake, and in February to March when the rains wash more nutrients from the land. Where information is available, it has been found that all haplochromine cichlid fishes, including all mbuna, are maternal mouthbrooders. They have elaborate courtship rituals that appear to be phylogenetically conserved, for there is little, if any, interspecific differentiation (Myers 1960; McElroy and Kornfield 1990; Ribbink 1990). Conspecific mbuna males hold adjacent but non-overlapping territories on the rocky shores. This has been considered a lek (Kellogg *et al.* 1995), but this is debatable, as leks are usually areas where male territories contain no resources. Male mbuna feed in their territories, and seek refuge from predators in caves under rocks. Many species spawn in these refuges, which may provide protection to females and eggs, as well as reduce the risks of sneaky matings. Males attract ripe females by darting in front of them and performing lateral displays and quivers. They then attempt to lead the female, using an exaggerated waggling movement called 'lead-swimming' in the direction of the male's preferred spawning site. Spawning sites vary between species: most species prefer to spawn in a secluded cave under rocks, although many *Pseudotropheus* (*Tropheops*) species seem to prefer to spawn in the open, often on the side of a steeply-sloping rock (G.F. Turner, pers. obs.). A receptive female will follow the male to his spawning site and they will both engage in protracted bouts of circling behaviour which may last for up to 1 h or more in the field (G.F. Turner, pers. obs.), before ultimately spawning. Eggs are laid singly or in small numbers (Ribbink 1990) and then rapidly collected in the mouth of the female (see illustrations in Konings 2001). Females rarely wait for the male to perform a fertilization run over the eggs before picking them up, and it is likely that fertilization usually takes place inside the female's mouth (Konings 2001). Clutches vary in size, but rarely number more than 50 (Trendall 1988a). After spawning, males play no further role in parental care. Brooding females generally hide away under rocks, often in groups, and do not seem to move much. They probably feed little, if at all. This may in part be because conspecific males court brooding females with great enthusiasm, behaviour that might attract predators of eggs and fry.

Eggs and larvae are brooded for a period of 20–30 days before free-swimming juveniles are released. Females of many haplochromine cichlids stand guard over broods of independently-feeding fry and allow the young fish to return to their mothers' mouth when threatened by predators (see Konings 2001). In contrast, mbuna females have never been observed to do this in the lake. Instead, it seems likely that fry are deposited into refugia among rocks, and do not return to their mothers' mouths. There is no pelagic dispersal phase and it is not known whether females migrate to release offspring or if they release fry in the vicinity of the brooding sites. Once in refugia, juveniles vigorously defend their space from intruders (Trendall 1988a), before eventually leaving to become free-swimming 'floating' individuals, until they become sexually mature.

Molecular data has shown multiple paternity in wild broods (Kellogg *et al.* 1995; Parker and Kornfield 1996) and as there is no evidence for sneaky mating occurring in mbuna populations (Ribbink and Chan 1989), it would appear that females are actively choosing to mate with more than one male. This behaviour is also apparent in laboratory studies, when females are given a choice of several conspecific males that are prevented from dominating each other, or from sneak mating, by separating partitions that only females can pass through (Knight *et al.* 1998; Turner *et al.* 2001). It is possible that females are adopting a 'bet-hedging' strategy to avoid paying the potential costs of entrusting all their maternal investment to the sperm of one male. Such costs might include inbreeding (in case he is a close relative), or mating with males with other undesirable heritable traits that she cannot reliably assess (Kellogg *et al.* 1995; Parker and Kornfield 1996).

Males of most mbuna species are territorial, although Ribbink *et al.* (1983) suggest that some less abundant species are not territorial (Fig. 4). In general, conspecific males tend to have very clearly defined and non-overlapping territories, but many heterospecific territories may overlap (Holzberg 1978), although 'core' spawning areas are defended against all fish (Robinson 1995). Male *Pseudotropheus aurora* have been recorded occupying the same territories for as long as 18 months, and 13 of 17 individuals remained on the same locations for 6 months (Hert 1992). Males that relinquished a territory over this time were in poor condition, suggesting that competing individuals had forcibly expelled them. In several removal studies, it was found that vacant territories were re-occupied by conspecifics (Hert 1990, 1992, 1995). Fidelity of males for specific territories was also manifested in homing behaviour. Male *P. aurora* were found to return to their home territories after experimental displacement from as far as 2.5 km away along continuous rocky habitat (Hert 1992). Five other mbuna species were able to return from over 1 km away (Hert 1992). At present, the homing mechanism is not known, but the function of this behaviour is likely to be closely linked to the dominance hierarchies based on individual recognition that establish in mbuna populations (Andries and Nelissen 1990). It may be easier for experienced males to return to a familiar location, than to take over a new territory in an already established 'foreign' social system.

Adult mbuna are typically non-shoaling, but subordinate males and females have been recorded as forming or entering both single- and multi-species schools, sometimes apparently as a mechanism of gaining access to otherwise unavailable benthic food resources. These schools sometimes raid the territories of other fish, and feed on the benthic algal turf and material within it (Marsh and Ribbink 1986). There is evidence that females of some species are actively territorial, perhaps defending feeding territories (Ribbink *et al.* 1983), but in general adult females appear to be less territorial than males. Even where females are not overtly territorial, they may still occupy restricted home ranges (Knight 1999) and have favoured refuges, particularly at night. Hert (1992) recorded that females have communal 'sleeping areas' that they regularly returned to. In tagging experiments, 26 of 33 *P. aurora* females remained in the same area, and seven of 12 returned to the same night-time locations after being in a separate enclosure for some time. Knight *et al.* (1999) used molecular methods to test for sex differences in dispersal distances. It seems that females are more likely to be found near to a close relative than are males, indicating greater dispersal by males. Why males should disperse further is not known, but it is

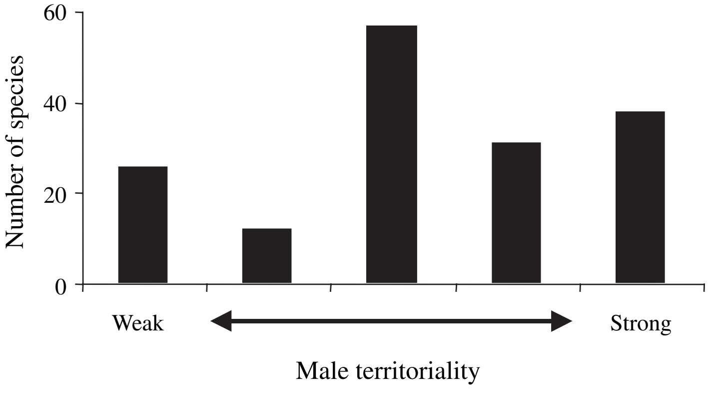

Figure 4 The strength of adult male territoriality in mbuna species. Data derived from Ribbink *et al.* (1983). Where data were present for the same species from more than one site, a mean value was used. Units of territoriality are not presented in the original charts from which the data are taken.

possibly linked to intense male-male competition that results in males having to spend a long time ranging around looking for a vacant territory. Male-biased dispersal is likely to reduce inbreeding and be more conducive to (parapatric) speciation based on divergent sexual selection when compared with an equivalent amount of female dispersal.

Mbuna juveniles occupy refugia that are defended vigorously from intruders. Such juvenile territoriality is unusual among cichlids. As natural selection favours the evolution of territorial behaviour when the benefits to an individual's fitness in terms of resource acquisition and loss outweigh the costs in terms of energy, injury and time (Kaufmann 1983), it may be best to view territoriality from the perspectives of the costs and benefits to the individual. Mortality of juvenile mbuna is estimated to be more than 95% within the first 40 days after release by the mother (Trendall 1988a), and predators appear to be numerous (Ribbink *et al.* 1983). It is possible that sharing of a refuge may attract predators or inhibit juvenile growth through reducing food availability within a safe distance of the refuge. Prior residents in refuges may learn the best escape routes, and have the best chance of survival.

For adults, it would appear that predation is less of a threat (Holzberg 1978), but the benefits of territoriality must outweigh the costs, which probably include reduced vigilance, increased conspicuousness to predators, lack of access to transient food resources and aggression from competing individuals. It is probable that the primary benefit of territorial behaviour to adult males is the control of a spawning site. Males of sandy shore cichlids of Lake Malawi appear to be chosen as mates for their ability to command specific positions on a breeding arena (McKaye 1991; Kellogg *et al.* 2000), and for their large (McKaye *et al.* 1990) or symmetrical bowers (Taylor *et al.* 1998). Thus, territory quality appears to be one cue that females use in mate choice. It is possible that female mbuna also require at least a minimum standard of territory quality when making spawning decisions, but we are unaware of any work that has specifically addressed this question.

Mbuna are unusual among Malawi cichlids in that males of almost all species appear to be territorial all year round. Even among other species that breed on rocky shores, males are usually only territorial for a few months in a year (Robinson and Ribbink 1998). Perhaps the low year-round incidence of breeding is enough to make it worthwhile for a male to be ready to breed at any time. Alternatively, male-male competition may be so intense and the benefits of being a resident are high enough that it would not pay a male to abandon a territory and try to re-establish himself in the next peak breeding season.

Once a male has become territorial, he needs to eat and most males spend much of their time feeding in their own territory (Robinson 1995). Thus, protection of food resources may be critical to individual males. If this is the case, we might expect territorial males to preferentially exclude from their territories species that have similar diets to their own. This tendency should be most marked in species with more specialized diets. There is some evidence that this is the case. *Pseudotropheus* (*Tropheops*) are specialist epilithic herbivores and territorial males direct intense aggression at other *Pseudotropheus* (*Tropheops*), even those of different species, perhaps because they are competing for the same limited food resources (Genner *et al.* 1999a). In contrast, males of the more generalist *Pseudotropheus* (*Maylandia*) complex were found to preferentially exclude only conspecifics. Interestingly, all studied species excluded conspecific females in addition to conspecific males. This may be because males are unable to distinguish accurately between non-ripe females and subadult males, or because the presence of non-ripe females reduces male mating success (Genner *et al.* 1999a).

Sexual dimorphism and mate choice

Most mbuna species are sexually dimorphic. Males almost always attain larger sizes than females, and often have longer pelvic, dorsal and anal fins. Territorial males are also usually brighter than females, although in some species both sexes are bright but differently coloured, for example male *Melanochromis johanni* are black, with iridescent blue horizontal stripes, while females are bright yellow-orange (Ribbink *et al.* 1983). In a few species the sexes are bright and similar, such as *L. caeruleus*, although even in such species courting males are generally brighter.

It has been suggested that the bright body coloration traits typical of males have evolved as a consequence of intense directional sexual selection. To date few studies have tested this empirically, but those that have imply that this is likely to be the case. Laboratory experiments have demonstrated that female *Labeotropheus fuelleborni* respond significantly more to males with brighter and more contrasting body colour (Pauers *et al.* 2004). Similarly, it would appear that the bright yellow 'eggspots' on male anal fins are also traits used in sexual selection. It has been proposed that these evolved to mimic the appearance of eggs and originally served to increase fertilization rates (Wickler 1962). Female *P. aurora* have been found to spawn more frequently with males with a greater number of these spots (Hert 1991), but female *Pseudotropheus lombardoi* showed a behavioural preference for males with one large spot, as opposed to those that had been experimentally manipulated to have more or smaller ocelli (Couldridge 2002). Thus, females of different species appear to prefer different spot traits.

Male breeding coloration is usually only expressed fully when a sexually mature male takes over a territory, or a dominant role in a hierarchy (Nelissen 1985). Adult females, even in species where females are bright, tend to have body coloration similar to juveniles and young males. This suggests that female colour serves the same function in juveniles and is thus not principally a sexual signal. In aquaria, aggressive females of many cichlids can occasionally adopt a drabber version of the male territorial colour (Turner and Falter 1989). This is true of at least some mbuna, particularly as females approach readiness for spawning (G.F.Turner, pers. obs.). Drab 'male' coloration has also been occasionally seen on mouthbrooding mbuna in the field, which are presumed to be females (Konings 2001). It seems unlikely that the adoption of male-type colour is a consequence of (or a precursor to) sex change as there is no published evidence of sex change in mbuna, although it has been demonstrated in distantly related cichlids (Barlow 2000; Carruth 2000).

It is generally believed that predation plays a major role in shaping animal colour. However, mbuna mostly live over complex rocky substrates where mortality of adult fish induced by predators using vision may be of negligible importance. It has been proposed that the 'poster colours' of coral reef fish have evolved mainly to serve in intraspecific communication because of the limited importance of visually mediated predation in a habitat with lots of hiding places (Lorenz 1962). Comparative analyses have shown minimal association between male mbuna colour and a series of ecological variables measured, such as water depth, rock size or substrate types (McElroy *et al.* 1991; Deutsch 1997). This is consistent with the poster colour theory, but it is difficult to draw firm conclusions from negative results: perhaps a more subtle measurement of habitat parameters might reveal some associations.

The bright courtship dress of male mbuna is shown during territorial defence as well as mate attraction. Seehausen and Schluter (2004) have suggested that rare males with a distinct territorial colour may find it easier to secure and defend a territory, a proposal consistent with some observations of distributions of individual male Lake Victoria cichlids and with an analysis of the colour composition of rocky shore cichlid communities. A similar analysis has yet to be attempted for mbuna. An alternative view may be that unusual male colour is not recognized as a territorial defence signal and so is less effective for repelling intruders. This would suggest that there might be selection for convergence of male colour between different species. It is possible that both processes may be operating, perhaps on different elements of male breeding dress. If colour is important in male-male competitive interactions, it may thereby provide fitness indicators upon which females can base mating decisions.

Pseudotropheus zebra, and perhaps other mbuna possess the ability to see ultraviolet (UV) wavelengths (Carleton *et al.* 2000), and territorial males of some species have been shown to reflect UV (Jordan *et al.* 2004). There may be more variation in male colour and pattern than perceived by the human visual system although to date UV reflectance seems to be mainly focused on the iridescent blue-white areas of male breeding dress, and no 'cryptic patterns' have been detected where UV-enhanced artificial lights have been employed in laboratory mate choice experiments (Pauers *et al.* 2004). It has also been shown that species such as *P. zebra* actually have as many as five different cone opsin genes which code for sensitivity to different colour wavelengths (Carleton and Kocher 2001), although at any time only three are expressed to any great extent. Although they may possess similar cone opsin genes, individuals of the same and of different species may have very different kinds of colour vision as a result of differences in gene expression.

Although much interest has focussed on mate selection based on colour, it is also possible that mating decisions are made on a suite of other characters including territory quality, male size, pattern symmetry, courtship vigour, length and condition of fins, courtship sounds as well as chemical cues such as pheromones. Statistically differences in male courtship calls have been demonstrated in a study of three closely-related sympatric species of the *P. zebra* complex (Amorim *et al.* 2004), although it is not known whether females can distinguish mates on the basis of such difference in calls. To date, there have been few investigations of sounds or other non-visual courtship traits in mbuna.

Colour polymorphism

Several species of mbuna exhibit striking within-population colour polymorphism, most notably, in the BB/OB/O system first characterized for Lake Malawi cichlids by Fryer (1959a) and worked out more fully for the Nkhata Bay population of *P. zebra* by Holzberg (1978) and Knight (1999). The common male form in *P. zebra* is bright blue, while the most common female form is dark brown. Both sexes have dark vertical bars, and this form is called 'barred' or 'BB'. Females of the other morphs have an orange background colour overlain with a number of darker blotches: those with many blotches are called 'orange blotch' or 'OB', while those with few or no blotches are 'orange' or 'O' morph. At Nkhata Bay approximately 10–15% of the apparent females (i.e. possibly including smaller non-territorial males) were OB (Knight 1999). At one headland, the O morph females comprised 18%, while at another a few hundred metres away they were less than 4% of the apparent female population (Knight 1999). Among Malawi cichlids, so far as we know, OB/O morphs are found only in some populations of *Pseudotropheus* (*Maylandia*), *Pseudotropheus* (*Tropheops*), *Labeotropheus* and *Genyochromis*. A similar polymorphism occurs in *Pseudotropheus* (*Maylandia*) *callainos* at Nkhata Bay, where the common form is blue without bars (B) and the equivalent of O is white (W). In this species, the blotched (WB) form is much rarer than the W form: the ratio of W to WB is more than 10:1.

Generally, such polymorphisms are largely female-limited. Males of the OB/O or WB/W morphs are very rare, making up less than 1% of the Nkhata Bay *P. zebra* or *P. callainos* population (Knight 1999), and probably no more in most other *P. zebra* populations. However, some populations of *P. callainos* appear to be fixed for the W morph in both sexes, and we have also recorded populations where all males are blue, but females are white or OB (Katale and Chirwa Islands) or all females are white, but males split roughly evenly between W and B morphs (Luwino Reef). Most individuals belonging to the OB/O/W morphs start out BB or B, but metamorphose a few weeks or months later (Holzberg 1978). An exception is *P. estherae*, where matings between a B-morph male and an O-morph female produce fry which can be assigned immediately after release as yellow-orange O-females and dark blue B-males (G.F. Turner, pers. obs.). Fry of populations of *P. callainos* fixed for W also start out white (G.F. Turner, pers. obs.). Similar blotched polymorphisms are also found in a number of other African cichlids, including *Oreochromis variabilis*, *Tropheus moorii* from Lake Tanganyika, several Lake Kivu haplochromines and numerous Lake Victoria species (Seehausen 1996).

The rarity of OB/O males in most populations is believed to be due to the OB gene being linked to a dominant female-determining locus. Holzberg (1978) proposed that BB females are XX, BB males are XY and OB females can be WX, WY or WW. Seehausen *et al.* (1999a) working with a similar system in a Lake Victoria cichlid proposed that the OB males are produced when a WY individual has an autosomal 'male rescue' gene. They suggest that the BB/OB polymorphism may provide the raw material for an unusual speciation process requiring polymorphisms in colour, mate preferences, sex determining chromosomes and male rescue genes (Seehausen *et al.* 1999a; Lande *et al.* 2001). In this model, invasion of the rare colour form requires an undetermined selective advantage to the dominant female determiner locus (W-chromosome). Kocher (2004) suggests that a gene that increases the proportion of females in the offspring will be favoured when population sizes are small and brothers are likely to compete for mates. Streelman *et al.* (2003a) have mapped the position of the OB locus in an F2 hybrid cross between *P. zebra* and *L. fuelleborni*. The BB/OB system is still relatively poorly known, and in particular that it often plays a major role in cichlid speciation seems highly speculative.

The fin-biting *Genyochromis mento* also exhibits colour polymorphism, and can be grey-green, brown, black, yellow or orange-blotch (OB). As this species feeds mainly on fins of mbuna, it has been suggested that it is mimicking its victims or other harmless species to avoid detection by its prey (Konings 2001). The relative abundance of colour forms at a site may be a consequence of frequency-dependent natural selection, although this has yet to be tested.

Diet and functional morphology

Within the rocky shore communities, some roles are not occupied by the mbuna. There are no really big predators of fish or invertebrates. Mbuna all seem to be strictly diurnal. Few feed far from the substrate. None feed deep in the sediments and none appear to specialize in extracting eggs or fry from the mouths of brooding female cichlids. Most species eat algae, plankton, tiny invertebrates or fish fry. There are just a couple of truly eccentric specialists. *Genyochromis mento* eat the fins and scales of other cichlids (Fryer 1959a). *Pseudotropheus* (=*Melanochromis*) *crabro* frequent the nests of huge predatory *Bagrus* catfish, where they feed on catfish parasites, as well as their eggs (Ribbink and Lewis 1982), although they also eat algae and plankton (Konings 2001). Morphologically the most bizarre is *M. labrosus*, which has inflated rubbery lips that are used to seal cracks between rocks when it is sucking prey out from within (Konings 2001). Similar lips and feeding behaviour are shown by the Malawian *Eclectochromis* (=*Protomelas*) *ornatus*, *Placidochromis milomo* and *Cheilochromis* (=*Chilotilapia*) *euchilus*, by the Tanganiykan *Lobochilotes labiatus* and by the Victorian *Paralabidochromis chilotes*.

From stomach content analyses, Fryer (1959a) was the first to delimit different functional groups and their associated trophic morphological characters (Table 3). Typically many rows of bicuspid or tricuspid widely spaced teeth tend to be found in fish, such as *Pseudotropheus* (*Maylandia*) and *Petrotilapia*, that 'comb' algae from the rocks, and collect loose strands and periphyton. Tightly packed bicuspid or tricuspid teeth characterize fish such as *Pseudotropheus* (*Tropheops*) and *Labeotropheus* that scrape or pull algae from rocks. Planktivores, such as *Cynotilapia*, have widely spaced, but short, unicuspid teeth, while predators of larger benthic organisms, like some *Labidochromis*, usually have longer unicuspid teeth. Mbuna also show differences in internal anatomy – for example, longer intestines are related to more herbivorous diets (Reinthal 1990a).

It might be imagined that each mbuna morphotype is optimally adapted to exploit narrowly defined food resources, but it has not been convincingly demonstrated. Although apparently close links between morphology and diet were emphasized by Liem and Osse (1975), later Liem (1980) observed that many apparently specialized taxa were able to feed opportunistically on other resources. This finding was supported by field observations by McKaye and Marsh (1983). *Pseudotropheus zebra* and *Petrotilapia genalutea* appear to be specialized for combing through epilithic algae. However, they were also seen exploiting plankton when it was abundant. Indeed most mbuna taxa seem to have broad diets – for example, even the apparently specialized fin biter *G. mento* sometimes eats epilithic algae (Ribbink *et al.* 1983), and the facultative parasite cleaner *Pseudotropheus pursus* mainly feeds on periphyton (Stauffer 1991). A further example is *Pseudotropheus crabro*, a species that is 'specialized' on eating the parasites and eggs of the catfish *Bagrus meridionalis*, but which also eats plankton, epilithic algae and insect larvae (Ribbink and Lewis 1982). Thus, Liem observed an apparent paradox. How could cichlid trophic morphology have evolved as a response to natural selection if one set of trophic tools could perform a multitude of tasks? McKaye and Marsh (1983) suggested that when favoured food was scarce during 'ecological bottlenecks', selection favoured specialized trophic morphological traits that provided energetic advantages, but normally, these morphological traits were selectively neutral. This explanation for Liem's paradox was later formalized in a mathematical model by Robinson and Wilson (1998), prompting Liem and Summers (2000) to suggest that competition should be re-evaluated as potential driving force behind cichlid morphological design.

An alternative viewpoint is that Liem and Osse (1975) were correct, and there are indeed strong associations between the diet used and trophic morphology. Morphological and dietary studies on mbuna may not have been conducted thoroughly enough. In detailed studies of Lake Victoria rocky shore cichlids, Bouton *et al.* (1999, 2002) were able to demonstrate clear relationships between the available diet and the trophic morphology of geographically separate conspecific populations. This suggests that local selective forces may be driving fine-scale morphological character differentiation in these fishes. We are unaware of any study of equivalent thoroughness on mbuna and thus the true function and selective forces operating on their

Table 3 Morphological variation among the twelve main groups of mbuna and their primary food sources.

Genus	Prominent features of trophic morphology	Primary food sources
Cyathochromis	Closely packed unequally bicuspid upright outer teeth, inner rows with tricuspid teeth. Lateral teeth conical. Terminal mouth vertically compressed. Teeth in outer row oblique	Epiphytic algae
Cynotilapia	Evenly, but widely spaced unicuspid conical upright outer and lateral teeth. Irregularly spaced inner teeth. Terminal slightly laterally compressed mouth	Zooplankton, phytoplankton
Genyochromis	Lower jaw rigid and prominent, outer margin lined with unequally bicuspid teeth. Five inner rows of tricuspid teeth.	Fish fins, scales, epilithic algae
Gephyrochromis	Five rows of teeth. Closely packed, but long, equally bicuspid or conical outer teeth. Lateral teeth conical. Terminal mouth vertically compressed.	Sedimented diatoms, epilithic algae
Iodotropheus	Loosely packed unequally biscupid outer teeth, inner teeth tricuspid. Terminal laterally compressed mouth. Distinctive frenum connecting upper lip to snout.	Epilithic algae, plankton, benthic invertebrates.
Labeotropheus	Large fleshy protuberant snout. Jaw margins very straight. Each tooth with widened and flattened crown, but curved inward. Tightly packed equally tricuspid teeth. Lateral teeth unicuspid. Lower jaw inferior subterminal.	Epilithic algae
Labidochromis	Loosely packed prominent unicuspid (or unevenly biscupid) teeth. Outer teeth procumbant, long and recurved. Terminal laterally compressed mouth	Epilithic algae, benthic invertebrates.
Pseudotropheus (*Maylandia*)	Closely packed equally bicuspid upright outer teeth, inner rows with widely spaced tricuspid teeth. Usually four or five rows in total. Lateral teeth conical. Terminal mouth vertically compressed.	Loose epilithic algae, plankton
Pseudotropheus (*Tropheops*)	Very closely packed equally bicuspid upright outer teeth, inner rows with tricuspid teeth. Usually eight rows in total. Lateral teeth conical. Head profile steeply sloping. Mouth subterminal and vertically compressed.	Epilithic algae
Pseudotropheus (others)	Closely packed equally bicuspid upright outer teeth, inner rows with tricuspid teeth. Lateral teeth conical. Terminal mouth vertically compressed.	Epilithic algae, plankton, benthic invertebrates.
Melanochromis	Closely packed equally bicuspid upright outer teeth, inner rows with tricuspid teeth. Lateral teeth conical. Terminal vertically compressed mouth	Epilithic algae, plankton, benthic invertebrates, fish fry.
Petrotilapia	Numerous rows of loosely packed irregularly spaced tricuspid upright outer teeth. Small lateral conical teeth. Terminal mouth vertically compressed. Teeth with long shaft, curved inward	Loose epilithic algae, plankton

Data compiled from Fryer and Iles 1972; Ribbink *et al.* 1983; Reinthal 1990a; Genner *et al.* 1999b,c.

trophic morphological characters remains unclear. To demonstrate that trophic morphological characters are indeed adaptive, as is widely assumed, it still needs to be shown that genetically based variation in trophic morphology results in different feeding efficiencies upon different limited food resources.

Recent studies have begun to investigate the genetic basis of differences in mbuna feeding morphology, particularly oral jaw design (Albertson and Kocher 2001; Albertson *et al.* 2003a,b; Streelman *et al.* 2003b). This approach was based on exhaustive morphometric measurements analysed with ‘thin plate spline’ methods of modelling multivariate shape data (Albertson and Kocher 2001; Kassam *et al.* 2003a,b). This was carried out by estimating the effective number of genetic factors controlling differences in the cichlid head through a comprehensive morphological assessment of two Lake Malawi mbuna species (*P. zebra* and *L. fuelleborni*) and their F1 and F2 hybrid progeny. It was estimated that between one and 11 factors controlled shape difference of individual bony elements (Albertson *et al.* 2003a). A difference in tooth shape (bicuspid vs. tricuspid) appeared to be controlled by a single major gene (Albertson *et al.* 2003a), suggesting that relatively few mutations might be required to accomplish this change, and therefore that parallel evolution of tooth shapes might be common. By identifying DNA markers linked to these genetic factors, Albertson *et al.* (2003b) found that several chromosomal regions contain a disproportionate number of these quantitative trait loci (QTL) suggesting that many genes controlling these functionally linked head characters are physically linked. This would make it easier for directional selection to shape their rapid divergence. Furthermore, the consistent direction of differences between the species in the effects of loci influencing differences in head characteristics is consistent with divergence as a result of strong directional selection (Albertson *et al.* 2003b).

Species coexistence

Mbuna live in high diversity assemblages, often with more than 30 species coexisting side-by-side, in addition to the many non-mbuna found on the rocky habitats (Ribbink *et al.* 1983). The authors of many studies have found interspecific differences in utilization of food or habitat resources and have suggested that such differentiation can help explain species coexistence, although this has been the subject of debate (e.g. Fryer 1959a; Fryer and Iles 1972; Reinthal 1990b; Genner *et al.* 1999a,b). For example, Galis and Metz (1998) suggest that competitive exclusion will occur rapidly unless there is niche differentiation. Fine-scale niche partitioning is usually reported as being facilitated by anatomical and behavioural specialization.

Dietary partioning

Liem and Osse (1975) suggested that food resource partitioning was the rule, while trophic resource sharing was rare in cichlid communities. In fact, most studies have found great similarity in the diets and habitat use of many mbuna species (Fryer and Iles 1972; Ribbink *et al.* 1983; Reinthal 1990b; Genner *et al.* 1999b,c). If dietary segregation does help to maintain coexistence, then small differences between the diets of coexisting species must be sufficient to prevent competitive exclusion. Such small, yet statistically significant, niche differences appear to be reasonably commonplace (Genner *et al.* 1999b,c). However, the question of whether dietary niche partitioning is necessary for mbuna coexistence depends on whether food resources limit populations. To our knowledge, evidence for resource limitation is limited to several pieces of anecdotal evidence. First, benthic algae, the primary food sources of most mbuna, rarely seem to be in luxuriant abundance except in inaccessible places, such as extreme shallows, narrow crevices and occasionally the ‘algal gardens’ of some territorial males (Ribbink *et al.* 1983). This suggests that available resources are efficiently cropped. Second, Marsh *et al.* (1986) identified two seasonal breeding peaks in mbuna that appear to be synchronized with periods of increased food availability, suggesting increased food supply is a critical factor determining reproductive output. However, the hydrographic conditions during these periods may act a cue for breeding activity independent of trophic resource abundance. Third, Duponchelle *et al.* (2000) report that both male and female mbuna decline in body condition during the rainy season when a large sediment plume causes a decrease in benthic productivity on the rocky habitats of the Maleri Islands. Fourth, we have noticed that most mbuna species attain much larger sizes than usual at sites such as Mphanga Rocks and Mara Rocks where strong upwelling currents may carry nutrients up from deep water and enable greater productivity of benthic and planktonic food sources. Finally, all species of mbuna grow larger in the aquarium than in the lake, possibly because of a more substantial diet, although this may also be attributable to reduced mortality.

Goldschmidt *et al.* (1990) suggest that the importance of cichlid dietary differentiation for coexistence has been underestimated because few studies have taken into account temporal variation in resource abundance. They proposed that to gain a more comprehensive picture of the extent of dietary niche partitioning stomach content studies need to be extended over longer periods (e.g. Bouton *et al.* 1999). However, such regular re-sampling requires extensive periods in the field, and the number of samples required may impact on the populations, particularly of rarer species. In order to overcome this, stable isotope and fatty acid signatures of muscle tissues have been employed as dietary tracers. The advantage of these biochemical signatures is that they accumulate in the body tissue over periods of weeks to years, thus potentially providing a longer view than stomach content analysis alone (Bootsma *et al.* 1996; Genner *et al.* 1999b; Kuusipalo and Käkelä 2000; Genner *et al.* 2003). These techniques are likely to find further uses for investigating questions of dietary partitioning and trophic adaptation in future.

Where species appear to share the same food resources, spatial segregation of preferred feeding microhabitats might maintain coexistence (Ribbink *et al.* 1983; Reinthal 1990b; Lowe-McConnell 1993). For example, species might differ in preferences for particular substrate slopes, levels of shelter and sediment cover. Quantitative studies have shown that there are significant differences in these parameters between species, but again there are extensive overlaps in feeding microhabitat, as well as diet (Genner *et al.* 1999b). By contrast, we consider that temporal partitioning of food resources is unlikely to contribute to coexistence. All mbuna are inactive at night, and throughout the day there appears to be no interspecific differentiation in temporal feeding patterns (Robinson 1995). Moreover, the benefits of temporal partitioning of resources are critically dependent on the replacement time of resources. If resources are slow to regenerate, as might be expected for epilithic algae or benthic invertebrates, temporal partitioning may reduce direct behavioural interference, but will not prevent resource depletion.

Habitat partitioning

Rocky shorelines of Lake Malawi are characterized by considerable habitat heterogeneity, with variation in the slope of the shorelines, the sizes of rocks, the prevalence of crevices and the amounts of sediment present. Within the mbuna community at a site, there does appear to be some degree of specialization for these habitats, and this may help to facilitate coexistence. Moreover, many mbuna show considerable differences in their depth distributions (Fig. 5), and such depth changes co-vary with habitat conditions – for example, deeper habitats tend to be more sediment rich. Although few species tend to be found throughout the full depth range surveyed at a site (Ribbink *et al.* 1983), the great majority of species pairs will overlap in depth distribution.

Often cichlids differ in spawning site preferences and a number of authors have suggested that spatial partitioning of breeding territories may facilitate coexistence (Ribbink *et al.* 1983). If juveniles were reared at the spawning site, as is true for example of Lake Tanganyika lamprologine species, the availability of breeding territory will clearly have a direct influence on the number of new recruits to a population. However, young mbuna are not reared in parental territories. Mbuna have a polygamous mating system and males provide no parental care. Females are thought to spawn just once or twice per year, while males are continually receptive. So, population sizes will not be regulated by a shortage of male territories, except under the unlikely scenario that females cannot find mates (Turner 1996). Thus, except in extreme cases, population sizes of mbuna are unlikely to be influenced by interspecific competition for territories.

Nevertheless, the behaviour of territorial males may affect the levels of competition among non-

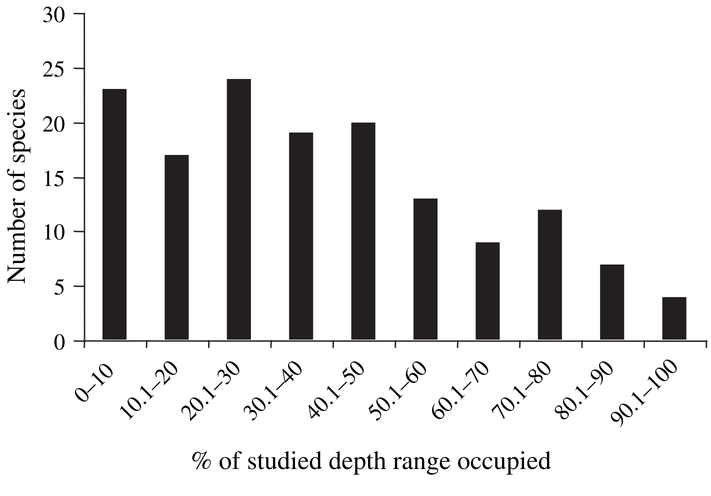

Figure 5 The depth range of mbuna species over the rocky shores of Lake Malawi. Data derived from Ribbink *et al.* (1983). Where data were available on the same species at more than one site, a mean value was used. Studied depth ranges were between 0 and 15, and 0–40 m.

territorial individuals that may in turn influence coexistence. Marsh and Ribbink (1985) studied feeding site utilization of three sympatric *Petrotilapia*. Males of these species scarcely shared space, but in our view this is unlikely to make much impact on their coexistence. This is because males of all three species excluded all female *Petrotilapia*, irrespective of species, leaving them to feed predominantly in undefended space or in territories of *Pseudotropheus* (*Tropheops*) 'orange chest'. So, in this case, male territoriality would result in increased competition among the species, by restricting female foraging sites and thus the reproductive output of the population. Additionally Genner *et al.* (1999c) showed that male mbuna tend to exclude conspecifics, but tolerate heterospecific intruders with a different diet to their own. Thus, it would appear that territorial behaviour may favour coexistence of species with different or generalist feeding strategies, while enhancing competition among species sharing a specialization.

Perhaps one of the strongest lines of evidence for habitat niche partitioning facilitating species coexistence comes from a recent study examining the quantitative association of community structure with habitat structure in transects at 16 geographically separate survey sites in north-western region of the lake (Genner *et al.* 2004b). It was found that although the geographic distance between sites was most important in explaining variance in community structure, significant proportions of the variance were also explained by depth and substrate composition. This implies that 'assembly rules' operate in mbuna communities, in other words constituent species possess fine-scale habitat preferences that are expressed in species distribution patterns across habitats in geographically and genetically communities. However, most of the variance in community structure remained unexplained. This may be simply because if a species is found in a particular habitat, it does not mean that it prospers there. Some habitats may be 'sources' and other 'sinks'. So species with different habitat preferences may overlap through dispersal of surplus individuals from their preferred habitat type (Iwasa and Roughgarden 1986). Alternatively geographically and genetically isolated populations may no longer be ecologically equivalent because of adaptation to local ecological regime. Finally, the low variance explained by habitat variables may also be due to purely stochastic influences on population sizes and hence community structure.

Other mechanisms

Overall, the weight of evidence suggests that some level of habitat or dietary differentiation is present among many mbuna species. However, whether such niche partitioning is sufficient to reduce interspecific competition to a level that prevents competitive exclusion, and thus maintain coexistence is not known. Moreover, that coexistence is maintained by niche partitioning alone is difficult to disprove as a hypothesis using field observations alone. If we find insufficient separation on one niche axis, we can never rule out the possibility that there are unsuspected dimensions in which niche differentiation has taken place (Silvertown and Law 1987). Nevertheless, alternative explanations for the co-occurrence of ecologically indistinguishable species have been proposed (reviewed by Silvertown and Law 1987; Chesson 1991; Tokeshi 1999). For example, the 'lottery model' (Sale 1978) proposes that juveniles occupy refuges on the basis of arrival order, irrespective of species and so population size is controlled by stochastic events. Juvenile survival may be one of the most important factors influencing the population size of Malawi cichlids (Trendall 1988a), and it remains to be investigated if juvenile refugia are limited in cichlid communities, but if they are, it is possible that such a mechanism may be in operation. Another possibility was suggested by Fryer (1959a) who believed interspecific competition is prevented because populations were regulated below carrying capacity by density-dependent predation. These alternatives warrant further research.

Biogeography and population subdivision

The shoreline of Lake Malawi switches between sandy, muddy and rocky substrate, and there are numerous offshore islands and reefs. McKaye and Gray (1984) calculated that in 1972, 18% of the western shoreline was rocky habitat, 61% sand and 21% weed. Notably, rocky habitats were found to be very small and patchily distributed. The longest stretch of continuous rock was a mere 8.5 km in length, and in general rocky substrates were heavily skewed towards small lengths of less than 1 km with a median of 300 m.

Apart from those species, such as *P. livingstonii*, that have established themselves over muddy/sandy habitats, mbuna are rarely seen far from rocky substrates. Cichlids from open water or sandy bottoms tend to be pale, silvery or sandy coloured, to live in shoals, and to avoid predators by speed, camouflage and schooling. From when they are first released as independent fry, mbuna are bright or darkly coloured, usually solitary and avoid predators by hiding among rocks. They would probably be very conspicuous and vulnerable to predators on sandy bottoms or in open waters. Mbuna probably have limited abilities to cross deep-water barriers by following the bottom. Cichlids have closed swim bladders. This is likely to limit their ability to undertake rapid depth changes. It is estimated that mbuna can move up or down no more than 4 m per day (Marsh and Ribbink 1981). Moreover, many mbuna species appear unable to control buoyancy in waters deeper than 40 m (Hill and Ribbink 1978).

Given such apparent barriers to dispersal, it is not surprising mbuna show genetic population differences. McKaye *et al.* (1984) found significant differences in the frequency of isozyme alleles from populations of *P. zebra* from opposite ends of the lake, and using more sensitive microsatellite DNA markers, it has been shown that population subdivision may take place over much smaller spatial scales. Muddy or sandy bays of around 1 km wide have been found to be associated with significant genetic differences among populations of four species of mbuna (Van Oppen *et al.* 1997). Moreover, a narrow cold stream entering the lake at the end of a 30 m wide sandy beach near Ruarwe appears to be a barrier to gene flow between populations of *P. callainos* ‘pearly’ (Rico and Turner 2002). In general, it has been found that populations separated by deep water tend to be the most genetically divergent and in contrast only slight genetic differentiation tends to have been found between samples collected along continuous rocky coast (Markert *et al.* 1999). Microsatellite markers have also shown that in the south of the lake, which is perhaps the youngest section (Owen *et al.* 1990), there are strong patterns of decreasing genetic similarity over increasing distances. This pattern suggests that colonization of new habitat takes place following a stepping stone model (Arnegard *et al.* 1999; Markert *et al.* 1999).

While molecular data are revealing that habitat discontinuities represent significant barriers to gene flow between mbuna populations, direct observations have been made of mbuna rapidly colonizing habitats across such barriers. McKaye and Gray (1984) placed artificial reefs 1 km from the nearest headland, at Otter Point on the Nankumba peninsula. Within a year at least five species of mbuna had colonized the reefs, and within 5 years at least 10 mbuna species were established. This inconsistency has not been investigated.

Reproductive isolation

Many animal species are reproductively isolated because mating with closely-related species either produces no offspring (hybrids are inviable), or sterile progeny. Sometimes species are simply incompatible in terms of courtship behaviour or their physical mating structures. Among haplochromines, matings among distantly related species can produce apparently healthy fertile hybrids, although there are exceptions (Crapon de Caprona and Fritzsch 1984).

This is by no means uncommon in fishes. Many recently diverged fish taxa are reproductively isolated by differentiation of breeding seasons or preferences for spatially separated breeding grounds. However, Van Oppen *et al.* (1998) found little spatial and no apparent temporal segregation of breeding activities among eight sympatric *Pseudotropheus* species at Nkhata Bay, despite almost all comparisons of species revealing genetic differences across six microsatellite loci. A laboratory study by Knight *et al.* (1998) demonstrated that three of these species, all belonging to *Pseudotropheus* (*Maylandia*), did not interbreed when given a free choice of mates in the laboratory. One pair of these species (*P. zebra* and *P.* ‘gold zebra’) was found to produce viable fertile hybrids when females were kept with males of the other species, but without males of their own species. Knight and Turner (1999) found that males of this species pair did not seem capable of distinguishing conspecific from heterospecific females, although there was good discrimination from the (differently coloured) females of *P. callainos*. Couldridge and Alexander (2002) suggested that not only did females prefer conspecific males, but they also seemed to have a ‘secondary’ preference for the heterospecific male of the closest colour to those of their own population. In combination, this evidence suggests that among mbuna reproductive isolation may often be maintained by direct mate preference, in many cases mainly by female preference for male colours. Knight and Turner (2004) demonstrated that allopatric populations of the *P. zebra* complex where males have blue and black barred breeding dress mate partially assortatively in laboratory trials. Assortative mating was related to the degree of differentiation of breeding dress. Well-differentiated populations, such as the Mphanga Rocks form (*P. emmiltos*), which has an orange dorsal fin, showed a high level of assortative mating. The Nkhata Bay and Chisumulu populations with more similar breeding dress mated randomly with each other.

The role of non-visual signals in assortative mating has yet to be thoroughly investigated. Amorim *et al.* (2004) demonstrated statistically significant differences among the sounds made by courting males of three sympatric *Pseudotropheus* (*Maylandia*) species, although it has yet to be demonstrated whether females of the different species can differentiate males on the basis of sound.

Speciation

Speciation is recognized to have taken place when intrinsic reproductive isolating barriers prevent interbreeding between two or more populations under natural conditions. Theoretical biologists have proposed that speciation can be caused by genetic drift, by natural (ecological) selection or by sexual selection. Selection may be divergent, selecting for evolution along two different pathways, such as different ecological niches or uniform, where similar selection pressures lead to fixation of incompatible mutations in different parts of the range of a species, leading to reproductive isolation. A subcategory of divergent selection, operating without geographic isolation, is disruptive selection, where two extreme forms are favoured and there is selection against intermediates.

Genetic drift

It is generally thought that genetic drift can only cause speciation after geographical barriers have already prevented interbreeding between populations, although some recent models challenge this (Gavrilets 1999). Genetic drift operates much more rapidly in small populations, and early workers felt that mbuna appeared to have the right kind of life history and biology to facilitate this process (Fryer 1977; Ribbink *et al.* 1983). Mbuna populations are easily isolated. Some populations are indeed small. It would be possible for a single mouthbrooding female to found a new isolated population. The small and unrepresentative sample of the gene pool would render such a population very different from its ancestor – just the conditions more likely to generate speciation by the Founder Effect, a most extreme form of genetic drift, considered by many biologists in the mid-20th century to be likely to be a major mechanism of speciation (e.g. Mayr 1942), but now generally considered to be a minor process (e.g. Coyne and Orr 2004). However, in such cases, we would expect to find low levels of genetic diversity in recently evolved species, particularly in mitochondrial DNA. One study showed a low mitochondrial genetic diversity in a population of an island endemic form, *Pseudotropheus* 'zebra black dorsal' on Maleri Island (Moran and Kornfield 1995). However, there is no evidence that this taxon is actually a biological species endemic to this island, and it is now known that very similar forms are found in a number of other locations (see Konings 2001, pp. 154–155). Generally, molecular studies of mbuna have reported high levels of diversity (Klein *et al.* 1993; Moran and Kornfield 1993). The polygamous mating system and the high level of multiple paternity may reduce the probability of genetic bottlenecking (Turner 1999).

Natural selection

Speciation is associated with diversification of numerous traits, and the extent of differentiation between incipient species in a given trait may be an indication of the importance of that trait in the speciation process (McKinnon and Rundle 2002). The radiation of trophic morphological traits in mbuna while other aspects of their body plan remain conservative indicates that trophic morphological diversification may be in some way linked to high speciation rates. It has been suggested that one reason why they have the capability to speciate is linked to the cichlid labroid-style decoupled pharyngeal jaw, a proposed 'key evolutionary innovation' (Galis and Metz 1998). However the possession of such a structure is no guarantee of speciation, for it is also present in numerous non-speciose cichlid lineages, as well as other groups of labroid fishes (Turner 1999).

Nevertheless, the potential for morphological evolution may have been important in speciation. There is an increasing body of evidence that ecological selection, for example as a result of competition for limited resources, can result in ecological and morphological divergence, and ultimately speciation (Schluter 2000; McKinnon and Rundle 2002). However for speciation to take place by this mechanism it is critical both that novel phenotypes are able to evolve, and that intermediate phenotypes suffer a fitness disadvantage that ultimately prevents gene-flow between the divergent forms.

Novel morphologies may arise through hybridization. Hybrids between *L. fuelleborni* and *P. zebra* are strikingly different to either of the parental species in many traits (Albertson and Kocher 2001), and do not necessarily possess intermediate morphologies (McElroy and Kornfield 1993). At present the relative fitness of hybrid forms, and back-crosses with their parental species, remains to be investigated empirically.

While it is possible that ecological forces may have promoted divergence, if speciation within the mbuna has occurred largely by ecological selection, it might be expected that diverging taxa would possess significant differences in functional morphology. This would not appear to be the case among mbuna (Albertson *et al.* 1999). Instead, ecological differences tend to be very small among closely related taxa, and increase among more distantly related taxa (Barraclough and Nee 2001).

Sexual selection

Recent models suggest that, under certain conditions, speciation can take place rapidly if there is variation in mate preferences within a population or if individuals prefer to mate with those similar to themselves (Turner and Burrows 1995; Van Doorn *et al.* 1998; Dieckmann and Doebeli 1999; Higashi *et al.* 1999; Kondrashov and Kondrashov 1999; Lande *et al.* 2001). Many Malawi mbuna species have now been shown to recognize, preferentially court and spawn with conspecifics, despite the presence of individuals of closely related species in both laboratory and field situations (Knight *et al.* 1998; Van Oppen *et al.* 1998; Knight and Turner 1999). Thus, direct mate choice may be important in maintaining reproductive isolation, and so it has been proposed that divergent sexual selection may have been important in the origin of species (Holzberg 1978; McKaye 1991; Turner 1994a; Deutsch 1997). Divergent mate preferences may result from many processes, including selection on female sensory systems for other purposes, variation in conspicuousness against different backgrounds, evolution of novel fitness indicator traits (Kirkpatrick and Ryan 1991; Coyne and Orr 2004). This is consistent with recent evidence for a correlation between divergent male colour and female preference among allopatric races of *P. zebra* (Knight and Turner 2004) and with evidence of intraspecific sexual selection in mbuna (e.g. Hert 1991; Couldridge 2002; Pauers *et al.* 2004).

Allopatric or sympatric speciation

The water level in Lake Malawi has changed a great deal although the timing and magnitude of these events is controversial (compare Owen *et al.* 1990; Nicholson 1998; Johnson *et al.* 2001, 2002). During major falls in lake level, patches of formerly continuous rocky habitat would have been split into fragments, while other formerly isolated patches would have been united. This is obviously a possible means whereby populations of species could be subdivided, allowing allopatric speciation to occur (Trewavas 1947; Fryer 1959b, 1977; Dominey 1984; Owen *et al.* 1990). It would also permit species like mbuna, which are normally restricted to rocky habitat patches to expand their geographical ranges and come into sympatry, resulting in increasing alpha diversity. Population genetic studies show restricted gene flow among habitat patches, which is a key prerequisite for this mode of speciation to operate (e.g. Van Oppen *et al.* 1997).

Although allopatric speciation is plausible and supported by a good deal of circumstantial evidence, it may not be the only mechanism in operation. Danley *et al.* (2000) reported that they had evidence for genetic divergence of neighbouring populations despite evidence of some current or recent gene flow. Moreover, if narrow distributions and strong habitat associations are important in speciation, then we might expect to find a strong association between dispersal ability and the species richness. At present, the evidence seems weak (Turner 1994a). When artificial reefs were placed a few hundred metres from a rocky shore, among the first colonizers were members of the most species-rich groups of mbuna, the *Pseudotropheus* (*Maylandia*) and *Pseudotropheus* (*Tropheops*) complexes (McKaye and Gray 1984).

Parallel speciation and introgression

Given the clear evidence for parallel origin of similar trophic morphotypes in different lakes (e.g. Kocher *et al.* 1993), it would seem reasonable to suggest that parallel evolution of trophic types might occur among more closely related forms within a lake. Using mtDNA sequences, Reinthal and Meyer

(1997) proposed that they had found evidence for parallel origin of trophic forms of *Pseudotropheus* (*Tropheops*) from two sites within Lake Malawi. However, Kornfield and Parker (1997) suggested that incomplete mitochondrial lineage sorting rendered their results unreliable.

Many pairs of species belonging to the same genus or subgenus differ in the same colour contrasts. Blue males may either have blue or yellow/orange dorsal fins in the *Pseudotropheus* (*Maylandia*) *zebra* complex, the *Pseudotropheus perspicax* group, *Petrotilapia*, *Labeotropheus trewavasae*, *L. fuelleborni*, *Labidochromis*, and *Cynotilapia*. Other repeating contrasts include the presence of absence of a dark submarginal band in the dorsal fin, blue or yellow body colour, presence or absence of dark flank bars or dark interorbital bar and presence or absence of a contrasting yellow/orange throat, chest or pelvic fins. Some patterns are absent. It seems there are no yellow mbuna with bright blue throats or chests, although this pattern occurs in some *Aulonocara* species. So, there are constraints on colour patterns, but the frequency with which similar pattern contrasts distinguish pairs of morphologically similar species is remarkable. Among the few studies which have shown reasonable phylogenetic resolution, there are no indications that species belonging to different genera/subgenera, but having the same male colour are more closely related than those of the same genus/subgenus with different colour (Albertson *et al.* 1999; Rico *et al.* 2003; Allender *et al.* 2003). So, it seems that the same male colours have indeed evolved repeatedly in different lineages. The same appears to be true of the rare female morphs, OB and O (Allender *et al.* 2003).

If male colour is critical in reproductive isolation, and the same male colours can evolve repeatedly, it seems possible that the same biological species could evolve more than once in different parts of the same lake. Rico *et al.* (2003) failed to find any evidence for parallel speciation among some of the *Pseudotropheus* (*Maylandia*) and *Pseudotropheus* (*Tropheops*) species around the Nkhata Bay-Ruarwe area of the lake. However, Smith and Kornfield (2002) did find evidence for parallel origin of the red dorsal form of *P. zebra*, when comparing sites from the far north (Mpanga Rocks) and far south (south-eastern and south-western arms). Allender *et al.* (2003) found evidence for several additional cases. One possible explanation for this apparent parallel evolution of male colour is introgressive hybridization (Smith and Kornfield 2002). However, the occurrence of similar colour variants in Lake Victoria suggests that at least some of the variation has either arisen in parallel or else a great deal of genetic variation in such traits has persisted often unexpressed for a long period in riverine as well as lacustrine species (Seehausen *et al.* 1999b). Which of these explanations is more plausible will depend on whether the traits in question are found to be the result of many or a few genes.

Tempo of speciation and radiation

Has speciation and radiation generally taken place like it is doing at present, or were processes different in the past? Danley and Kocher (2001) suggest a three stage process: (i) After colonization of the lake by generalist ancestors, habitat specialization resulted in divergence into sand and rock associated (mbuna) clades. During this period they believe that the primary divergence of morphological traits, melanin patterning and reproductive behaviour also took place. (ii) Next came a period when resource competition drove the refinement of trophic morphological traits. Finally they suggest that (iii) intense sexual selection has resulted in the evolution of species-specific reproductive characters, including the vast array of male reproductive traits that can be seen today. Liem and Osse (1975) also proposed that morphological differences evolved early in the radiation, while Sturmbauer (1998) suggested a similar process, mainly considering Lake Tanganyika.

In our view, there is no compelling evidence for any of these scenarios. If all speciation were driven by sexual selection, one would predict that recent species would differ mostly in sexually selected traits, but greater morphological differences would evolve later under interspecific and/or intraspecific competition. The split into ‘sand’ and ‘rock’ clades is an oversimplification, with deep water or sandy shore *Aulonocara* and *Lethrinops* in the mbuna group, and obligate rocky shore species such as *Protomelas taeniolatus* and *Tyrannochromis* in the ‘sand clade’.

In another recent paper, Sturmbauer *et al.* (2001) propose that the finding of individuals with identical mtDNA haplotypes in distant parts of the lake provides evidence that a recent low lake level stand had permitted populations to disperse right round the lake. In our view, it may also be consistent with a very low rate of fixation of mtDNA within populations that were maintained at very large sizes for a protracted period. At present, these issues remain interesting speculations.

Why are there so many species of mbuna?

It is generally thought that mbuna comprise about half or more of the haplochromine cichlid species of Lake Malawi. Genner *et al.* (2004a) estimate a maximum of 225 mbuna of 600 Malawian haplochromine species (38%). However, this high figure depends critically of the allocation of species status to geographically restricted morphologically undistinguished colour forms (Turner *et al.* 2001). Minimum estimates of species richness can be obtained by an iterative process. Pairs of taxa with the largest geographical ranges are compared for co-occurrence in sympatry and if they do not co-occur, they are considered conspecific and their ranges added together. By this means, Genner *et al.* (2004a) estimate that there may be as few as 66 species of mbuna. Assuming that their estimate of non-mbuna Malawian haplochromines is accurate, mbuna could comprise as little as 15% of the flock. However, it is likely that some species of non-mbuna are also geographic races, while assortative mating trials indicate that some allopatric mbuna may indeed be species, or at least incipient species (Knight and Turner, 2004).

If we grant that mbuna are unusually species rich among Malawian cichlids, the obvious explanation is the potential for allopatric speciation. Few other cichlids seem so tightly tied to the rocky lakeshore and other habitats may not be so patchily distributed. Niche differentiation among mbuna seems relatively low compared to the non-mbuna haplochromines, and both groups seem to show roughly equal opportunities for sexual selection. However, predation by visual predators is probably higher among sandy shore species, perhaps limiting the range of male courtship colours. Deep water and swampy shore species live in habitats where light penetration is limited and confined to a relatively narrow band of wavelengths, so female choice of colour may be constrained. On the contrary, rocky-shore non-mbuna share the visual environment and patchy habitat of mbuna. Pereyra *et al.* (2004) have shown that population structure in the non-mbuna rocky shore cichlid *P. taeniolatus* is comparable to that of mbuna species studied to date, while related *Protomelas* species preferring sandy habitats show lower levels of genetic differentiation in space. It is notable that *P. taeniolatus*, like some of the mbuna groups, shows geographic variation in male colour. These findings suggest that non-mbuna haplochromines may show equal potential for allopatric speciation to the mbuna.

Vulnerability and conservation

Many mbuna have small geographic ranges and narrow habitat preferences. All lack a pelagic dispersal phase, have low fecundity and slow growth rates. These traits render them vulnerable. One of the primary threats to the cichlids of Lake Malawi is overfishing (Turner 1994b, 1996). At present, mbuna in some parts of the southern Malawian sector of the lake are protected by the imposition of no-fishing zones within 100 m of the rocky shore areas of the Lake Malawi National Park. So far, in our view, mbuna have not been under direct threat from fishing primarily because they have little commercial value as a food and are not caught in high numbers as by-catch by artisanal fishers targeting other species. Indeed those fishers who do target other fish species groups found on rocky reefs, such as utaka, usually avoid setting nets too close to the rocks for fear of tangling. Few fishers actively target mbuna, apart from a few children angling for subsistence and collectors for the aquarium trade. Both appear to take small numbers at present.

Unlike Lake Victoria, to our knowledge, there have been no introductions of competitor or predatory fish into Lake Malawi. However, mbuna have been translocated to non-native sites within the lake (Table 4). This has principally been the result of the aquarium trade (Ribbink *et al.* 1983). Many of the introduced species have spread from their point of introduction onto neighbouring rocky shorelines (Trendall 1988b; M.J. Genner and G.F. Turner, pers. obs.). These introductions are almost certainly irreversible, although long-term culling programmes could possibly reduce population numbers, but at the risk of native species in by-catch. At present there is no evidence of competition between endemic and introduced species, and if displacement of endemic taxa were taking place it would appear to be a slow process. A high diversity community had been maintained at one rocky headland for between 9 and 18 years in 1987 (Trendall 1988b). However, introduced species may mate with native taxa and produce viable hybrids. There are reported sightings at Thumbi West Island of unusual fish that may have been hybrids between the native

Table 4 Reported translocations of mbuna species within Lake Malawi.

Species	Source site	Introduced site(s)	Reference
Cynotilapia afra	Likoma Island	Thumbi West Island	Ribbink *et al.* 1983
		Otter Point	GFT, MJG, pers. obs.
Labeotropheus fuelleborni 'yellow flank'	Nakantenga Island	Thumbi West Island	Ribbink *et al.* 1983
Labeotropheus trewavasae	Nkhata Bay	Likoma Island	Konings pers. comm.
Labidochromis flavigulus	Chisumulu Island	Likoma Island	Ribbink *et al.* 1983
Labidochromis freibergi	Likoma Island	Thumbi West Island	Ribbink *et al.* 1983
Labidochromis gigas	Likoma or Chisumulu Island	Thumbi West Island Otter point	Ribbink *et al.* 1983
Labidochromis strigatus	Chisumulu Island	Thumbi West Island Likoma Island	Ribbink *et al.* 1983
Melanochromis interruptus	Chisumulu Island	Thumbi West Island	Ribbink *et al.* 1983
		Likoma Island	Konings pers. comm.
		Nkhata Bay	
Melanochromis joanjohnsonae	Likoma Island	Thumbi West Island	Ribbink *et al.* 1983,
Melanochromis parallelus	Unknown	Thumbi West Island	Ribbink *et al.* 1983
Melanochromis perileucos	Likoma Island	Thumbi West Island Otter Point Domwe Island	Ribbink *et al.* 1983
Pseudotropheus (*M.*)*aurora*	Likoma Island	Thumbi West Island Otter Point	Ribbink *et al.* 1983
Pseudotropheus (*M.*)*callainos*	Nkhata Bay	Thumbi West Island	Ribbink *et al.* 1983
		Otter Point	GFT, MJG, pers. obs.
		Likoma Island	Konings, pers. comm.
		Namalenje Island	
		Maleri Island	
		Mumbo Island	
		Harbour Island	
Pseudotropheus (*M*) 'livingstoni likoma'	Likoma Island	Thumbi West Island	Ribbink *et al.* 1983*
Pseudotropheus (*M.*)*lombardoi*	Mbenji Island	Namalenje Island	Ribbink *et al.* 1983
Pseudotropheus (*M.*)*pyrsonotus*	Nakantenga Island	Maleri Island	Ribbink *et al.* 1983
Pseudotropheus (*T.*) 'red cheek'	Likoma Island	Thumbi West Island	Ribbink *et al.* 1983
Pseudotropheus (*T.*) 'membe'	Likoma Island	Thumbi West Island	Konings, pers. comm.

*This species may not have been introduced, rather it may have been confused with the indigenous *P. elegans* (A. Konings, pers. comm.).

P. zebra and the introduced *P. callainos* (Stauffer and Hert 1992) and *Cynotilapia afra* (Stauffer *et al.* 1996). Recently molecular studies have given support for idea of introgression between *P. zebra* and *C. afra* (Streelman *et al.* 2004). Interbreeding may occur most readily when an alien conspecific race is introduced.

Perhaps the most significant threat to mbuna may come from habitat modification as a consequence of pollution. Lake Malawi has been subject to increased levels of sediment input from inflowing rivers over recent years, and this change has been attributed to higher rates of erosion in the lake's catchment due largely to alterations in agricultural land use practices (Bootsma and Hecky 1993; Duponchelle *et al.* 2000; Mkanda 2002). At present it is difficult to gauge the likely effects of changes in sedimentation, but it is possible that it may result in concomitant changes in local community structure. Given the nature of this threat, and as the primary aim of biodiversity conservation is to find mechanisms of protecting the greatest genetic and functional biological diversity from anthropogenic impacts given the finite resources available (Reinthal 1993), perhaps efforts to conserve mbuna should be focussed on a macro-scale perspective. It might be more profitable, from both conservation and development perspectives, to tackle the broader causes of environmental change, rather than focussing efforts on small numbers of taxa or narrowly defined locations. However, it remains to be seen whether the resources, the knowledge and the political will are available to fundamentally alter the agricultural practices of millions of people for the sake of preserving some interesting fish. The existing no-take reserve policy of the National Parks Department at least has the merit of publicising the aesthetic and scientific interest of the fish, and of spreading a conservation ethos while doing little harm to the local human communities.

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