

Chapter 29

Pelagic cichlid fishes of Lake Malawi/Nyasa: biology, management and conservation

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Abstract

Survey work carried out in the early 1990s indicated that the biomass of cichlid fishes in the pelagic zone of Lake Malawi/Nyasa was around 180 000 t. It appeared that this may represent the last major underexploited fishery resource of Lake Malawi, but several major questions remained unanswered, particularly in relation to species identification, stock movements and nursery areas. In addition to extensive field sampling work, detailed morphological and molecular analyses were carried out. Approximately 21 species of the genera *Rhamphochromis*, *Diplotaxodon* and *Pallidochromis* were recorded, at least nine of which are presently undescribed. All species studied in detail are abundant and widespread in all suitable habitats. Molecular studies indicated minimal population structuring in the three species investigated. The spawning and nursery areas of all known species of *Diplotaxodon* are in deep water, and largely inaccessible to fishing. Spawning areas of *Rhamphochromis* also appear to be in deep water, but the nursery grounds of some species are at least partially in shallow waters. It was concluded that there is minimal risk of species or population extinctions as a result of current patterns of exploitation. Implications of the results for management and conservation of fish stocks are discussed.

Keywords: cichlidae, exploitation, extinction, genetics.

29.1 Introduction

29.1.1 *The lake and its importance*

Lake Malawi is bordered by three of the world's poorest countries, Malawi, Mozambique and Tanzania. It is one of the largest lakes in the world, with a surface area of 30 800 km², and a maximum depth of over 700 m. It probably contains more

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endemic fish species than any other lake in the world. At least 650–700 species of cichlid fishes have evolved within the lake basin within the last 700 000 to 2 million years. The production of so many species at such a high rate is surpassed only by the closely-related cichlid fishes of Lake Victoria (Turner 1999). With the devastation of the Victorian cichlids by recent human-induced changes to the lake ecosystem, the Malawian cichlids represent a priceless asset to researchers studying the mechanisms of the evolution of biological diversity. The fish resources of Lake Malawi and its associated water bodies are of tremendous importance as a source of protein and revenue to the people living along the lake shore, particularly in the Malawian sector where the fisheries are most thoroughly developed. Since the beginning of the 1990s, there have been worrying signs of overfishing, particularly in the heavily exploited and highly productive southern areas of the system (Turner 1994a; 1995; Turner, Tweddle & Makwinja 1995; Tweddle, Turner & Seisay 1995). To date, despite a substantial investment in research and development, aquaculture has made little or no contribution to meeting the needs of the rapidly expanding human populations of this region. The initiation of a substantial new capture fishery on the lake would be a major contribution to the development of the region.

29.1.2 *The pelagic zone*

The lake is steep-sided, deep and permanently stratified. Below a depth of 200–250 m there is insufficient oxygen to support fish. At present, both artisanal and mechanised fisheries are largely confined to the shores of the lake, except in the south where there is a large shallow shelf area of high productivity. FAO (1982) concluded that the pelagic zone of the lake was seriously deficient in its fish community and recommended the introduction of a clupeid fish, *Limnothrissa miodon* (Boulenger), from Lake Tanganyika. The reasoning behind this was that large swarms of adult lakeflies, *Chaoborus* sp., were seen on Lake Malawi, but not in Lake Tanganyika. The larvae of these flies are carnivorous and large by the standards of freshwater zooplankton. In the absence of adequate equipment for deep water fishing in the offshore habitat, FAO believed that the principal offshore fish were small shoaling cyprinids, *Engraulicypris sardella* (Günther), known as 'usipa' in the Malawian part of the lake, which they believed were unable to feed on *Chaoborus* larvae. The introduction of the slightly larger clupeids was seen as way of establishing an efficient planktivore which would convert zooplankton into food fish.

In the early 1990s, extensive acoustic and plankton surveys were carried out in the offshore pelagic zone (Menz 1995). Initially, little attention was paid to sampling the fishes, as it was assumed that they would mostly be usipa. However, toward the end of the project, it was realised that cichlid fishes of the genera *Rhamphochromis* and *Diplotaxodon* comprised more than 80% of the fish biomass in the pelagic zone, and that this included a number of species which fed principally on *Chaoborus*. The overall fish biomass was estimated to be between 120 000 and 200 000 t. This suggested that a large fishery could be developed, yielding up to 30 000 t year⁻¹ on a sustainable basis (Menz 1995).

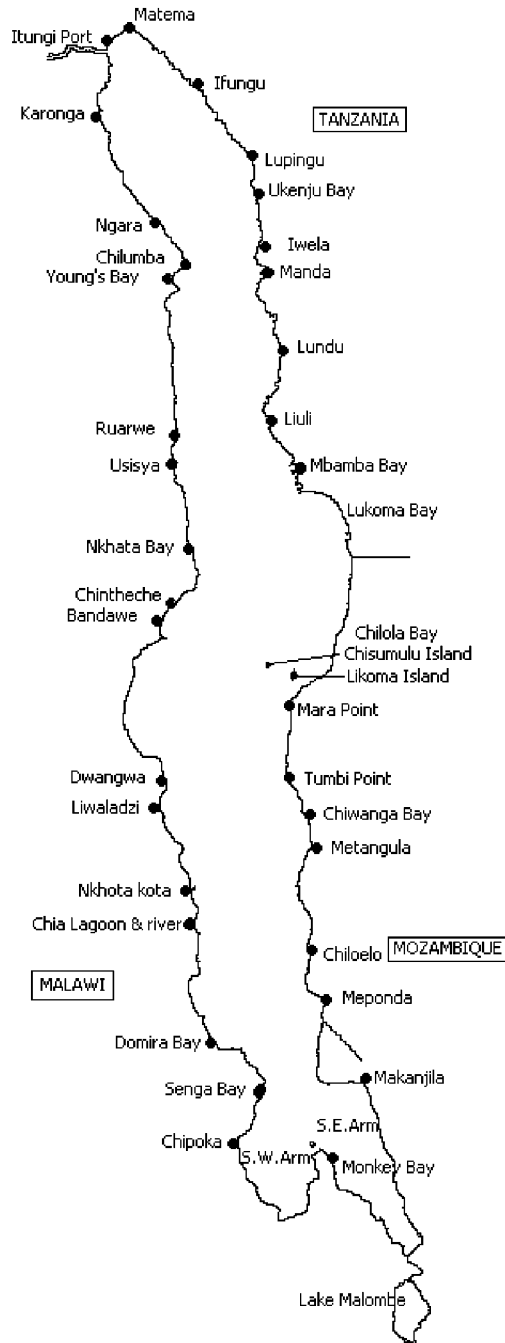


Figure 29.1 Map of Lake Malawi, showing major sampling locations along the shore

This study left several questions unanswered. Inshore waters were not investigated, nor were the catches of existing fisheries. It was possible that the offshore stocks were already heavily exploited, perhaps during the breeding season or on their nursery areas. This might mean that a rapid expansion of offshore fishing could lead to a crash in the populations of these fishes. It was difficult to appraise this possibility, as many of the species could not be reliably identified in the field, and it was believed that many were still undescribed (Fryer & Iles 1972). The UK Department for International Development (DfID) Ncheni Project, initiated in 1996, aimed to address these deficiencies.

29.2 Methods

Most of the samples were obtained from catches made by artisanal fisheries or by commercial trawl fisheries. On the Malawian shores, from 1996 to 1998, more than 4500 individually-labelled specimens were collected from more than 4.5 months field work. On the Tanzanian shore of the lake, experimental longline surveys were also conducted by staff from the Tanzanian Institute for Fisheries Research (TAFIRI). It was also possible to send personnel to accompany demersal trawl surveys being carried out by the GEF/SADC project in the south-western part of the lake, and by the Malawi Fisheries Department in the southern arms. The research vessel *Usipa* was hired for a single lake-wide cruise, from 18 to 27 January 1998. A pelagic trawl was used for 20 hauls, totalling 39 h 40 min fishing time. Material was collected from Mozambican waters during a demersal trawl survey carried out in collaboration with an EU-funded project. Many more specimens were examined in the field or in museum collections made by other projects, notably 1355 *Rhamphochromis* and *Diplotaxodon* specimens collected by the GEF/SADC project.

For many specimens, tissue samples were preserved in alcohol for subsequent molecular analysis, using mitochondrial DNA sequencing or genotyping of microsatellite nuclear DNA.

29.3 Results

29.3.1 *Species identification and taxonomy*

Eleven species of the genus *Diplotaxodon* were recognised (Table 29.1, Fig. 29.2). Of these, five were considered undescribed. Six of the seven previously described species were collected but it was not possible to confirm the identity of *Diplotaxodon ecclesi* Burgess & Axelrod. In general, there were few clear-cut counts or measurements which were useful in the diagnosis of new species. Although a few species had distinctive morphologies, many did not, but they differed in male breeding dress. Several forms were present in small numbers and could not be positively assigned to any of the 11 species. These remain unclassified for the present. A molecular phylogenetic study based on mitochondrial DNA sequences carried out as part of the project demonstrated

Table 29.1 Cichlid species of the genera *Diplotaxodon*, *Pallidochromis* and *Rhamphochromis*

Species	Maximum SL (mm)	Morphological group	Description
<i>Diplotaxodon</i>			
<i>D. limnothrissa</i>	154	Slender small mouth	Turner 1994b
<i>D. 'holochromis'</i>	160	Slender small mouth	Undescribed
<i>D. argenteus</i>	204	Elongate big mouth	Trewavas 1935
<i>D. 'similis'</i>	203	Elongate big mouth	Undescribed
<i>D. aeneus</i>	140	Big-eye	Turner & Stauffer 1998
<i>D. apogon</i>	117	Big-eye	Turner & Stauffer 1998
<i>D. macrops</i>	125	Big-eye	Turner & Stauffer 1998
<i>D. 'offshore'</i>	140	Big-eye	Undescribed
<i>D. 'deep'</i>	224	Deep-body, big-eye	Undescribed
<i>D. greenwoodi</i>	247	Deep-body, big mouth	Stauffer & McKaye 1986
<i>D. 'brevimaxillaris'</i>	212	Deep-body, big mouth	Undescribed
<i>Pallidochromis</i>			
<i>P. tokolosh</i>	280	Big-eye, big mouth	Turner 1994c
<i>Rhamphochromis</i>			
<i>R. esox</i>	420	Cylindrical	Boulenger 1908
<i>R. ferox</i>	209	Slender, small mouth	Regan 1922
<i>R. 'grey'</i>	347	Slender, small mouth	Undescribed
<i>R. longiceps</i>	195	Slender, small mouth	Günther 1864
<i>R. 'longfin'</i>	250	Large mouth & teeth	Undescribed
<i>R. 'maldeco'</i>	312	Large mouth & teeth	Undescribed
<i>R. macrophthalmus</i>	298	Large mouth & teeth	Regan 1922
<i>R. 'stripe'</i>	322	Large mouth & teeth	Undescribed
<i>R. woodi</i>	402	Large mouth & teeth	Regan 1922

that the benthic species *Pallidochromis tokolosh* (Turner) is properly considered a member of the *Diplotaxodon* clade. *Pallidochromis* differs from *Diplotaxodon* in having larger, more widely-spaced teeth and in having a less upwardly-angled mouth.

Nine species of *Rhamphochromis* were tentatively identified, four of which are certainly undescribed. Some of the formally described species will probably have to be synonymised. *Rhamphochromis ferox* Regan has previously been misidentified in the field as a big, large-mouthed predator (Menz 1995). Based on type specimens, it was considered to be small, delicate-looking species, similar to *R. longiceps* (Günther). The big predators were probably *Rhamphochromis woodi* Regan.

29.3.2 Habitat preferences

Inshore-living haplochromine cichlids are well-known for their habitat specificity (Fryer & Iles 1972; Ribbink, Marsh, Marsh, Ribbink & Sharp 1983), but prior to the current work, it had not been established whether the same was true of pelagic cichlids.

The eupelagic community was dominated by five species commonly found in this habitat (Table 29.2); the most abundant species were *Diplotaxodon limnothrissa* Turner and *Diplotaxodon 'offshore'*, the latter mainly in deeper water. Most of the

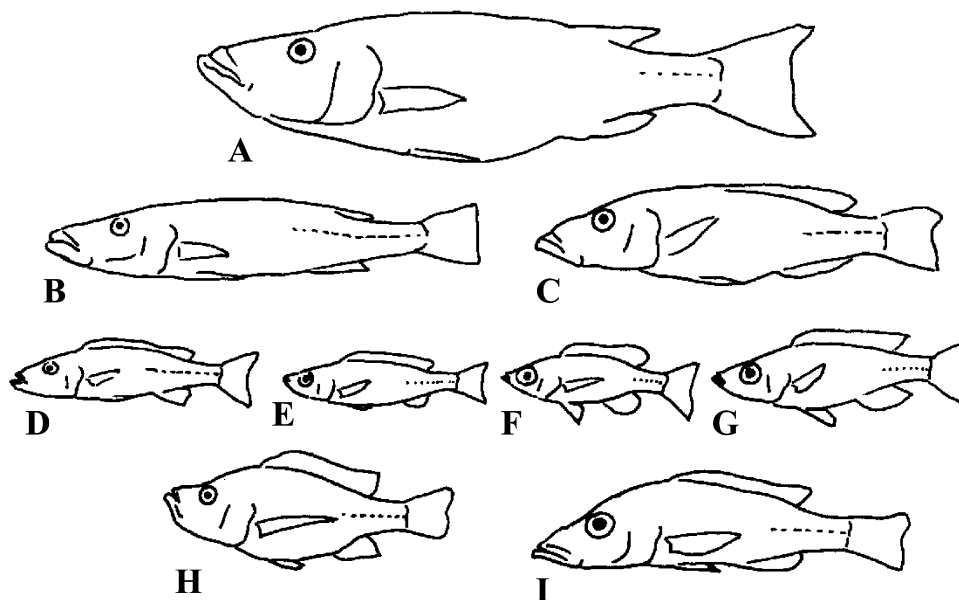


Figure 29.2 Representative pelagic cichlids of Lake Malawi. A. *R. woodi*; B. *R. esox*, C. *R. macrophthalmus*; D. *R. longiceps*, E. *D. limnothrissa*, F. *Diplotaxodon* 'offshore', G. *D. argenteus*, H. *Diplotaxodon* 'brevimaxillaris', I. *P. tokolosh*. Drawings by G.F. Turner, from photographs by the authors

eupelagic forms also occurred in the reef zone, but several species appeared to be confined to this habitat, including *Rhamphochromis* 'grey' and the rare *Diplotaxodon aeneus* Turner & Stauffer. The shelf zone is accessible to bottom trawling and most of this habitat lies in the southern arms of the lake, although there is another large area in the far north. Apart from the deep-water pelagic *Diplotaxodon* 'offshore', all the eupelagic species were encountered in this habitat, but there were also several species which were rarely, if ever, found elsewhere (Table 29.2). *Diplotaxodon* in particular, formed a far greater proportion of the biomass in deeper waters, especially at depths of 100 m or more (Fig. 29.3). Only immature *Rhamphochromis* were collected in the shallower part of the littoral zone, with adult *Rhamphochromis* 'stripe' apparently confined to the deep rocky littoral.

29.3.3 Distributions and stock structure

All of the eupelagic species seemed to have lake-wide distributions. Some inshore species seemed not to have very specific habitat requirements, and were also widely distributed. Although several species appeared to have strict habitat requirements, all were collected from several different areas of this habitat, although these areas were sometimes a long distance apart. For example, *Diplotaxodon apogon* Turner & Stauffer was described from the southern arms of the lake, where it is abundant on the

Table 29.2 Habitat preferences of pelagic cichlids in Lake Malawi (all = all developmental stages; a = adults only; f = fry; i = immature)

Habitat	Description	Common species	Others
Eupelagic	Open water above anoxic bottom	<i>D. limnothrissa</i> (a, f), <i>D. 'offshore'</i> (all), <i>R. longiceps</i> (a), <i>R. ferox</i> (a), <i>R. woodi</i> (a)	
Deep shelf	Soft bottom, 100–220 m	<i>D. macrops</i> (all), <i>D. apogon</i> (all), <i>D. limnothrissa</i> (a, i), <i>D. greenwoodi</i> (all), <i>D. 'similis'</i> (all), <i>P. tokolosh</i> (y), <i>R. woodi</i> (a, y), <i>R. macrophthalmus</i> (all), <i>R. longiceps</i> (a)	<i>D. 'brevimaxillaris'</i> <i>R. 'longfin'</i>
Shallow shelf	Soft bottom, 50–100 m	<i>D. limnothrissa</i> (a, f, i), <i>D. argenteus</i> (all), <i>R. ferox</i> (a), <i>R. longiceps</i> (a), <i>R. esox</i> (a), <i>R. 'maldeco'</i> (all)	<i>R. woodi</i> , <i>D. 'deep'</i> <i>D. 'holochromis'</i> <i>R. macrophthalmus</i>
Reefs	Water column near and above rocky shores and submerged reefs	<i>D. 'holochromis'</i> (all), <i>D. 'similis'</i> (a), <i>D. limnothrissa</i> (all), <i>D. greenwoodi</i> (all), <i>R. woodi</i> (all), <i>R. 'grey'</i> (all), <i>R. longiceps</i> (all), <i>R. ferox</i> (all)	<i>D. aeneus</i> <i>D. argenteus</i> <i>R. esox</i>
Rocky littoral	Benthic habitat on rocky shores	<i>R. 'stripe'</i> (all), <i>R. esox</i> (f, i), <i>R. ferox</i> (f, i)	<i>R. longiceps</i>
Margins	Sandy/muddy shores, lagoons, etc.	<i>R. longiceps</i> (all)	

shelf area at depths of 100 m or more (Turner & Stauffer 1998). This species then turned up in samples from similar habitats in the South-West Arm, Senga Bay, Domira Bay and off Nkhotakota in the south-western part of the lake, off Metangula on the eastern shore, and in Weissmann Bay in the far north.

Many inshore-living cichlids have high levels of population structure on a small spatial scale, suggesting very limited powers of dispersal (van Oppen, Turner, Rico, Deutsch, Ibrahim, Robinson & Hewitt 1997). In contrast, comparing the frequency distributions of allele sizes at six microsatellite DNA loci, little or no genetic differentiation was found between populations of *D. limnothrissa*, *D. macrops* Turner & Stauffer or *D. 'offshore'* collected hundreds of kilometres apart.

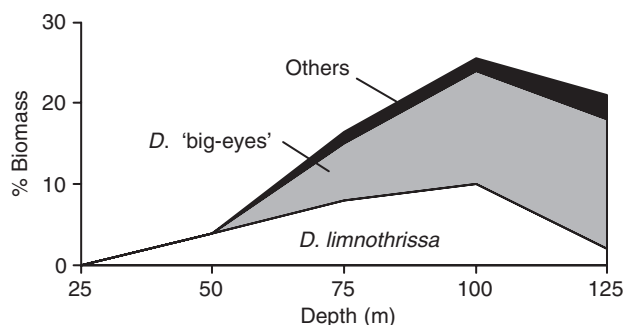


Figure 29.3 *Diplotaxodon* and *Pallidochromis* as percentage biomass of experimental demersal trawl catch in SW Arms (data reanalysed from F. Duponchelle, personal communication). *Diplotaxodon* 'big-eyes' is mainly *D. macrops* and *D. apogon*

29.3.4 Reproduction

All haplochromine cichlids previously studied were found to be maternal mouth-brooders. The present studies indicate no reason to doubt that the same is true of the pelagic haplochromines.

Many Malawian cichlids from sandy shores and the shelf habits aggregate in breeding arenas or 'leks'. In trawls, large numbers of ripe males were sometimes collected together with smaller numbers of ripe and spent conspecific females, but relatively few immature fishes. This suggests that the trawl had been fishing over leks. Such aggregations were observed for *D. macrops*, *D. apogon* and *D. greenwoodi* Stauffer & McKaye at around 100–120 m in the southern arms of the lake, and for *Rhamphochromis macrophthalmus* Regan at a depth of 100 m off Metangula in Mozambique.

Females of several species, including *D. limnothrissa*, *D. macrops*, *D. argenteus* and *R. woodi*, were collected carrying eggs, larvae or independently-feeding juveniles in their mouths. Like other mouthbrooding cichlids, females of both of these genera have large, yolky, non-adhesive eggs. Mature eggs were large, generally 4–6 mm in diameter. Some of the largest eggs were found in the smallest *Diplotaxodon* species: *D. limnothrissa*, *D. macrops* and *D. apogon*. These species reach maximum sizes of only 12–15.5 cm SL and 40–60 g. Consequently, they have very low fecundities (10–40 eggs per ripe female). Such low fecundity is probably unique for a small pelagic zooplanktivore, although it is by no means unusual for a small haplochromine cichlid. *Rhamphochromis* were found to attain rather higher fecundities, 27–680 eggs per ripe female, according to size and species. With such low fecundities, it is unlikely that these species could rapidly recover from population crashes caused by overexploitation.

Breeding seasons were generally long: March–August for *D. limnothrissa* in the SW Arm, all year round for *D. 'similis'*, November–April for *D. apogon*, January–September for *D. macrops*, and October–February for *P. tokolosh* (F. Duponchelle, personal communication). *R. ferox* and *R. longiceps* also appear to breed for most of the year, ripe fish being taken from January and February, respectively, until October.

29.3.5 *Breeding and nursery grounds*

Small *Rhamphochromis* of the *ferox/longiceps* group were often seen underwater, and were caught by gears operating near the surface or in shallow waters. These small fish were found to penetrate into swampy areas, including Lake Malombe, the Upper Shire River and Chia Lagoon. Young *Rhamphochromis esox* (Boulenger) were also sometimes found at depths of a few metres or less, mainly on sandy shores, while young *R.* 'stripe' were abundant in shallow rocky areas. Fully ripe or mouthbrooding *D. limnothrissa* were found in all habitats with a bottom depth greater than 20 m, but young of 2–10 cm were most abundant near the surface over shelf areas. Mouthbrooding female *R. woodi* were generally collected over deep bottoms, but immatures of 5–15 cm were mostly collected in the shelf zone near the bottom at depths of 50–100 m. Ripe females and small juveniles of *Diplotaxodon* 'offshore' were often collected far offshore in deep waters, but ripe males were found at depths of 99–184 m from a variety of sites along the mid-western shore from Senga Bay to Nkhata Bay. It seems likely that this species breeds deep-down along the steeper shelving coasts, but that mouthbrooding females rapidly return to the eupelagic zone where they release their fry. All other pelagic cichlids seem to breed in the normal adult habitats, which are mainly in deep waters.

29.3.6 *Diet*

From stomach contents, all *Diplotaxodon* and *Rhamphochromis* specimens examined seem to have fed on prey from the water column (Allison, Irvine, Thompson & Ngatunga 1996; unpublished data). Small individuals fed on crustacean zooplankton, *Chaoborus* larvae and pupae, and young stages of the cyprinid *Engraulicypris*. Larger individuals ate fish, mainly *Engraulicypris* or small pelagic cichlids. Two individual *P. tokolosh* contained remains of benthic cichlids of the genera *Aulonocara* and *Lethrinops* (Turner 1994c).

29.3.7 *Exploitation*

Turner (1995) summarised the mechanised fisheries operating in the south of the lake up to 1991. Four main gears were operating at that time. The ring net (purse seine) fishery employed a 102-mm mesh, too large to catch pelagic cichlids, apart from the occasional *R. woodi*. The other gears all employed 20–38 mm meshes. The midwater trawl was operated with otter boards on the bottom, but the net set to float higher in the water column. In 1990–1991, *D. limnothrissa* comprised 20% of the total catch of the midwater trawl and 53% of the 'small fish' component (Fig. 29.4). *Rhamphochromis* comprised 12% of the 'small fish' element, and other *Diplotaxodon*, mainly *D. argenteus*, about 4%. In the early 1990s, the main target of this fishery was the high-value *Oreochromis* 'chambo' species. The 'small fish', mainly haplochromine element, comprised just 38% of the catch. By 1994, it had risen to 56%, and according to catch

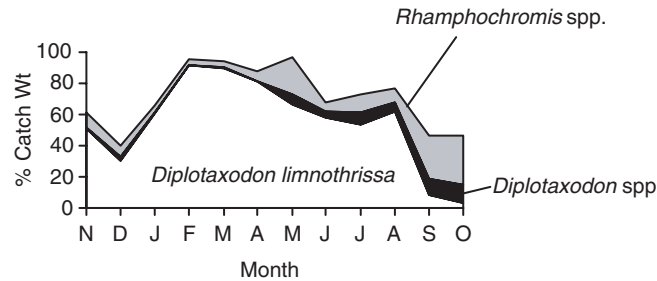


Figure 29.4 Monthly pelagic cichlid catches in midwater trawl, as percentage weight of 'small fish' catch, i.e. excluding large *Oreochromis* and catfish. The category '*Diplotaxodon*' includes all members of this genus, excluding *D. limnothrissa*. The highest catches of *D. limnothrissa* correspond closely to the peak breeding season of that species. Data collected by G.F. Turner in 1990–1991, based on 35 samples, totalling 16,987 fish weighing an aggregate 361 kg

statistics, pelagic cichlids comprised 43% of the total catch. Up to this time the fishery had been operating on the main chambo grounds, in 'Area B' just to the north of Boadzulu Island in SE Arm. With the collapse in chambo stocks in the mid-1990s, the fishery moved its main landing site from Maldeco in the middle of the SE Arm to Monkey Bay in the north of the arm. This permitted the trawlers to exploit the remaining, smaller chambo stocks in the shallower areas around the north of the SE Arm. By 1996–1997, the main by-catch of the fishery was no longer *Diplotaxodon*, but inshore zooplanktivores of the *Copadichromis virginalis* (Iles) complex, along with various benthic cichlids. By August 2000, Maldeco had largely abandoned the semi-pelagic trawl and was operating two fully pelagic trawlers targeting *Diplotaxodon* and *Rhamphochromis* species.

The remaining mechanised fisheries in the early 1990s were demersal trawls. Pair trawlers using illegal double-bagged cod-ends of 20–25 mm mesh fished in shallow waters around the southern arms and Domira Bay, often refusing to submit catch returns to the Malawian Fisheries Department. Despite fishing mainly in shallow waters, pelagic cichlids comprised a surprisingly high proportion of the catch: around 5% by weight, of which *Diplotaxodon*, mainly juveniles of more surface-living species, such as *D. limnothrissa* and *D. argenteus* (Trewavas), along with around 15% *Rhamphochromis*, mainly small individuals of the *ferox/longiceps* type. Although highly profitable in the SE Arm (Turner & Mdhaili 1992), the pair trawl fishery collapsed in the late 1990s, apparently due to lack of investment in maintenance of the boats and engines by proprietors who had been accustomed to anticipate that the government or development aid programmes would provide them with favourable loans or even free boats and engines.

In the early 1990s, larger single boat demersal trawls operated in deeper water in the SE Arm, catching mainly benthic cichlids, but also a fair proportion of pelagic cichlids (Fig. 29.5); around 18% *D. limnothrissa* and 8% *Rhamphochromis*. In the late 1990s, with loans from the World Bank and the Icelandic Government, this fishery was greatly expanded with two large Icelandic trawlers capable of fishing in deeper waters, one operated for research, but also as a revenue raising activity by the Malawi

Government Fisheries Department. Both vessels covered larger areas than the smaller vessels, frequently fishing in the SW Arm or even further to the north. Perhaps because of their greater power and speed, or because they operated in areas previously not exploited by trawlers, the catches of these vessels frequently included a larger proportion of larger fish, such as big *R. woodi*. Deeper water species, such as *D. macrops* and *D. apogon*, were also landed in large numbers.

Outside of the main chambo grounds in the southern arms, large *Rhamphochromis* are the highest value fish commonly taken in the lake. The rise in tourism along the northern lakeshore of Malawi has led to an increased demand from restaurants for these big 'batala'. Off the steep rocky shores of the Nkhata Bay area, most large *Rhamphochromis* are caught by targeted, size selective angling from dugout canoes fished by day. The main species are *R. woodi* and *R. 'grey'*. Deep-set gillnets tend to land lower value fish, including large numbers of *D. limnothrissa*. The nocturnal light attraction fisheries for *Engraulicypris* land a substantial by-catch of smaller *Rhamphochromis*, mainly *R. ferox* and *R. longiceps*. These species, along with *D. limnothrissa* and *D. 'holochromis'* are also taken in day-fishing 'chirimila' (lift net) catches targeted on reef-living 'utaka', zooplanktivores of the genus *Copadichromis*.

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to 441 t, and by 1994 to 43 t. Although these fisheries have not landed large numbers of pelagic cichlids, apart from some juvenile *Rhamphochromis*, it indicates the potential dangers of unregulated expansion of small-meshed artisanal gears, particularly with regard to species with a spawning/nursery area within range of such gears.

29.4 Discussion

29.4.1 Conservation of biodiversity

The widespread populations and lack of stock structure are favourable for the conservation of pelagic cichlids. Extirpation of locally distributed species or genetically unique populations of a species seems a remote possibility. Thus, there seems little cause for concern over the preservation of these species.

29.4.2 Fisheries management and stock assessment

If the populations of pelagic cichlid species are comprised of single vast stocks, local overexploitation is likely to be compensated by immigration of fish from elsewhere. However, from the point of view of fisheries management, a note of caution is warranted. The frequencies of selectively neutral alleles (as microsatellites are presumed to be) can be homogenised with a rate of migration between populations as low as five individuals successfully immigrating and breeding per generation. At this rate, a locally overexploited stock might take a very long time to build itself back up to an economically-viable level, particularly given the low fecundity of many of the species. However, given the lack of alternative sources of protein and employment in the region, application of the precautionary principle seems a luxury that cannot be borne by the peoples of the region.

D. limnothrissa: At the height of its exploitation by the midwater trawl in the early 1990s, the total mechanised catch of *D. limnothrissa* was of the order of 700 t year⁻¹ (Turner 1996) and it seems likely that the artisanal catch was lower. The total standing stock of this species in the offshore pelagic zone alone was estimated at 87 000 t (Menz 1995). It seems safe to conclude that this species is presently underexploited and expansion of the fishery is feasible.

The presence of the wide-ranging *D. limnothrissa* in trawl catches in the southern arms poses a problem for stock assessment. If the southern arm stock of this species exhibits a high rate of mixing with the vast offshore populations, then the catch per unit effort (CPUE) is likely to be unaffected by the level of fishing effort, violating the fundamental assumptions of the surplus production models presently used. Ideally, the *Diplotaxodon* catch would be subtracted from the analysis, which would then be performed on the data on resident demersal species alone. If an attempt is made to fully exploit the *D. limnothrissa* stock by expanding inshore trawl fisheries, this is likely to lead to heavy pressure on the demersal species, and it seems probable that the stocks of the demersal species are neither so large, nor so mobile, and could more easily be

fished out. It would be better if an alternative method could be found to exploit *D. limnothrissa* in the offshore habitat.

Diplotaxodon 'offshore': As with *D. limnothrissa*, there is a huge eupelagic stock of *D.* 'offshore'. At the beginning of the project, *D. macrops* had not been distinguished from *D.* 'offshore'. As *D. macrops* could be exploited by deep-water demersal trawling, it seemed possible that this might be a way to access this component of the eupelagic stock. This, however, is not the case. At present, it seems that *D.* 'offshore' is only lightly exploited by deep-water artisanal fisheries.

R. ferox and *R. longiceps*: *R. ferox* and *R. longiceps* were not accurately distinguished from each other until late in the project. The offshore stock of these species is large, but they are presently exploited by a wide range of gears, and the current total yield is difficult to estimate. The presence of many immature specimens of these species in catches by small-meshed beach seines and chirimilas is potentially a cause for concern.

R. woodi: Exploitation of the high-value *R. woodi* is likely to be increasing in the north-western part of the lake. At present, the use of size-selective angling methods and the limited range of fishing canoes probably means that there is little risk of over-exploitation of this wide-ranging stock. However, large numbers of immature fishes are presently caught by demersal trawls, and it would be useful to estimate the levels of mortality from this cause, and to determine what proportion of the juvenile population lies in the trawlable area.

Other species: Other *Rhamphochromis* and *Diplotaxodon* species, along with *P. tokolosh*, are principally caught as small components of multispecies fisheries. Management of these fisheries must take into account the biology of these other, mainly demersal cichlid fishes and *Engraulicypris*.

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References

- Allison E.H., Irvine K., Thompson A.B. & Ngatunga B.P. (1996) Diets and food consumption rates of pelagic fish in Lake Malawi, Africa. *Freshwater Biology* **35**, 489–515.
- Boulenger G.A. (1908) Diagnosis of new fishes discovered by Captain E. C. Rhoades in Lake Nyasa. *Annals and Magazine of Natural History* **8**(2), 238–243.

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- Burgess W.E. & Axelrod H.R. (1973) New cichlids from Lake Malawi. *Tropical Fish Hobbyist* **1973** (October) 14 & 87–89.
- FAO (1982) Fishery Expansion Project, Malawi: Biological Studies on the Pelagic Ecosystem of Lake Malawi. Rome, FAO, *Technical Report 1*, Fi: DP/MLW/75/019, 109 pp.
- FAO (1993) Fisheries Management in the SE Arm of Lake Malawi, the Upper Shire River and Lake Malombe. Rome, FAO, *CIFA Technical Paper 17*, 106 pp.
- Fryer G. & Iles T.D. (1972) *The Cichlid Fishes of the Great Lakes of Africa*. Edinburgh: Oliver & Boyd, 641 pp.
- Günther A (1864) Report on a collection of reptiles and fishes made by Dr. Kirk in the Zambesi and Nyassa regions. *Proceedings of the Zoological Society of London* **1864**, 303–314.
- Menz A. (ed.) (1995) *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Chatham, UK: Natural Resources Institute, 386 pp.
- Regan C.T. (1922) The Cichlid fishes of Lake Nyasa. *Proceedings of the Zoological Society of London* **1921**, 675–727.
- Ribbink A.J., Marsh A.C., Marsh B.A., Ribbink A.C. & Sharp B.J. (1983) A preliminary survey of the cichlid fishes of rocky habitats of Lake Malawi. *South African Journal of Zoology* **18**, 149–310.
- Stauffer J.R. & McKaye K.R. (1986) Description of a paedophagous deep-water cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. *Proceedings of the Biological Society of Washington* **99**, 29–33.
- Trewavas E. (1935) A synopsis of the cichlid fishes of Lake Nyasa. *Annals and Magazine of Natural History Series* **10**(16), 65–118.
- Turner G.F. (1994a) Fishing and the conservation of endemic fishes of Lake Malawi. *Archiv fur of Hydrobiologie Advances in Limnology* **44**, 481–494.
- Turner G.F. (1994b) A description of a commercially important new pelagic species of the genus *Diplotaxodon* (Pisces: Cichlidae) from Lake Malawi, Africa. *Journal of Fish Biology* **44**, 799–807.
- Turner G.F. (1994c) *Pallidochromis tokolosh*, a new genus and species of deep water cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. *Ichthyological Explorations of Freshwaters* **5**, 377–383.
- Turner G.F. (1995) Management, conservation and species changes of exploited fish stocks in Lake Malawi. In T.J. Pitcher & P.J.B. Hart (eds) *The Impact of Species Changes in African Lakes*. London: Chapman & Hall, pp. 365–395.
- Turner G.F. (1996) *Offshore Cichlids of Lake Malawi*. St. Leon Rot (Germany), Cichlid Press, 240 pp.
- Turner G.F. & Mdhaili M. (1992) *A Bioeconomic Analysis of the Industrial and Semi-industrial Fisheries of Southern Lake Malawi*. FI:DP/MLW/86/013. FAO Field Document 22, 12 pp.
- Turner G.F. & Stauffer J.R. (1998) A description of three deep water cichlids of the genus *Diplotaxodon* (Teleostei: Cichlidae) from Lake Malawi, Africa, with a redescription of *Diplotaxodon ecclesi* Burgess & Axelrod. *Ichthyological Explorations of Freshwaters* **8**, 239–252.
- Turner G.F., Tweddle D. & Makwinja R.D. (1995) Changes in demersal cichlid communities as a result of trawling in southern Lake Malawi. In T.J. Pitcher & P.J.B. Hart (eds) *The Impact of Species Changes in African Lakes*. London: Chapman & Hall, pp. 387–412.
- Tweddle D., Turner G.F. & Seisay M.B.D. (1995) Changes in species composition and abundance as a consequence of fishing pressure in Lake Malombe. In T.J. Pitcher & P.J.B. Hart (eds) *The Impact of Species Changes in African Lakes*. London: Chapman & Hall, pp. 413–424.
- van Oppen M.J.H., Turner G.F., Rico C., Deutsch J.C., Ibrahim K.M., Robinson R.L. & Hewitt G.M. (1997) Unusually fine-scale genetic structuring found in rapidly speciating Malawi cichlid fishes. *Proceedings of the Royal Society of London, Series B* **264**, 1803–1812.