The Natural History of the Satellite Lakes of Lake Malawi

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Abstract

Large, long-lived lakes, such as Lake Baikal and the African Great Lakes are known for their diverse endemic faunas. Nearby smaller isolated lakes have long been hypothesised to facilitate allopatric speciation, such as Lake Nabugabo at the edge of Lake Victoria, helping seed the radiation in the large lakes. Furthermore, crater lakes, formed by volcanic activity are often deep, long-lived and relatively isolated, and often host a number of closely-related endemics, becoming model systems for testing theories of sympatric speciation and adaptive radiation, such as Lakes Barombi Mbo in Cameroon, and Apoyo in Nicaragua. Here we report on studies of 9 crater lakes in southern Tanzania: Lakes Ikapu, Ilamba, Itamba, Itende, Kingiri, Kyungululu, Masoko (=Kisiba), Ndwati and Ngozi, plus the shallow satellite lakes Chikukutu and Chilingali in central Malawi. Additional notes are presented about fish species present in nearby river systems. The lakes differ considerably in surface area, depth and water chemistry. No permanently aquatic animals were observed in Lake Ngozi, the largest of the lakes, nor in Lake Ndwati. All of the other 7 craters lakes were found to contain cichlid fishes, comprising a total of 29 populations of which 24 are considered likely to be native, many meriting recognition as distinct species. At least one lake (Masoko) contains a diverging pair of cichlid ecomorphs likely to be undergoing sympatric ecological speciation. Another case might be the dwarf and large ecomorphs of *Rhamphochromis* in Lake Kingiri. In addition, 4 crater lakes are reported to contain members of other fish families: Clariidae, Cyprinidae, Danionidae and Procatopodidae. The lakes also hosted a variety of macro-invertebrates, including crabs, bivalves and gastropods. There is evidence of repeated attempts to stock all of these lakes with non-native fish species, in at least one case leading to the establishment of breeding populations of two species. This represents a major threat to these unique ecosystems. In Malawi, Lakes Chilingali and Chikukutu were recently joined as a result of damming of the outflow of the former. This 'large Chilingali' hosted a diverse fish fauna, including two apparently endemic haplochromine cichlid fishes of the genera *Lethrinops* and *Rhamphochromis*. The lake was heavily fished and attempts had been made to stock cages for tilapia culture using non-native populations of species already present in the lake. However, the dam was allowed to erode and it finally collapsed in 2011-13, resulting in the restoration of the previous condition of two inter-connected lakes. Little is known of the pre-impoundment lakes, but post-collapse, the lakes became shallow and swampy, with apparently greatly reduced fish diversity. Neither endemic species could be found when the lakes were sampled in 2016. Our work has indicated that the satellite lakes of Lake Malawi are important reservoirs of biodiversity that can play a major role in our understanding of speciation and adaptive radiation, but they are fragile systems currently threatened by poor management practices including intentional stocking of non-native fish.

Introduction

Freshwater ecosystems contain a disproportionately high concentration of unique species, with around 1/3 of all vertebrates, despite occupying less than 1% of the Earth's surface (Strayer & Dudgeon 2010). They are heavily threatened by human activities (Reid *et al.* 2019), including catchment disturbance, water resource development, pollution and biotic factors including capture fisheries and introduction of non-native species, with additional pressure expected from human population growth and climate change (Vörösmarty *et al.* 2010). However, distribution, abundance and population trends of freshwater species are often poorly known and use of information from data-rich terrestrial species is believe to provide a relatively inaccurate guide to freshwater conservation needs (Darwall *et al.* 2011).

Among freshwater habitats, crater lakes are particularly diverse and vulnerable because of their isolation and small size. The cichlid fishes of Cameroonian (Poelstra *et al.* 2018) and Nicaraguan (Kautt *et al.* 2018) crater lakes are celebrated as important model systems for the study of ecological speciation. Recently, Malinsky *et al.* (2015) reported a detailed interdisciplinary study of a pair of diverging haplochromine cichlid ecomorphs from Lake Masoko (Kisiba) in southwestern Tanzania, including characterisation of the genomic basis of adaptive divergence in situ. Other satellite lakes, such as Lake Nabugabo near Lake Victoria, have been suggested to be important in the generation of biodiversity in larger lakes, through a process of intermittent isolation and connection leading to allopatric speciation and secondary contact (Greenwood 1965) and are valuable as they host both satellite lake endemics and species at risk from anthropogenic change in the main lake (Mwanja *et al.* 2001). Previous studies of Lake Chilingali, a small shallow satellite lake to the West of Nkhotakota in central Malawi demonstrated assortative mating between native haplochromines of the genera *Rhamphochromis* (Genner *et al.* 2007) and *Lethrinops* (Tyers *et al.* 2014) and their putative closest relatives from the main lake, indicating that this satellite lake hosted narrow endemics arising through allopatric speciation. Here, we put these discoveries into the context of preliminary surveys of nine crater lakes within the Tanzanian part of the Lake Malawi (Nyasa) catchment and Lake Chilingali/ Chikukutu in the Malawian sector.

Methods

The Malawian lakes were visited between 2004 and 2016 in a number of expeditions involving UK universities in collaboration with the Malawi Government Department of Fisheries or Bunda College (now Lilongwe University of Agriculture and Natural Resources, LUANR,) and Chancellor College, Malawi. The Tanzanian lakes were visited through a series of collaborative expeditions from 2011 to 2018, involving staff and students from Tanzanian & UK Universities and the Tanzanian Fishery Research Institute (TAFIRI), later augmented by Operation Wallacea in 2017-18. Survey methods were diverse and varied among lakes and visits, but included experimental fishing with seines, angling, mosquito nets, gillnets, snorkelling and SCUBA, along with observations by ROV, underwater cameras, SCUBA and snorkelling. Additionally, fish were sometimes obtained from local fishermen, using a variety of methods, such as gillnets, angling, seines and castnets. Water depths were determined by surface sonar (fish finders) and water parameters sampled with a variety of probes and water bottles, deployed from inflatable or wooden boats. Invertebrates were collected by hand nets, while plankton nets and Secchi disks were also deployed. A number of fish specimens were brought back to the laboratory alive and reared to determine male breeding dress at sexual maturity. Tissue samples were obtained from dissection of fish humanely killed by anaesthetic overdose and preserved in ethanol, DMSO or RNAlater. Additional data was obtained from interviews, unpublished reports, museum collections and a variety of mapping resources.

Figure 1: Lake Malawi showing approximate location of the Tanzanian Crater lakes (based on Lake Masoko) and Lake Chilingali, in Malawi. From Google Earth, Landsat Copernicus, image dated 14 December 2015.

Results

Part 1. Lakes Chilingali & Chikukutu

Lakes Chilingali and Chikukutu lie in the Malawian part of the Lake Malawi catchment, to the West of the town of Nkhotakota, around 11.5km from the shore of Lake Malawi (Figure 2).

Along with various collaborators and local guides, we visited the lake(s) in April 2004 (GFT, MJG), July 2004 (MJG), May 2005 (MJG), June 2009 (GFT), January 2011 (MJG) and February 2016 (GFT). Access was by a dirt road, well-signposted (Lake Chilingali) on the right of the tarred road from Nkhotakota to Kasungu, but the easiest access point was at the former dam end of Chilingali about 6km away. In 2016, the southern tip of Chikukutu was only about 2km from the tarred road, but was not easy to find, and involved negotiating some narrow rough tracks and a substantial walk.

During our visits from 2004-2011, there was a single large lake held behind a dam, but in 2016, following the collapse of the dam, there were several much smaller lakes. According to information from the Malawi Government Department of Surveys, the dam was constructed in 1992 (Genner et al. 2007). Satellite photographs show a single large lake in November 2010 (Figure 3). At the time of visiting in January 2011, the dam was badly eroded but was still holding. However, satellite photos from September 2013 onwards show two or more much smaller lakes (Figure 4).

Evidence of a longstanding pre-impoundment pair of lakes comes from maps by Stewart (1883) referring to Lakes Chikuputa and Chiningala and by Money & Kellett Smith (1897) showing Lakes Chukuputu and Chiningara on the Kaombwe River. Harrison & Chapuwa (1975) mention Lakes Chilingali and Chikukutu. The National Atlas of Malawi (Malawi Government Department of Surveys, 1983) shows 3 separate lakes (the largest two named as Chilingali and Chikukutu), as does the 1996 map sheet for Kasungu based on a 1986 aerial photograph. These water bodies appear to be much larger than the lakes shown on recent satellite photos, and are almost contiguous (Figure 5). This might be the result of inaccurate representation in these maps, or changing rainfall patterns, but it may also indicate that the period of impoundment was characterised by a high level of siltation, perhaps resulting both from increased soil erosion due to cultivation of the catchment and reduction in water flow as a result of impoundment. When visited in 2016, the remnant Lakes Chilingali and Chikukutu both appeared shallow and swampy, and far fewer fish species were found than before: notably neither of the two apparently endemic haplochromines could be found, nor could the Lake Malawi endemic tilapia *Oreochromis squamipinnis*.

Physico-chemical analysis of the ‘large’ lake in 2009 indicated a pH of ca 7.9, conductivity of ~76µS/cm, Secchi depth of 93-108cm, Chlorophyll *a* of 20.6µg/l (Table 1). The chlorophyll and Secchi depth figures would put the large lake at the lower end of eutrophic status (Carlson 1977). The deepest part of the lake found was 4.4m, but a more extensive bathymetric survey in 2005 indicated 2 basins of approximately 5m depth (Figure 6). Previously depth had been reported to be 4m on average, with a maximum of 9m (Government of Malawi 2008). In June 2009, at 4m depth, some photosynthetically active radiation penetrated to the bottom, which was oxygenated and had a similar temperature to the surface of ~23.6C (Ferris 2010).

When visited on 17 February 2016, Lake Chilingali was estimated to be ca 1m deep, muddy and fringed with emergent macrophytes. The section just upstream of the road bridge (on the site of the former dam) was a separate lake, deeper (2m+), rocky and with patches of water lillies (*Nymphaea caerulea*). Just downstream of the bridge, was a separate small pool, less than 0.5m deep, completely covered with floating weed (*Pistia*). On 18 Feb 2016, Lake Chikukutu was also shallow and muddy with extensive emergent macrophyte beds. Physio-chemical parameters were recorded: pH 6.1-6.4; TDS 60, EC 130µS/cm; T=28.8C. These parameters are notably rather different to those of the large lake phase, indicating a transition from a cool, clearer water, alkaline lake to a more eutrophic, hot (or variable-temperature), muddy, acidic system.

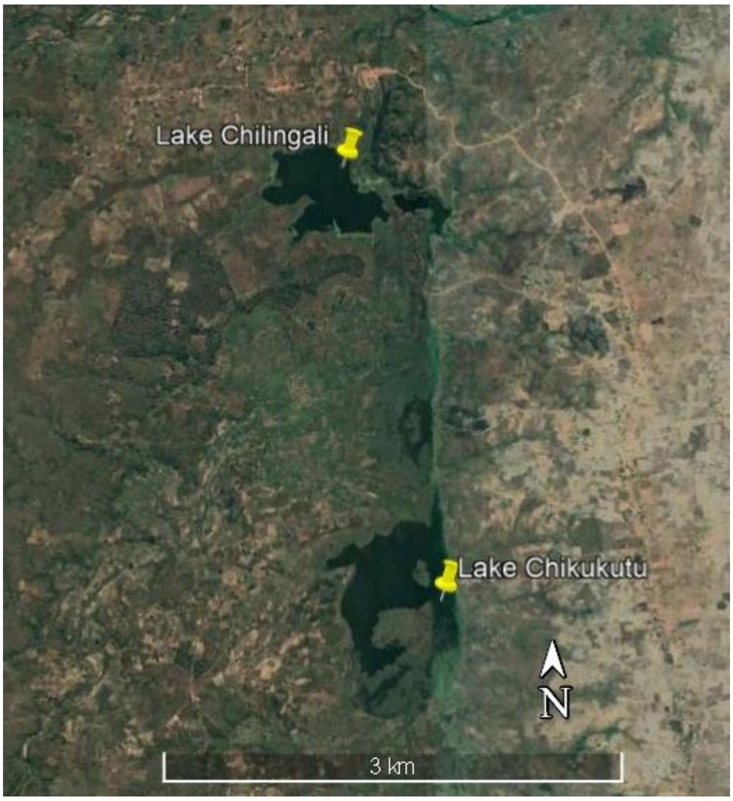

Figure 2. Satellite image of Lakes Chilingali and Chikukutu taken on 5th June 2018. Chilingali was visible as three small lakes, the largest of which was about 900 x 750m, Chikukutu was also split into three, of which the largest of which was ca 1,300 x 750m (Google Earth, © 2018 CNES/Airbus; © 2018Digital Globe).

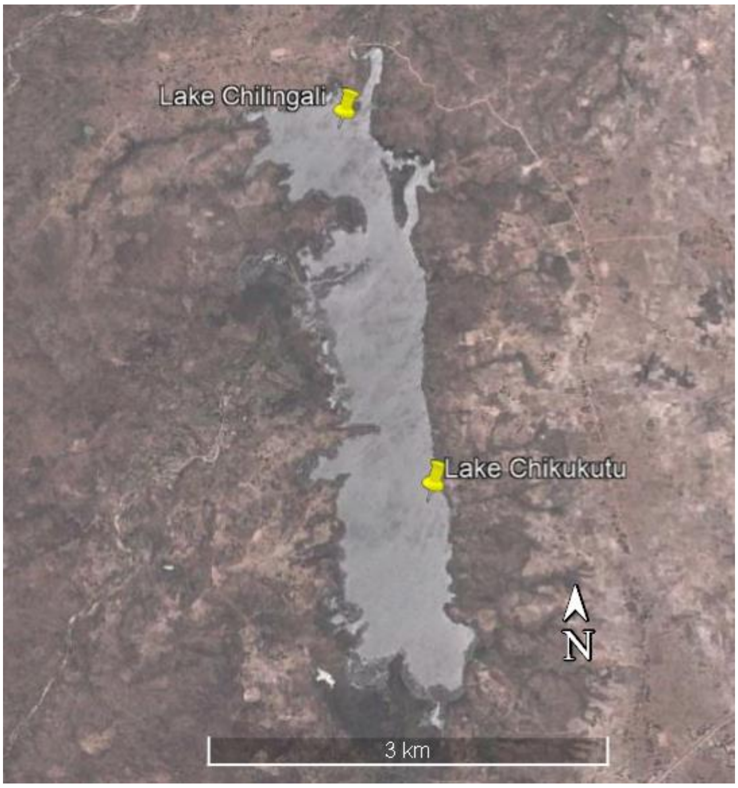

Figure 3. Satellite image of the single Lake Chilingali-Chikukutu on 4th November 2010, measuring approximately 5.5 x 1.5km. The marker positions are the same as those on Figure 2. From Google Earth, © 2019 Digital Globe.

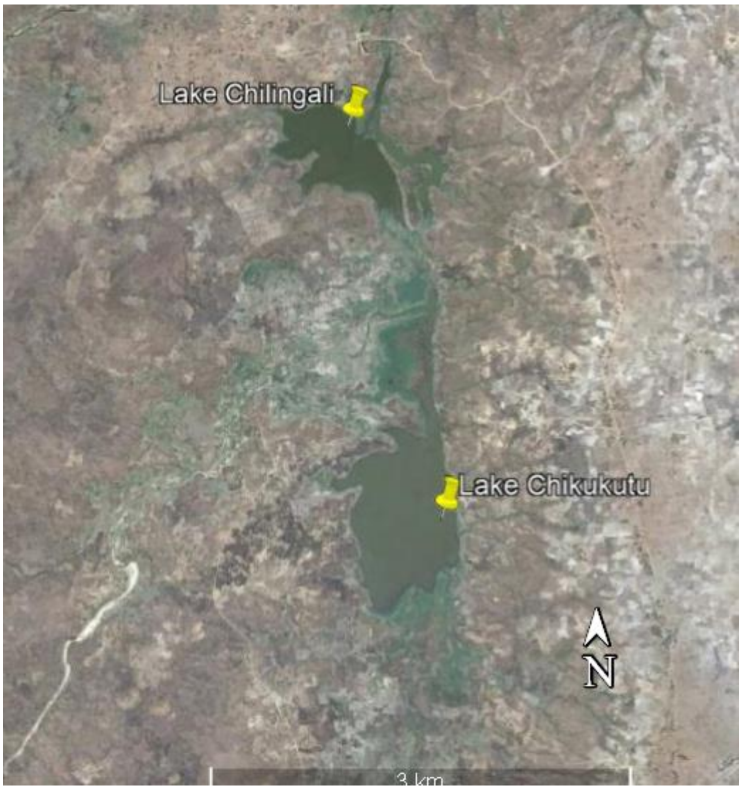

Figure 4. On Google Earth, the earliest satellite image of the separate Lakes Chilingali and Chikukutu appears on 11 September 2013, almost 3 years on since the last image of the single lake. There is notably more open water visible than in 2018 (figure 2). This could be due to seasonal or annual rainfall variations, but it might also reflect that in the subsequent 5 years, substantial beds of emergent vegetation are likely to have grown in the shallower areas of the lakes (© 2019 CNES/ Airbus).

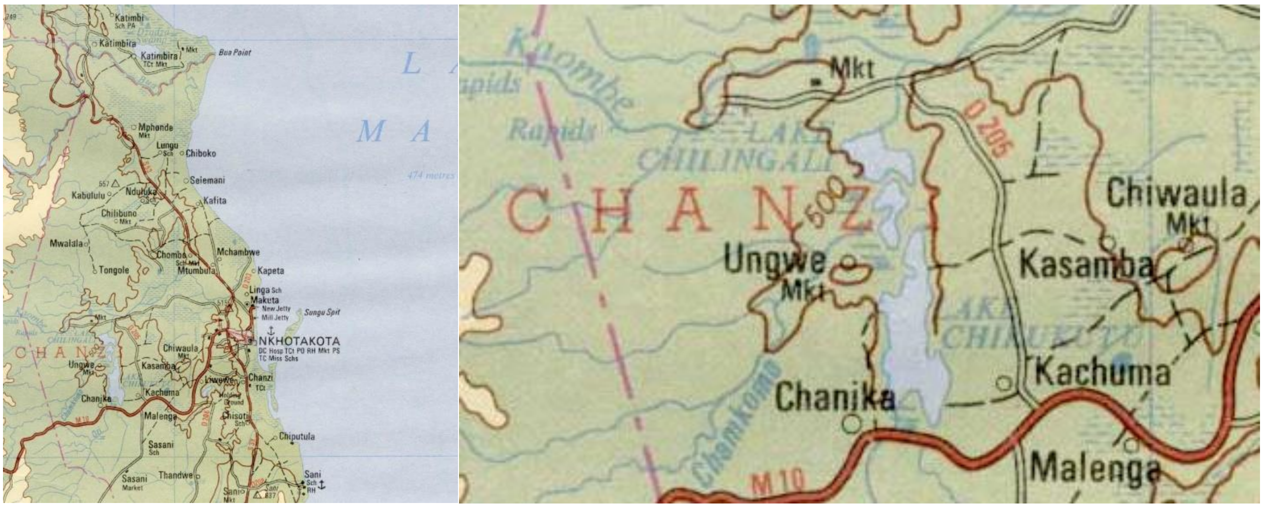

Figure 5. Maps from the Malawi National Atlas (1983) show three large lakes that are almost contiguous and approach close to the main road (M10). This suggests that the lakes that formed since the collapse of the dam are much smaller than the pre-impoundment lakes, possibly as a result of siltation.

Table 1: Comparison of the chemical compositions of Lakes Chilingali and Malawi (modified from Ferris 2010; units are mg l^{-1}).

Ion	Chilingali	Malawi	Malawi Reference
Phosphate	0.260	0.031	3
Nitrate	0.200	0.014	1
Ammonium	0.037	0.007	3
Chloride	1.038	3.545	2
Sulphate	0.288	2.882	2
Sodium	4.804	19.311	2
Potassium	1.758	5.865	2
Magnesium	2.342	7.292	2
Calcium	5.239	18.036	2

1: Gondwe *et al.* (2008); 2: Bootsma & Hecky (2003) (All values used converted from µmol L^{-1} to mg L^{-1}); 3: Bootsma & Hecky (1999)

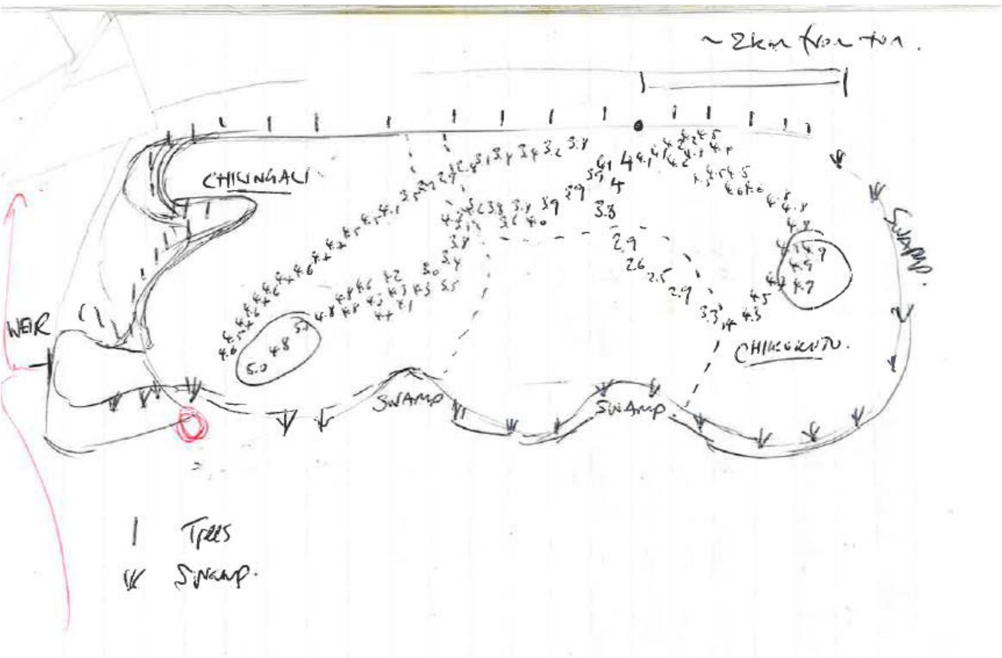

Figure 6. Sketch map of depth soundings in the impounded ‘large’ Lake Chilingali, 4th May 2005 (by M.J. Genner), showing 2 deeper basins (circled) of approximately 5m depth, representing the two original pre-impoundment lakes. North is to the left.

Plankton and Invertebrates.

In 2009, plankton hauls were dominated by diatoms and cyanobacteria (especially *Microcystis*), with rotifers and copepods numerically dominant among zooplankton, with occasional cladocerans (Ferris 2010). *Chaoborus* larvae and pupae were not found in plankton hauls (all taken in the daytime) but were abundant in fish gut contents (Griggs 2010), suggesting a possible use of refugia, perhaps in the bottom mud. In the large lake conditions of 2009, numerous benthic invertebrates were collected, particularly in the weedy shoreline habitats. These included a high diversity of gastropods, including the huge *Lanistes ovatus*, the ubiquitous *Melanoides tuberculata* and a *Bulinus* species, an intermediate host of human schistosomes. We are not aware of any investigations of the invertebrate community since the collapse of the dam wall.

Fish Fauna of Lake Chilingali

The fish fauna of ‘large’ Lake Chilingali was diverse, comprising at least 25 species from 9 families, most notably including 2 apparently endemic haplochromines of the Lake Malawi radiation. By contrast, surveys in 2016 revealed only 6 non-endemic species of 3 families: cichlidae (3), cyprinidae (2) and clariidae (1).

Table 2. Fishes of Lake Chilingali/ Chikukutu, Malawi.

Genus	species	family	local name	other names	2009	2016
Astatotilapia	*calliptera*	Cichlidae	Mkwetu		y	y
Brycinus	*imberi*	Alestidae			y	
Clarias	*theodorae*	Clariidae	Ncheka		y	
Clarias	*gariepinus*	Clariidae	Mlamba		y	y
Coptodon	*rendalli*	Cichlidae	Ningwichali	Nyungutsale, Katakuzi	y	
Cyphomyrus	*discorhynchus*	Mormyridae	Mputa		y	
Hemigrammopetersius	*barnardi*	Alestidae			y	
Enteromius	*kerstenii*	Cyprinidae	Chitimera	Chilasa	y	
Enteromius	*litamba*[1]	Cyprinidae	Tamba		y	
Enteromius	*paludinosus*	Cyprinidae	Chitimera	Chilasa	y	y
Enteromius	*spp.* [2]	Cyprinidae	Chitimera	Chilasa	y	y
Labeo	*cylindricus*	Cyprinidae	Ningwe		y	
Lethrinops	"sp. Chilingali"[3]	Cichlidae	Kang'khongo		y	
Marcusenius	*spp*	Mormyridae	Nthache		y	
Mastacembelus	*shiranus*	Mastacembelidae	Njola	Solomon fish	y	
Micropanchax	*johnstoni*	Procatopodidae			y	
Mormyrops	*longirostris*	Mormyridae	Panda	Pyopyo (small ones)	y	
Opsaridium	*tweddleorum*	Danionidae	Sanjika		y	
Oreochromis	*shiranus*[4]	Cichlidae	Nkututu	Makumba, Lifalili	y	y
Oreochromis	*squamipinnis*[5]	Cichlidae	Kababa	Chambo	y	
Pseudocrenilabrus	*philander*	Cichlidae	Kapalamoto		y	y
Rhamphochromis	"sp. Chilingali"[3]	Cichlidae	Sangwe	Ncheni	y	
Serranochromis	*robustus*	Cichlidae	Sungwa		y	
Synodontis	*njassae*	Mochockidae	Nkholokolo		y	
Tilapia	*sparrmanii*	Cichlidae	Kambuzi[6]		y	

Notes: 1. Possibly found only in river; 2. Species not yet identified, but collected; 3. Probably endemic; 4. Mature males called 'Kankuda'; 5. Mature males called 'Ngwalu'; 6. 'Kambuzi' is used for shallow water haplochromines elsewhere.

Rhamphochromis sp. 'chilingali' (Figure 18)

During our first visit to the lake in 2014, we observed small *Rhamphochromis* specimens in the catch of seine net fishers. Stomach contents were generally dominated by the larvae and pupae of *Chaoborus* midges, with smaller volumes of crustacean zooplankton, and occasional benthic items such as odonatan nymphs (Griggs 2010). This species proved to be numerous and to mature at a much smaller sizes than any known population from Lake Malawi. The largest wild specimen recorded was 106mm SL (Genner *et al.* 2007), compared to a maximum size of 205mm SL for *Rhamphochromis longiceps* Günther. The male breeding dress was different from that of *R. longiceps*, notably lacking anal fin eggspots. Laboratory experiments showed that *R. longiceps* and *R.* sp. 'chilingali' showed strong assortative mating when specimens of similar sizes were used: size at maturity in aquarium-raised fishes can be rather different from that of wild populations. When large males of *R. longiceps* were kept with small individuals of *R.* sp. 'chilingali', females of the latter tended to mate with males of the former, but this is likely to be a laboratory artefact resulting from dominance interactions in relatively small aquaria. Another relatively small undescribed species (maximum 206mm SL) from Lake Malawi was collected by Genner *et al.* (2007) and named *Rhamphochromis* sp. 'longiceps yellow belly'. This form was also noted to lack eggspots in the anal fin, but had more orange in the dorsal fin than normally found in mature male *R.* sp. 'chilingali'. The two populations were also very divergent in mitochondrial DNA sequence (Genner *et al.* 2007). Live specimens of this population were not available for assortative mating trials, as the species seems to be confined to offshore habitats. However, it seems likely that the *R.* sp. 'chilingali' represents an endemic satellite lake species, but one which is likely extinct in the wild. Since the collapse of the dam, the species has not been observed in nature, and it was not seen in the catches of fishermen in Lakes Chilingali or Chikukutu in 2016. When shown photographs of the species, local fishermen recognised it, but claimed that this fish had not been found in the lakes since the collapse of the dam. The species is presently maintained in a number of research facilities, its small size and ease of breeding making it a tractable representative of the pelagic cichlid subclade of the Malawi haplochromine radiation (Malinsky *et al.* 2018). Genomic studies by Machado *et al.* (2014) provided evidence for gene duplications in comparison to the generalist *Astatotilapia burtoni* from the Lake Tanganyika catchment. *Rhamphochromis* sp. 'chilingali' has become established as an ornamental (pet) aquarium species, and videos of captive specimens have been posted online (https://www.youtube.com/watch?v=0I8FCazgOik) including courtship behaviour (https://www.youtube.com/watch?v=nfN6hp-0fTk). Breeding adults have not been observed to dig in the substrate, but court and spawn in midwater, the female catching the eggs in her mouth. Females mouthbrood the offspring until they are capable of independent feeding but have not been observed to guard free-swimming fry or readmit them to their mouths post-release.

Lethrinops sp. 'chilingali' (Fig. 19)

A small species of the Lake Malawi endemic genus *Lethrinops* was also numerous in the lake prior to the dam collapse. This closely resembled *Lethrinops lethrinus*, but differed in body shape, having a more terminal mouth and shorter snout (Tyers *et al*. 2014). Gut contents analysis suggested that this species was primarily a *Chaoborus* feeder, but cladocerans and occasional large benthic items, such as odonatan nymphs were also taken. The scarcity of detritus suggested that the species was primarily a midwater-feeder (Griggs 2010, Tyers *et al.* 2014). Females and juvenile fish generally exhibit a midlateral stripe that is broken into a series of spots and stripes, in contrast to the continuous stripe generally shown by *L. lethrinus*. Individuals also occasionally show dark spots at the base of the dorsal fin and sometimes also along the upper flank area between the midlateral stripe and the base of the dorsal. Male breeding dress is predominantly a bright metallic blue-green, with a conspicuous red and white dorsal fin margin and large bright yellow spots and stripes on the anal fin, which also has a red margin. Courting males tend to show more black on the lower parts of the body and particularly on the pelvic fins than is usual for *L. lethrinops*. The upper and lower margins of the caudal fin are also black (rather like *Mchenga* species), as is the proximal part of the anal fin. None of the other described species of *Lethrinops* show a similar body shape and melanin pattern and no similar populations have been fully documented from within the lake or its catchment, suggesting that the *L.* sp. 'chilingali' may be a satellite lake endemic. Laboratory mate choice trials revealed a high level of assortative mating between *L.* sp. 'chilingali' and *L. lethrinops* from the southeastern arm of Lake Malawi (Tyers *et al.* 2014). In captivity, males pile up substrate (mud or sand) in a small mound, and attempt to attract females to lay small batches of eggs on the bottom. The females immediately pick up the eggs in their mouth and brood them for around 3 weeks, until the young are capable of independent feeding. Females have not been seen to guard free-swimming fry or readmit them into their mouths. Like the *Rhamphochromis*, the *Lethrinops* from Lake Chilingali has not been recorded in the wild since the dam collapse, and may be extinct in the wild. At the time of writing, the species survives in a few research and private aquaria.

Astatotilapia calliptera (Günther 1894) (Fig. 20)

Astatotilapia calliptera was recorded from all surveys of Lake Chilingali, up to and including 2016, when it remained abundant within the remnant Chilingali, although it was not found in Chikukutu. Phenotypically, the population seemed typical for *A. calliptera* in Lake Malawi and its catchment, with males exhibiting a largely yellow breeding dress (Figure 20). Laboratory mate choice experiments indicated no assortative mating between this population and a similar-coloured population from near Salima on the western coast of Lake Malawi (Tyers & Turner 2013). Stomach contents analysis of specimens from the 'large lake' phase in 2009 showed a wide diet, dominated by *Chaoborus* midge larvae and pupae, cladocerans and detritus, with a few molluscs, indicating that much of their food was obtained from the bottom. Like other populations of *A. calliptera*, mature males are much larger and more brightly-coloured than females and attempt to attract females to accompany them to spawn on the bottom. Females brood the young for 2-3 weeks, guarding and retrieving free-swimming fry for a further week or so in aquarium conditions, adopting a characteristic 'warpaint' of dark stripes across the forehead and through the eye, with dark eyes, lips and throats.

Pseudocrenilabrus philander (Weber 1897) (Fig. 21)

At first sight, *Pseudocrenilabrus philander* can be confused with *A. calliptera*, but differs in its relatively smaller mouth and its more rounded head and caudal fin. Male breeding dress is also rather similar: yellow-green with blue lips and a dark stripe through the eye. However, male *A. calliptera* have several yellow-orange eggspots on the anal fin, each surrounded by a contrasting margin, while *P. philander* usually has a single bright red spot at the tip of the anal fin, along with rows of small blue-white spots. *Pseudocrenilabrus philander* was found in Lake Chilingali before and after the dam collapse and was also found in streams and pools elsewhere around the Nkhotakota area. Strangely, it has not been recorded in Lake Malawi proper, nor anywhere else in the catchment except in the far north near Kyela in Tanzania. The species is widespread in southern Africa, although it exhibits considerable geographic variation, particularly in male colour (Skelton 1993). The species is a maternal mouthbrooder and regarded as one of the more basal haplochromines.

Serranochromis robustus (Günther 1864) (Fig. 22)

This large (60cm) predator is a member of a cichlid lineage mainly found in the Congo and SW Africa. The species was formerly split into two subspecies, but the Western populations are generally now treated as a distinct form, *S. jallae*. Around Lake Malawi, the species is easily recognised by its huge mouth, and by the dark chocolate brown horizontal bands along the flanks of juveniles and females. It is a maternal mouthbrooding haplochromine. Within Lake Chilingali, small specimens were abundant prior to the dam collapse and were found to feed on a variety of items including fish and odonatan nymphs (Griggs 2010). The species was not found in samples collected in 2016, but it is widespread, inhabiting in shallow margins of lakes and deep pools on slow-slowing stretches of rivers all around the Lake Malawi catchment as well as within the lake itself.

Oreochromis squamipinnis (Günther 1864) (Fig. 23)

The large broad-headed maternal mouthbrooding ‘tilapia’ *Oreochromis squamipinnis* is endemic to the Lake Malawi catchment and rarely found outside the lake itself, except in the Shire River, Lake Malombe and the Tanzanian crater lakes. Healthy populations were seen in ‘large’ Lake Chilingali, but none were found in 2016. The species is almost impossible to distinguish from the closely-related *O. karongae* (Trewavas 1941), other than through the colour of the territorial male. Male *O. karongae* are black, apart from white margins to the unpaired fins, while *O. squamipinnis* males have an area of bright blue, green or white on the upper surface of the head and the back. The expeditions to Lake Chilingali were generally not carried out during the breeding season for these fishes (September to May), and no males in breeding dress were seen, but local fishermen reported that these fish would have blue heads during the breeding season, indicating that they were most likely *O. squamipinnis* rather than *O. karongae*, although it is possible that both species were present. The pale colour of some of the larger specimens is more consistent with maturing male *O. squamipinnis* than *O. karongae*. It is possible that this, and other larger tilapiines might have been stocked by local fisheries department staff, as the remains for aquaculture cage were seen in 2009. Gut contents of 7.5-15cm SL specimens collected in 2009 contained mainly *Chaoborus* larvae and pupae and some crustacean zooplankton and phytoplankton and almost no detritus (Griggs 2010), suggesting midwater feeding.

Oreochromis shiranus (Boulenger 1897) (Fig. 24 & 25)

Among the Malawian cichlids, this species is easily recognised because it has 4 anal fin spines instead of the more usual 3. This character is variable in the Tanzanian crater lakes, but all specimens examined from Lake Chilingali had 4. Adults males can also be distinguished by their black breeding dress, red fin margins, large lips and strongly concave head profiles. The species was abundant before the dam collapse, and was still numerous afterwards, but no large specimens were seen in 2016. In 9-19cm SL specimens collected in 2009, guts were largely filled with detritus, with some plankton (Griggs 2010), suggesting benthic feeding.

Coptodon rendalli (Boulenger 1897) (Fig. 26)

This large substrate-spawning species is widely distributed in southern and central Africa, but was originally described from Malawi, where it is abundant in shallow weedy habitats in Lake Malawi and most other water bodies. It is distinguished by its deep body, steep head profile and narrow head. Some individuals have bright red bellies. It is very similar to *C. zillii* from northern and western Africa. It was reasonably common prior to the dam collapse but was not seen in 2016. Gut contents were dominated by detritus with some copepods, phytoplankton and dipteran larvae (Griggs 2010).

Tilapia sparrmanii (Smith 1840) (Fig. 27)

This small substrate-spawning species has not been recorded in Lake Malawi. Like *Pseudocrenilabrus philander*, it occurs in rivers and lakes around at Nkhotakota and again in the

Tanzanian part of the catchment near Kyela at the north, but it has not been recorded from elsewhere in the catchment. It is easily recognised by its deep body, narrow head and bright colours, generally with a yellow base colour, strong brown or black barring, dark fins and red markings on the flanks and fins. In Lake Chilingali in 2009, guts mainly contained plant material, detritus and fly larvae (Griggs 2010). The species was not found in 2016.

Non-cichlid fishes

The lake contained a diverse set of non-cichlid fishes, all typical of rivers and lakes in the catchment and all found in Lake Malawi.

The mormyrids (Figure 28) recorded included the large long-snouted *Mormyrus longirostris* Peters 1852 and the medium-sized *Marcusenius* spp. species which have a large fleshy bump under the snout - likely *M. macrolepidotus* (Peters 1852) which has conical teeth or *M. nyasensis* (Worthington 1933) with bicuspid teeth). Smaller species recorded included *Cyphomyrus discorhynchus* (Peters 1852) and *Petrocephalus catostoma* (Günther, 1866). The taxonomy of these species is in flux, as it has been shown that many similar-looking species are reproductively isolated by divergent Electric Organ Discharge (EOD) patterns which are used in communication as well as navigation and prey detection. *Pollimyrus castelnaui* (Boulenger 1911) is common in similar habitats around Lake Malawi, but has not been positively recorded from Lake Chilingali.

Smaller cyprinids (Figure 29) recorded included the sawfin barb *Enteromius paludinosus* (Peters 1852), the red-cheeked *Enteromius kersteni* (Peters 1868) and the spotted *Enteromius trimaculatus* (Peters 1852). Several other small *Enteromius* species were likely to be present, but their taxonomy and identification is poorly documented. In 2009, larger species reported included the large surface-feeding *Enteromius litamba* (Keilhack 1908), which is endemic to the Lake Malawi catchment and the widely-distributed bottom-feeding *Labeo cylindricus* Peters 1852 (Figure 30). The smaller species were largely still to be found in 2016, but the larger species were not recorded. The danionid (formerly cyprinid) *Opsaridium tweddleorum* Skelton 1996 (Figure 30) and the alestids (formerly characins) *Brycinus imberi* (Peters 1852) (Figure 17) and *Hemigrammopetersius barnardi* (Herre 1936) were also recorded from the large Lake Chilingali, but are likely to have persisted in the river. These are all largely surface to midwater feeders.

Among the bottom feeders, catfishes (Siluriformes) were represented by the virtually ubiquitous *Clarias gariepinus* (Burchell 1822) (Fig. 31), the Lake Malawi catchment endemic *Synodontis njassae* Keilhack 1908 (Fig. 31), and the inconspicuous snake catfish *Clarias theodorae* Weber 1897 (fig. 31). The spiny eel *Mastacembelus shiranus* (Günther, 1896) was also recorded in ‘large’ Chilingali (Fig 30). The only one of these species found in 2016 was *Clarias gariepinus*.

Exploitation.

Active fisheries were observed prior to the dam collapse, with seines, gillnets and traps being operated from canoes and plank boats. Changadeya *et al.* (2001) reported that the ‘large’ Chilingali supported 293 fishermen using 61 canoes, 91 gillnets and 19 seines. Cage culture for tilapias had been trialled by government agencies at the time of visiting in 2009, but had been abandoned and the netting used to make seines. In 2016, canoes were seen at both Lakes Chilingali and Chikukutu, along with large piles of seine nets made from plastic mosquito netting. Local fishermen reported that these were supplied free of charge by the government. They were also used to make ropes for the nets, drying racks and for providing support for grass roofs. They were not generally used as mosquito nets. A single gillnet fisherman was seen on Lake Chiukutu, but his net was in very poor condition. Fishermen reported that catches were poor.

Figure 7: Lake Chilingali in 2009, showing extensive and varied marginal vegetation, and active fishing craft.

Figure 8. Lake Chilingali, the dam wall showing signs of erosion in 2004.

Figure 9. The crumbling dam wall of Lake Chilingali in 2009.

Figure 10. Lake Chilingali 2016: (Top left) the new bridge over the former dam site; (top right) the small lake (about 2m deep) just upstream of the former dam; (bottom left) seining in a weedy pool immediately downstream of the former dam; (bottom right) shallow main Lake Chilingali with a large bank of drying nets made from bed mosquito netting.

Figure 11: Lake Chikukutu 2016: on right, fishing with a net constructed from bed mosquito netting.

Figure 12: Invertebrates of Lake Chilingali: (left) leeches; (right) shrimp, from Griggs (2010).

Figure 13: Odonata nymphs of Lake Chilingali: (left) Coenagrionidae; (centre) Libellulidae; (right) Aeschnidae, from Griggs (2010).

Figure 14: Larger insects of Lake Chilingali: (left) water beetle, Hydrophiliidae; (centre) beetle larva, Dytiscidae; (right) giant water bug, Belostomatidae (from Griggs 2010)

Figure 15. Prosobranch gastropods of Lake Chilingali (large lake 2009): left: *Bellamya* spp, centre: *Lanistes ovatus*; right: *Melanoides* spp. Preserved material, from Griggs 2010.

Figure 16: Molluscs of Lake Chilingali (large lake 2009): left: Pulmonata: *Bulinus spp.*, *Lymnaea spp.*, right: Bivalve (*Coelatura* spp.): Preserved material, from Griggs 2010.

Figure 17: Sorting a local fishing crew's seine net catch on Lake Chilingali in 2009: mainly immature cichlids and (top) the characin *Brycinus imberi*.

Figure 18. *Rhamphochromis* sp. ‘chilingali’ males (above and bottom left); females (bottom right), 2004. Note the plain orange anal fin of mature males which lacks eggspots and the variation in head shape including snout length and profile and cheek depth.

Figure 19. *Lethrinops sp.* ‘chilingali’: mature male (2009, top); maturing male 2004 (middle left); juvenile ca 35mmSL, 2004 (middle right); mature courting male, subordinate male and female in aquarium (bottom left); two mouthbrooding females and juvenile, showing variation in melanic markings from spots to stripes (bottom right).

Figure 20. *Astatotilapia calliptera* males 2009, left; 2004, right. The differences in colour are largely related to mood and reproductive state and not polymorphism.

Figure 21. Lake Chilingali: male *Pseudocrenilabrus philander* (left) in 2009 and (right) in 2016.

Figure 22. Lake Chilingali: *Serranochromis robustus* juvenile with characteristic strong horizontal bands (above, from 2004); female or immature male (below left, 2009) and maturing male, indicated by bluish colour on cheeks and hints of anal fin spots (below right 2009).

Figure 23: *Oreochromis squamipinnis*. Lake Chilingali 2009.

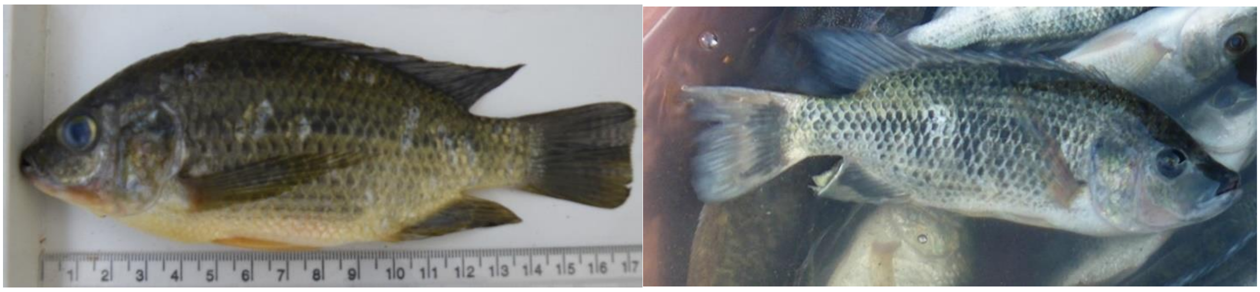

Figure 24.: Lake Chilingali 2009: *Oreochromis shiranus* female (left), male (right).

Figure 25. Sexually mature male *O. shiranus* in 'large' Lake Chilingali in 2009, and a maturing male (indicated by the blue sheen on the cheeks) in 'small' lake conditions in 2016. As can be seen by the size of the fingers in the background, these are shown approximately to the same scale, consistent with precocious maturation (stunting) in the small shallow lake conditions of 2016.

Figure 26. Lake Chilingali (2009): *Coptodon rendalli*.

Figure 27. Lake Chilingali (2009) *Tilapia sparrmanii*.

Figure 28: Lake Chilingali Mormyridae: *Marcusenius* spp. (above, 2009); *Cyphomyrus discorhynchus* (middle, 2004); *Petrocephalus catostoma* (below, 2009).

Figure 29. Smaller cyprinid fishes of Lake Chilingali: top left, *Enteromius paludinosus* (2016); top right, *Enteromius* spp. (2009); centre left, *Enteromius* spp. (2016); centre right, *Enteromius cf. lineomaculatus* (2016); bottom left, *Enteromius kersteni*; bottom right, *Enteromius trimaculatus*.

Figure 30. Lake Chilingali (2009): *Opsaridium tweddleorum*, Danionidae (top); *Labeo cylindricus*, Cyprinidae (middle); *Mastacembelus shiranus*, Mastacembelidae (below).

Figure 31. Lake Chilingali, Siluriformes: *Synodontis njassae* (top and middle left); *Clarias gariepinus* (middle right); *Clarias theodorae* (bottom), all from 2009.

Part 2. The Tanzanian Crater Lakes

The crater lakes lie in a volcanically active region to the north of Lake Malawi, known as the Rungwe Volcanic Province (Figures 32 & 33). Its volcanic history has been extensively reviewed by Fontijn *et al.* (2012). Vulcanism has been dated to 17-19Mya ago in the NNE part of Province, but the current major peaks are believed to date from a period commencing about 9Mya, but older lake bed are known from the Upper Miocene (5.3-11.6Mya) at a level well above the current level of Lake Malawi (Fontijn *et al.* 2012, figure 2). Over 100 volcanic cones have been detected in the area. Three major volcanoes are considered to be currently active. Mounts Rungwe and Ngozi have both erupted explosively (a so-called 'Plinian event') within the Holocene (<11.65kya): Ngozi perhaps as recently as 360 years ago, Rungwe perhaps 4kya. Eruption of Mount Kiejo has been characterised by extensive lava flows, the last recorded around 1800 AD, when flows of over 8km erupted over at least 3 days (Fontijn *et al.* 2012).

The best studied of the crater lakes, Masoko (or Kisiba) is a volcanic Maar lake (Garcin *et al.* 2007), and it is believed that most of the other crater lakes are too (Delalande *et al.* 2008). The exception is Lake Ngozi, which lies in the caldera of the active volcano (Delalande *et al.* 2015; Josephat 2016). Maar lakes are formed when uprising magma contacts a subterranean aquifer, resulting in explosive vapourization and rapid production of a steep-sided crater which rapidly fills in with water (Thomas & Goudie 2000). For Lake Masoko, sedimentation studies suggest an age of 50,000 years consistent with Argon/Argon dating of around 40 +/-10k years (Williamson *et al.* 1999). The lake is not believed to have dried out completely (Gibert *et al.* 2002), although lake levels were believed to have been much lower on several occasions, most recently around 1550-1850 AD (Garcin *et al.* 2007). No age estimates were found for the other Maar lakes.

In addition to the crater lakes containing permanent water, other craters including Katubwi and Kyambangunguru hold seasonal shallow pools or swamps (Delalande *et al.* 2008), which may formerly have been lakes.

The lakes lie among several major river systems that drain then highland of the Rungwe Volcanic Province: the Kiwira to the West, the Mbaka in the middle and the Mguwisi/Lufilyo to the East. Lake Masoko is a closed basin, largely dependent on groundwater and precipitation, while Lake Ilamba has both a surface inlet and an outlet (Delalande *et al.* 2008).

The biology of the crater lakes was relatively poorly known prior to our expeditions from 2011 onwards. The endemic *Oreochromis chungruruensis* (Ahl 1924) was described from Lake Kyungululu in the early 20th Century from 19th Century collections (Ahl 1924). Ricardo (1939) made a brief mention of *Astatotilapia calliptera* and *Oreochromis* in Lake Masoko. Trewavas (1976) considered some of the *Oreochromis* material collected by Ricardo, as well as Ahl's type material, and suggested Lake Masoko and Kyungululu were probably the same lake (which they are not). She also looked at some *Oreochromis* specimens collected from Lake Kingiri by Albrecht and registered in 1966. She considered much of this material to belong to the species *Oreochromis lidole*, a deep-water living species otherwise known only from the southern half of Lake Malawi. These opinions were repeated in an illustrated account in her later monograph (Trewavas 1983). A few notes also appeared in Seegers' (1996) monograph in Lake Rukwa, including an illustration of *Astatotilapia calliptera* from Lake Masoko.

The crater lakes can be divided into three groups, based on altitude and biota: **1. The Mguwisi system** lakes Kingiri, Ilamba, Itamba and Ikapu are located 529-831m above sea level, and have relatively high fish species richness (4-11 species); **2. The intermediate elevation** lakes, Masoko, Kyungululu and Itende, lie at 868-1026m above sea level and accommodate 2-4 fish species each, although some of these may not be native; **3. The high altitude lakes** Ndwati and Ngozi appear to be uninhabited by fish. These lakes will be discussed from lowest to highest elevation, followed by some notes on the biota of neighbouring river systems.

Table 3: Summary of the lakes visited and their faunas: 1. Mguwisi system lakes.

	Kingiri	Ilamba	Ikapu	Itamba
Elevation[1]	529m	563m	658m	831m
Height Above Lake Nyasa[1]	48m	83m	177m	350m
Diameter[1]	575-602m	613-839m	437-573m	424-473m
Depth	34m[2]	19m[2]	4m[2]	17m[2]
Conductivity (µS/cm)	120-230[3]	497-686[3]	81[2]	131-145[2]
TDS (mg/l)	70[3]	310[2]	55[2]	850[2]
Secchi Depth(m)	4.7[3]	1.5	3.5	4.5
Macrophytes	A few reeds, >95% shore overhung by trees	Lots of reeds, mostly overhung by trees	Abundant submerged plants, most shore reedy	Some reeds, mostly overhung by trees
Bottom	Gently sloping, muddy with some rocks, steep drop at 5m	Steep, muddy	Flat, weedy, muddy	Steep, overhung by trees
Dominant Invertebrates	Sponges, molluscs	Molluscs	Insects, gastropods	Sponges, crabs, bivalves
Bilharzia vectors	No	Yes	Yes	No
Tilapia	*Coptodon rendalli*	None	*T. sparrmanii*	None
Oreochromis	*O. shiranus,* *O squamipinnis*	*O. shiranus,* *O. cf. squamipinnis*	*O. cf. shiranus,* *O. cf. karongae*	*O. cf. shiranus,* *O. karongae* *O. cf. squamipinnis* *O. niloticus* (2011 only)
Astatotilapia	Black Males	Black Males	Dark Males	Dark males
Other haplochromines	*Rhamphochromis (2 taxa), Serranochromis robustus*	*Otopharynx* sp.	None	None
Catfish	*Clarias*	*Clarias*	*Clarias*	None
Cyprinids	*Enteromius. cf trimaculatus,* *E. cf. radiatus.*	*Enteromius paludinosus,* *E. cf trimaculatus,* *E. pseudotoppini,* *E. cf. radiatus.*	None	None
Others	*Micropanchax johnstoni*	*Engraulicypris cf. ngalala*	None	None

Sources: 1: Google Earth, 2 Delalande *et al.* 2008, 3 present study 2011 data,

Table 4: Summary of the lakes visited and their faunas: 2. Intermediate altitude lakes.

	Kyungululu	Masoko	Itende
Elevation[1]	937m	868m	1026m
Height Above Lake Nyasa[1]	457m	387m	546m
Diameter[1]	430-434m	670-700m	270x590m
Depth	45m (2017)	38m[2]	<3m
Conductivity (µS/cm)	-	38-120[2]	90-105/172
TDS (mg/l)	-	25[2]	65-78
Secchi Depth(m)	dirty	5.5	? Clear
Macrophytes	Some reeds, mostly barren	Some reeds, mostly open	Abundant submerged plants, completely surrounded by reeds
Bottom	Steep, rocky with some sand	Open, gently sloping, sandy with some rocks, steep drop after 5m	Flat weedy, surrounded by reeds
Dominant Invertebrates	Sponges, crabs	Sponges, molluscs, crabs	Insects, gastropods
Bilharzia vectors	No	Yes	Yes
Tilapia	*Coptodon rendalli,* *T. sparrmanii*	*C. rendalli*	None
Oreochromis	*O. chungruruensis*	*O. cf. squamipinnis*	Chambo spp?
Astatotilapia	None	Yellow males, blue males	Yellow males
Other haplochromines	None	None	None
Catfish	None	*Clarias*	None
Cyprinids	None	None	None
Others	None	None	None

Sources: 1: Google Earth, 2 Delalande et al. 2008, present study 2011 data,

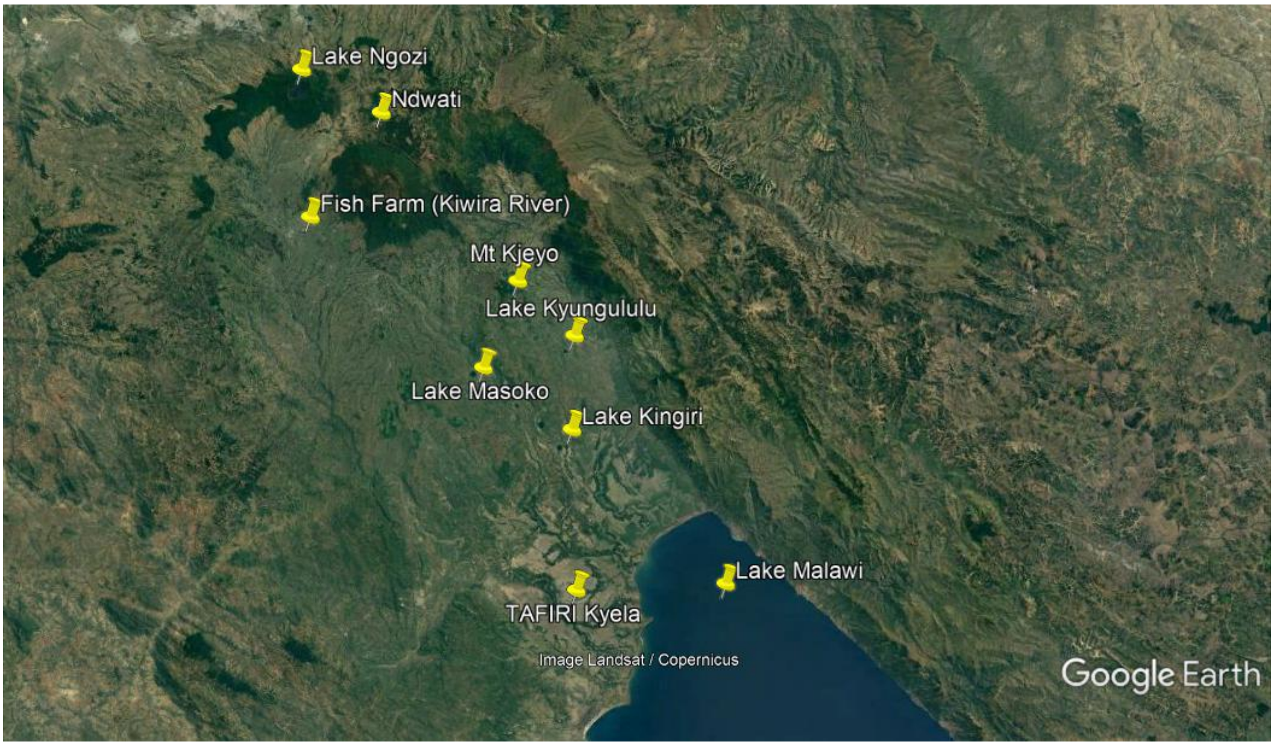

Figure 32. The major sampling sites in the crater lakes region (north-south map extent approximately 90km) and the laboratory of the Tanzanian Fisheries Research Institute (TAFIRI) in the town of Kyela.

Figure 33. Relative positions of the crater lakes known to be inhabited by fish: some of the pointers are deflected for clarity (map area ca 28 x 15km).

Lake Kingiri

(-9.419, 33.858)

At an elevation of around 530m, Lake Kingiri is less than 50m above the level of Lake Malawi (Nyasa). Tributaries of the Mguwisi river, a Lake Malawi afferent, at a higher level than the current lake surface come within 300m of the lake. Although most of the lake is surrounded by a low crater wall, the NE side is virtually on a level with the surrounding plains (presently used for agriculture). Thus, it is plausible that the lake could have been accessible to fish during flooding of nearby rivers or higher stands of Lake Malawi. The lake is approximately 580-600m in diameter and 34m deep (Delalande *et al.* 2008). A small open area (Site A) afforded the easiest access for sampling: here there is no crater wall and a gap among the trees. This area was extensively used for bathing, washing clothes and watering livestock (Fig. 35). The lake essentially seems to overflow here at high stands, submerging a flat muddy area of grasses. Underwater, there is an extensive shallow (<1m) muddy area with a few scattered rocks or tree-stumps, giving way to area of rocks on mud at depths of 1-2m. Below this, the bottom drops more quickly, but the slope is less steep than at other parts of the lake. At around 20m, the bottom becomes flatter and is covered in a deep layer of silt. Away from Site A, most of the shoreline is heavily wooded with a few narrow footpaths down to the lake (for example, at Site B). No fully submerged macrophytes were recorded, nor any floating plants nor plants with specialised floating leaves, such as waterlilies. In some more open places, there were small patches of emergent vegetation (reeds and other grasses) or tangled roots of trees (Figure 36). Underwater, the slope is initially gradual, with scattered rocks or pieces of wood of various sizes on mud or sand with areas of small rocks covered in sediment (Figs 36 & 37). However, the slope quickly becomes much steeper, in some places almost vertical and rocky (Fig. 38), plunging rapidly to the silt plain at a depth of about 20m. Many of the hard substrates, such as rocks and wood, are covered with encrusting sponges (Figs. 37 & 39). Other invertebrates seen include conspicuous large gastropods, often on rock surfaces (Fig. 39).

The lake was actively fished, with gillnets set in open water or along the shoreline, often supported by bamboo stakes. Fish traps made of reeds are also used. Tilapiine cichlids, *Clarias* and the larger *Rhamphochromis* appeared to be the target species.

Fish fauna.

We recorded a larger number of fish species from Lake Kingiri than from any of the other crater lakes surveyed in the area, with at least 11 species recorded, of which three – all haplochromines- are considered crater lake endemics.

Astatotilapia sp. ‘kingiri’ (Figures 40-41)

This haplochromine cichlid was numerically by far the dominant species in experimental fishing catches and underwater observations and was found close to the lake bottom in all areas surveyed. Females and immatures were pale sandy-coloured, with yellowish pelvic and anal fins, and dark spotting in the soft dorsal and caudal fins. They strongly resembled *Astatotilapia calliptera*, which inhabits virtually every water body in the Lake Malawi catchment. They were generally observed in loose feeding groups of 3-5 individuals, although they were occasionally seen in larger groups, particularly the smaller fish. The males were among the largest *Astatotilapia* recorded from a crater lake, attaining 105mm SL. Large males were often observed among rocks particularly where they lay on soft sediment. When disturbed, males often retreated into burrows under the rocks. When undisturbed, many males adopted a jet-black coloration, with bright orange-yellow eggspots on the anal fin; the margin of the dorsal and anal fins was usually dark red. These males were often seen courting or threatening conspecifics, and they appeared to be site-orientated and probably territorial. Males behaving in this way were observed during all visits to the lake, as were mouthbrooding females, so it can be proposed that breeding is not strongly seasonal. Males, even very large ones, were also observed in other habitats, including shallow areas among roots or on the steep rocky crater walls. However, these males were paler, generally grey (sometimes with dark pelvic fins or with a dark stripe through the eye) and did not appear to be territorial.

Rhamphochromis sp. 'kingiri dwarf' (Figs. 42-43)

In our first survey, in July 2011, numerous very small specimens (<75mm SL) of *Rhamphochromis* were collected by experimental gillnetting in Lake Kingiri. Many male individuals showed bright orange pelvic and anal fins. Some also had orange colour on the throat and lower half of the caudal fin. This was taken to be indicative of sexually active males, which was confirmed with visual inspection of the gonads. Females had largely colourless fins. Males in breeding colour were also observed in catches made in December 2011. In March 2015, very large numbers were seen underwater courting mouthbrooding females: groups of males often chased after females, which were often noticeably larger than the males. These were aggregated over a large sunken tree at depth of about 5m just to the south of Site A. This species appears to be endemic to Lake Kingiri; the genus is endemic to the Lake Malawi catchment (Eccles & Trewavas 1989).

Rhamphochromis sp. 'kingiri large' (Fig. 44)

On 15 July 2011, six larger *Rhamphochromis*, all males, were bought from local gillnet fishermen. Another two specimens, one male and one female were collected on 26 November 2011. These were not found in subsequent visits. These ranged in size from 83 to 210mm SL. Molecular analysis indicated identical mtDNA sequences to the dwarf specimens, which may indicate that this represents a conspecific ecomorph or a sympatric species pair. The male breeding colour is similar to that of the smaller fish (bright orange pelvic and anal fins). If it does represent a distinct species, it seems likely that the population of such a large piscivore in such a small lake must be very small and it is worrying that it seemed to be the object of a targeted gillnet fishery in 2011. The species/morph appears to be endemic to Lake Kingiri.

Serranochromis robustus (Günther 1864) (Fig. 45)

This large-mouthed haplochromine was collected in both 2011 surveys and occasionally seen underwater to the south of Site A, where it ranged from the shallows down to depths of ca 15m. It was observed to move rapidly over the rocky habitat, singly or in small groups of 2-3 individuals. This species is known from Lake Malawi (the type locality), although it has a wider distribution in southern and central Africa (Skelton 1994).

Oreochromis squamipinnis (Günther 1864) (Fig. 46)

Many small to medium-sized tilapias (up to 16cm SL) were collected in seine and gillnet catches during 2011, particularly from around site A. Many of these could be readily identified as members of the 'Chambo' group by their wide heads and silvery bodies with irregular dark vertical barring on the flanks, and by the possession of 3 anal fin spines. No adult males were collected in these or subsequent visits, but two males showing the characteristic breeding dress were filmed during expeditions in 2015 and 2017 (Fig. 46). This indicates that *O. squamipinnis* is found in the lake, but does not rule out the possibility that *O. karongae* is also present, as the two species are very hard to distinguish except through male breeding dress. *Oreochromis squampinnis* is endemic to the Lake Malawi catchment (Trewavas 1983).

Oreochromis shiranus Boulenger 1897 (Fig. 47)

Many individuals of *O. shiranus* were collected in the 2011 surveys and observed during later visits. Females and immatures were clearly diagnosable by their golden-yellow colour and largely horizontal dark stripes, while mature males (up to 18cm SL) were black with a red dorsal fin margin. In most of the rest of the range of this species, there are 4 spines in the anal fin: in Lake Kingiri, 17 out of a sample of 18 also had 4 anal spines, and the other individual had 3.

Coptodon rendalli (Boulenger 1897) (Fig. 48)

This species was collected in small numbers during the 2011 surveys. It was occasionally observed by snorkelling in shallow waters. Until recently, this species was known as *Tilapia rendalli*.

Other fish species

Among the non-cichlid fish fauna, we occasionally observed *Clarias gariepinus* in gillnet catches. *Enteromius paludinosus, Enteromius trimaculatus* and *Micropanchax johnstonii* (Günther 1864) (Fig. 49) were observed in shallow water while snorkelling near site A.

Figure 34. Lake Kingiri, showing main access points used in surveys: Site A is a shallow open area with seasonally submerged grasses, used for washing and livestock; Site B marks the approximate location of several narrow paths through dense woodland, leading to a rapid drop-off underwater. Meandering channels and tributaries of the Mguwisi River can be seen to the NE and NW of the lake. Satellite image from Google Earth (12 Nov 2018).

Figure 35: Lake Kingiri: (top left) Panoramic view from Site A, looking roughly SW; (top right) heavily wooded shoreline in the vicinity of site B, viewed from a boat on the lake; (bottom left) site A, showing heavy use for watering livestock; (bottom right) site A, flooded emergent grasses in the foreground with open beach used for drying clothes behind. All photos taken in July-November 2011.

Figure 36: Shallow habitats in Lake Kingiri: (left) a male *Astatotilapia* among roots of overhanging trees over a muddy bottom; (right) open rock habitat at 1-2m depth.

Figure 37: Lake Kingiri: (left) a crater likely dug by a male *Oreochromis squamipinnis* reveals the gravel underlying the thin layer of silt in many shallow water areas; (right) encrusting sponges on the underside of a small rock.

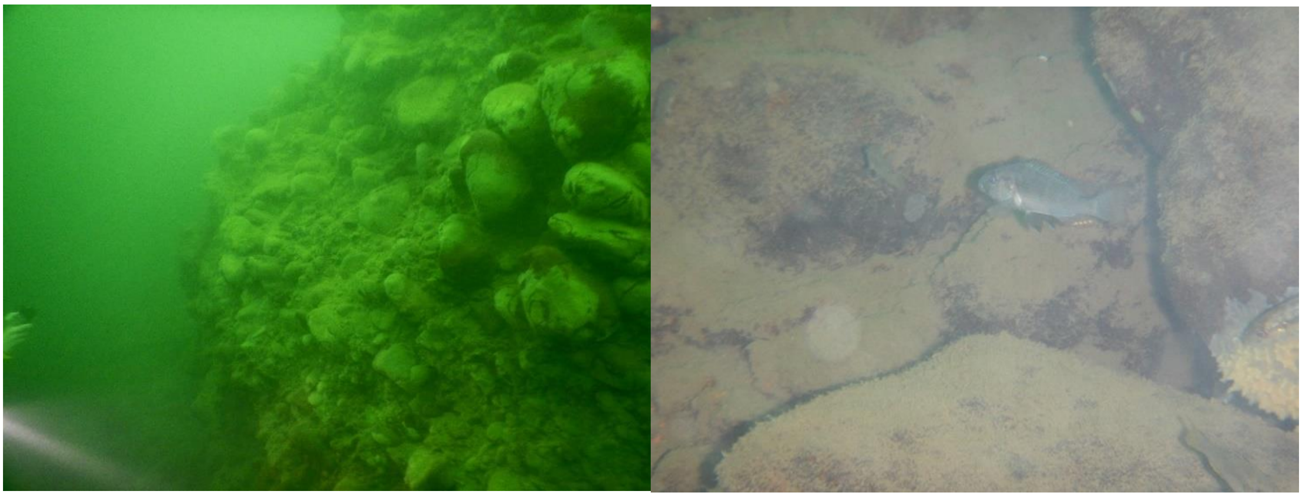

Figure 38. Lake Kingiri: (left) An area of steeply-dropping crater wall at around 8m depth, showing the natural lighting condition; (right) *Astatotilapia* spp among rocks at about 15m depth on the crater wall.

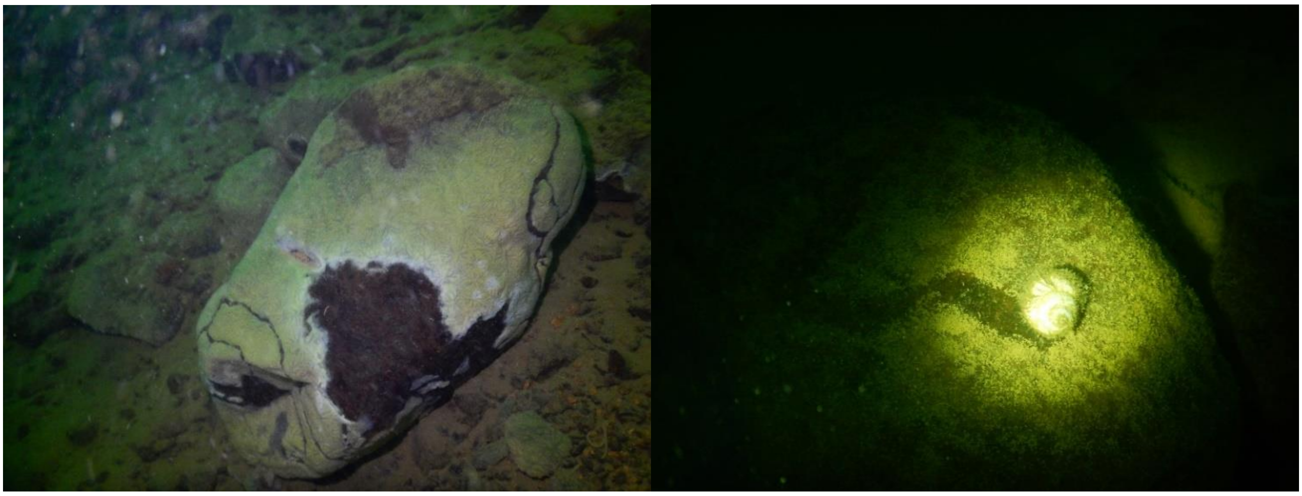

Figure 39. Lake Kingiri: (left) A sponge-encrusted rock showing star-shaped patterns; (right) a large gastropod leaving a conspicuous feeding trail through the biofilm.

Figure 40. *Astatotilapia* sp. 'kingiri': male (left) and female (right).

Figure 41. Lake Kingiri: Black male *Astatotilapia* 'kingiri' on territory among rocks on a muddy bottom, 3m depth, June 2017 (screen grab from video).

Figure 42. Lake Kingiri: *Rhamphochromis* ‘kingiri dwarf’: (left) mature male; (right) mature females.

Figure 43. Lake Kingiri: breeding aggregations of *Rhamphochromis* sp. ‘kingiri dwarf’ over a sponge-covered sunken tree at ~5m depth in March 2015. On the left, a male is pursuing a larger brooding female. Photos are screen grabs from video footage (youtube: Hq7zQwafSfY): date labels are erroneous.

Figure 44. Lake Kingiri: *Rhamphochromis* sp. ‘kingiri large’ male (left) and female (right) collected in November 2011.

Figure 45. Lake Kingiri: *Serranochromis robustus* male (top) and immature or female (bottom).

Figure 46. Lake Kingiri: *Oreochromis squamipinnis* (top left) large male showing early stages of developing secondary sexual markings; (top right) immatures.; (bottom left) Male defending territory at around 20m depth in March 2015; male in company with female *O. shiranus* at ~2m depth in June 2017 (screen grabs from videos).

Figure 47. Lake Kingiri: (left) *Oreochromis shiranus* male in breeding dress; (right) female.

Figure 48. Lake Kingiri: *Coptodon rendalli*.

Figure 49. Lake Kingiri: *Micropanchax johnstonii*.

Lake Ilamba

(-9.393, 33.836)

Lake Ilamba lies further north and at a slightly higher elevation (~560m) than Lake Kingiri. The lake measures about 877m north-south and ~733m east-west (Google Earth) and is about 19m deep (Delalande et al. 2008). The lake has a seasonal inflow to the north, which enters the lake through a thick mass of reeds, and a shallow outflow which emerges in a wooded area (Figure 50). Although Lake Ilamba is only about 700m away from the Mguwisi River, a tributary of the Lufilyo, the outflow (Figure 52) does not join the larger river until about 3 km to the south. The lake water is turbid and salty, with a Secchi reading of 1.5m, conductivity of 497-686 (2011) or 493-495 (2018) µS/cm and a TDS of 310-369 mg/l. An alkaline pH of 7.8-7.9 was recorded (2018). Most of the shoreline is overhung with trees (Figure 51), although there are patches of reeds in many places. No submerged macrophytes have been observed. Sponges are common (Figure 52) and numerous molluscs have been collected, including bivalves, and the gastropods *Lanistes, Bellamya, Melanoides,* and *Bulinus* spp.- the latter a known host of *Schistosoma*. Large crabs (*Potamonautes*) have been observed in the outflow stream and are presumably present in the lake. Monitor lizards (*Varanus niloticus*) have been seen. The lake is actively fished with offshore gillnets targeted on *Oreochromis* spp. and wicker fish traps aimed at tilapia and clarias: in 2018, a local fisherman reported that 15 fishermen were active, using 7 canoes from 4 landing sites. He stated that the catch was mainly for personal consumption, although surplus was occasionally sold. In both 2011 and 2018, fishermen warned of the presence of large crocodiles in the lake.

Fish Fauna

Like Lake Kingiri, Lake Ilamba was found to contain a diverse fish fauna. This included a number of non-cichlid fishes, a unique population of an endemic Lake Malawi haplochromine genus (*Otopharynx*), and a crater-lake speciality *Astatotilapia* with black breeding males. It was the only lake where we found danionids.

Astatotilapia sp. ‘Ilamba’ (Fig. 53)

Male *Astatotilapia* in this lake were recorded to attain a length of 90mm SL, which is among the smallest of the recorded maximum sizes. When dominant, they are uniformly black, apart from the orange eggspots on the anal fins and sometimes a hint of a reddish margin to the anal or dorsal fins. Immature or non-territorial males show a variety of colour elements, reminiscent of a dull version of the typical riverine *Astatotilapia calliptera*, but such specimens brought back to the aquarium at Bangor University developed into black territorial males. Females are sandy-coloured and resemble those of *A. calliptera*. Despite the poor visibility, underwater observations suggest that the bottom of the lake just off Site A has numerous rocks among mud, and these are inhabited by many territorial male *Astatotilapia*.

Otopharynx sp. ‘tetrastigma Ilamba’ (Fig. 54)

The males of this species are brightly-coloured, iridescent turquoise with orange highlights to most of the flank scales, and numerous orange markings in the dorsal and caudal fins. The dorsal fin margin is conspicuously white with a red edge. The anal fin is dark with large faint eggspots and an orange lower margin. Females and juveniles are silvery with several flank spots in an oblique line. The species closely resembles and may be conspecific with *Otopharnyx tetrastigma* (Günther 1894), a species which is commonly encountered in shallow weedy habitats, such as Lake Malombe (Turner

1996) and which is known to penetrate far down the Shire River (Tweddle *et al.* 1979). This species was found in much smaller numbers than the *Astatotilapia*, but seemed to inhabit the same microhabitats and territorial males were seen intermingled during underwater observations. Maximum recorded size: 12 cm SL. The genus *Otopharynx* is endemic to the Lake Malawi catchment (Eccles & Trewavas 1989).

Oreochromis cf. squamipinnis (Fig. 55)

When we visited, tilapiine cichlids were the main target of fishing operations on the lake, and the bulk of those landed were of the Lake Malawi 'chambo' complex. Many adult males in breeding dress were seen in July 2011 and June 2018 and all of those were dark blue to black with pale blue upperparts, characteristic of *Oreochromis squamipinnis*. Notably, the maximum size for this species was much smaller than in Lake Malawi or Lake Kingiri, at 137mm SL. No individuals were seen with genital tassels more than 1cm long.

Oreochromis shiranus (Fig. 56)

Among the local fishermen's catches, we collected a smaller number of specimens that exhibited most or all of the diagnostic traits of *Oreochromis shiranus*: relatively narrow head, stronger horizontal than vertical melanic markings, all-black males with red dorsal fin margin and enlarged jaws. Although the species normally has 4 anal fin spines, 3 out of 5 specimens examined from this lake had only 3 spines. The largest specimens were considerably larger than those of the co-occurring *O. cf squamipinnis*, but somewhat smaller than conspecifics from other water bodies, attaining no more than 180mm SL.

Other species

A few specimens of *Clarias gariepinus* were collected in 2011 (Fig. 57). At the northern end of the lake small-meshed nets yielded numerous small barbs, including *Enteromius paludinosus, E. trimaculatus* and *E. cf. macrotaenia* (Fig. 58). Near the shore at Site A, numerous small fish with a sinusoidal swimming action were observed feeding on fish guts discarded by local fishermen: when netted out, these proved to be a neobolines (Fig. 58), formerly classed as *Mesobola*, but recent taxonomic revision places them in *Engraulicypris* (Ridden *et al.* 2016). There are few distinguishing features among the species in this genus, but we refer our specimens to the species *Engraulicypris ngalala* Ridden, Villet & Bills 2016, on the basis of its recorded distribution in the Ruvuma River system and Lake Chilwa (Ridden *et al.* 2016).

Figure 50. Lake Ilamba, showing inflow and outflow streams, and the approximate location of the main sampling site visited (Site A). The oblique line of trees that meets the more curving line of the outflow stream just south of the lake is an old road, not a watercourse.

Figure 51. Lake Ilamba: (left) looking north from Site A; (right) dugout fishing canoe at Site A.

Figure 52. (Left) the outflow of Lake Ilamba in June 2018; (right) underwater view of a rock encrusted with sponge, with cichlid fish indistinctly visible in the background at less than 1m depth.

Figure 53. Lake Ilamba. *Astatotilapia sp.* ‘Ilamba’ males are black, when fully territorial (above), but non-territorial males (left) show a range of colour elements, including golden flank scales, a dark eye bar and blue highlights on the lower part of the head.

Figure 54. Lake Ilamba. *Otopharynx sp.* ‘tetrastigma Ilamba’. Mature males (above) are large and brightly-coloured. Females and immatures (left) are silvery with three indistinct small flank spots in an oblique line.

Figure 55. Lake Ilamba. *Oreochromis cf. squamipinnis*: (above) male in breeding dress and (below) adult female.

Figure 56. Lake llamba: large male *Oreochromis shiranus* collected in June 2018. The jaws are only moderately enlarged, but the characteristic red dorsal fin margin and 4 anal spines are clearly visible.

Figure 57. Lake Ilamba: *Clarias gariepinus.*

Figure 58. Lake Ilamba: cypriniform fishes. (top left) *Enteromius trimaculatus*; (top right) *Enteromius paludinosus*; (bottom left) *Enteromius macrotaenia*; (bottom right) *Engraulicypris cf. ngalala*.

Lake Ikapu

(-9.370, 33.808)

Lake Ikapu measures around 675 x 540m and is reported to be about 4m deep, although it is pretty difficult to say what should count as the bottom of the lake. The water is clear (Secchi depth ~3.5m) and has a low conductivity (80 µS/cm). The lake is most readily approached from the northern end, where a secondary school gives way to arable fields that run up to the crater wall, affording a spectacular view down to the lake, more than 10m below (Fig. 60). There is a footpath down the crater wall (Figure 59, Site A; Figure 61), leading to a track which follows half the circumference of the lake (although it can take some wading at least at certain times of the year). This path is almost entirely shaded by trees, as the lake lies well inside the wall of the crater (Fig. 61). There is a parallel path along the rim of the crater that periodically affords panoramic views of the lake. At the southern end, the tree cover is reduced and the crater wall indiscernible, as the lake gives way to a flat marshy area and then to cultivated land. There are pools more or less isolated from the main lake at both the SE and NW ends of the lake (Figure 59, Sites B & C; Figure 62). A small stream arises a short way to the south of the lake- this might be a subterranean outflow and might even form surface connections at high water levels.

The most obvious feature of Lake Ikapu is the spectacular dominance of macrophytes: reed beds give way to a wide band of blue water lilies (*Nymphaea caerulea* Savigny 1798: Fig. 63), underlain by a variety of submerged plants including carnivorous bladderwort (Fig. 66) and spectacular *Ottelia* (Fig.65) , but increasingly dominated by fully submerged hornwort (*Ceratophyllum*: Fig. 64) which makes a thick layer on the bottom of the lake for a considerable distance offshore.

Invertebrates are numerous and diverse in Lake Ikapu. Snails include *Bulinus* spp., a known schistosome host, *Lymnaea, Bellamya* and *Lanistes ovum*. Large dytiscid beetles (*Cybister*) were often seen in the shallows. Other invertebrates included water stick-insects (*Ranatra*), saucer bugs (Naucoridae) and dragonfly nymphs. Fishing on the lake appeared to be limited to half-hearted subsistence gillnet fishing, children angling and a single castnet fisherman who was semi-retired and plied his trade in a single pool to get fish for his family. This was surprising, as the fish populations seemed dense, and the lake was near to a main road and the market town of Mbambo.

Fish Fauna

Lake Ikapu was found to have a relatively low-diversity fish fauna, with 5 species, of which 4 were cichlids. However, most of the cichlids seemed to be unique populations or species.

Astatotilapia sp. ‘Ikapu’ (Fig. 67)

Haplochromine cichlids of the genus *Astatotilapia* are frequently seen in all habitats in the lake, but tended to be skittish and no courting or dominant territorial males were seen underwater. Large males, up to 100mm SL, collected by gillnetting, angling or castnetting showed an olive brown colour with hints of blue and yellow, which makes it hard to judge whether this is the final male breeding dress or if it will transition to black.

Oreochromis species (Figs. 69 & 70)

Oreochromis are abundant within the lake, often being seen in large, loose feeding schools, particularly just around the edge of the lily zone. These seem to be a mixture of *Oreochromis cf.*

karongae and *Oreochromis cf. shiranus*, with possible hybrids between the two. These two species co-occur within Lake Malawi, where they are quite easy to distinguish. However, in Lake Ikapu things are more complicated. Normally, female and juvenile *O. shiranus* within the Lake Malawi catchment are brownish-yellow with a metallic golden hue and strong horizontal bands. Female and juvenile *O. karongae* are more silvery with dark vertical bars. In Lake Ikapu, females of both species are golden yellow, and several individuals have been collected that seem to have a body shape rather like *O. shiranus*, but with vertical bars more typical of *O. karongae*. Furthermore, many of the specimens with *O. shiranus* body shape were found to have 3 anal fin spines (4 out of a sample of 11). In Lake Malawi, *O. shiranus* almost always has 4 anal spines and *O. karongae* 3. Adult males of both species are black, but they differ in the colour of the dorsal fin margins: white in *O. karongae* v red in *O. shiranus* and this difference was clear in the Lake Ikapu specimens we collected. The largest males collected were 176mm SL for *O. cf. shiranus* and 149mm SL for *O. cf. karongae*. However, in Lake Malawi, *O. shiranus* males often develop enlarged jaws and a strongly concave head profile, while male *O. karongae* develop enlarged genital tassels. Neither of these extreme traits have been identified among the (admittedly few) adult male *Oreochromis* collected from the lake. It seems possible that both populations are genetically divergent from other populations assigned to *O. karongae* and *O. shiranus*, perhaps due to local adaptation, founder effects and/or introgression.

It is unclear where these fish breed. Both species normally build bowers in mud or sand, but no open substrate has been seen in the lake (the bottom seems to be thickly covered with macrophytes) and the only territorial male seen underwater was guarding a large sunken tree. Peripheral pools may be used, or perhaps the centre of the lake has an open area.

Tilapia sparrmanii (Fig. 68)

This species was found to be numerous, particularly in the shallowest part of the lake, where brood-guarding pairs were often seen.

Other fish species

Clarias gariepinus was the only non-cichlid fish found in the lake. It has never been observed underwater but has been found in gillnet catches.

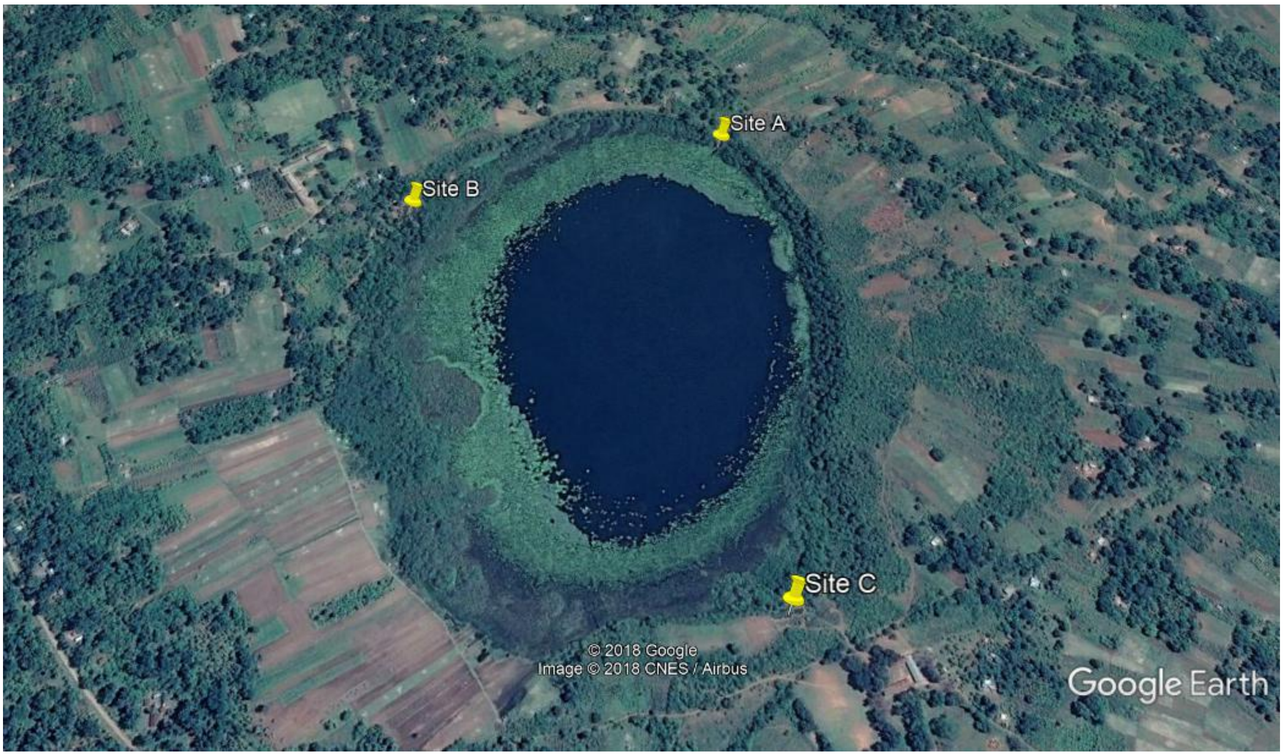

Figure 59. Lake Ikapu. The pale green ring around the dark blue open water is comprised of emergent macrophytes. The darker green areas are tree cover. Site A is an area under the shade of trees where a small open patch of land is sometimes used to land fish catches. There was a narrow channel through the macrophytes at the time of visiting from 2011 to 2017. This was the main area where underwater observations were made. Site B is a pool off the lake, again shaded by trees, where we were able to obtain fish collected by a local castnet fisherman. Site C is an open area where pools appeared not to be connected to the lake: numerous invertebrates but no fish were seen.

Figure 60. Lake Ikapu viewed from the crater rim at the northern end (left) and from the shore at Site A (right).

Figure 61. Lake Ikapu: ascending the crater wall at site A (left) and walking the woodland path around the eastern shore of the lake (right).

Figure 62. Marginal habitats around Lake Ikapu: (left) Site B: open pool to the north of the lake where *Oreochromis* and *Astatotilapia* were collected with a castnet; (right) flooded forest at the SE of the lake where a few small cichlids were seen over the leaf litter, near to site C.

Figure 63. Lake Ikapu: waterlilies (*Nymphaea caerulea*) are dominant in a wide zone around the lake.

Figure 64. Lake Ikapu: beyond the waterlily zone, the bottom of the lake is mainly a thick layer of hornwort (*Ceratophyllum*).

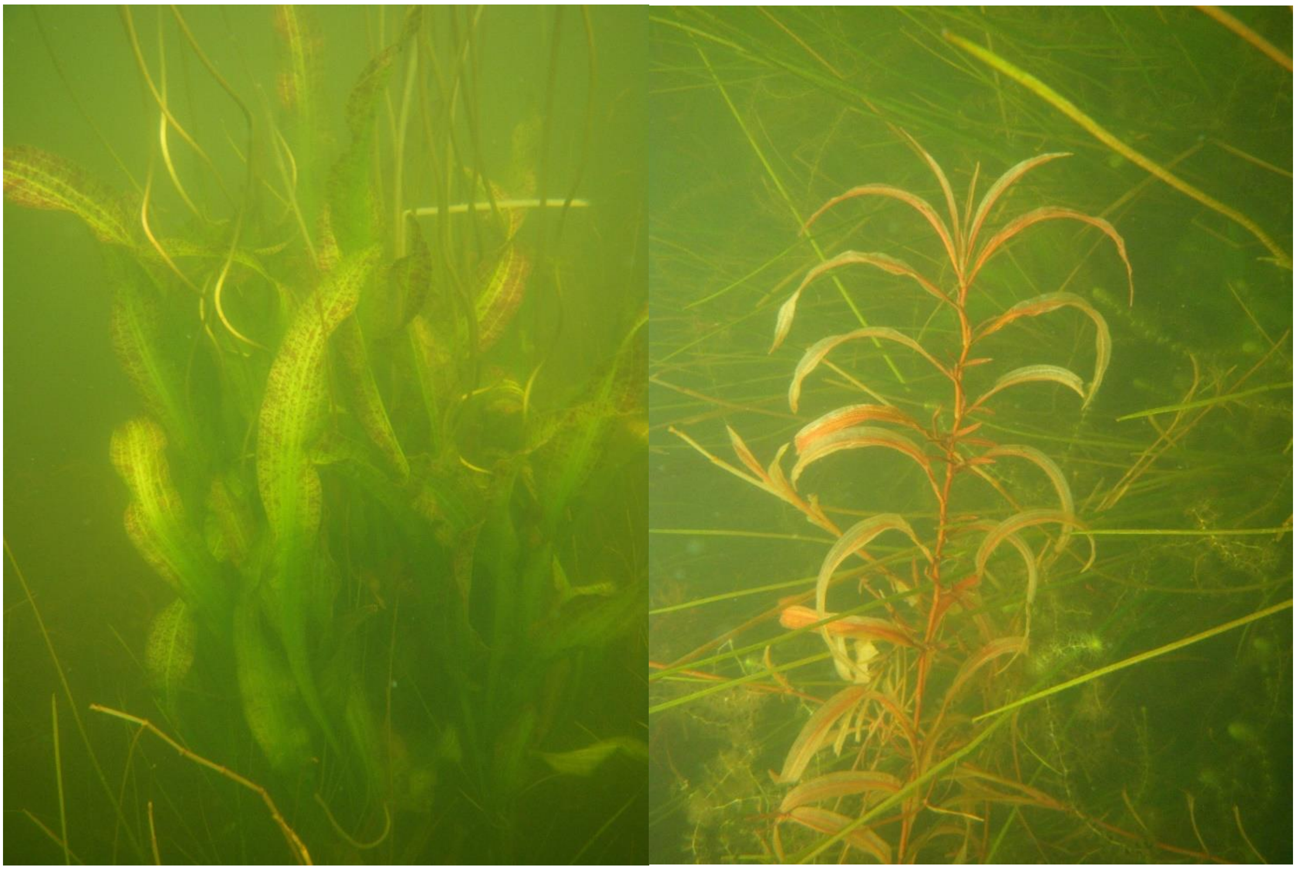

Figure 65. Lake Ikapu: submerged macrophytes, *Ottelia ulvifolia* and *Ammania* spp.

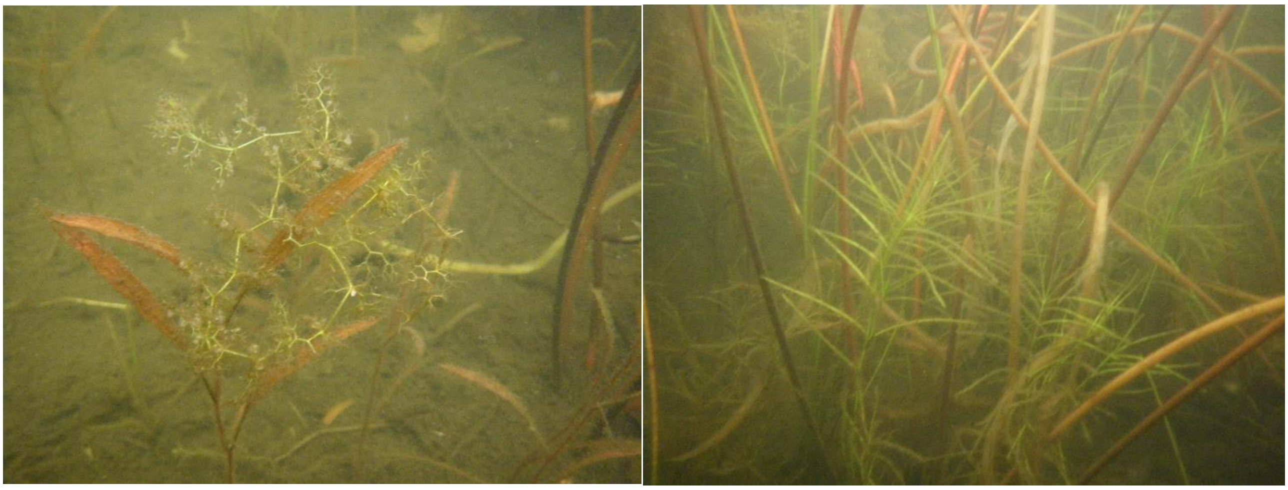

Figure 66. Lake Ikapu: submerged macrophytes in the lily zone: bladderwort, *Urticularia* spp. (left) and *Zannichellia* spp.? (right)

Figure 67. Adult male *Astatotilapia* sp. ‘Ikapu’. It is not clear whether this olive-brown colour represents the full breeding dress or not (photo digitally edited to remove labels and pins).

Figure 68. Lake Ikapu: *Tilapia sparrmanii*.

Figure 69. Lake Ikapu: Male *Oreochromis karongae*, collected March 2015 (above) and male *Oreochromis shiranus*, collected July 2011 (below). The species are readily distinguished by the colour of the dorsal fin margin and the ‘brow ridges’ seen in *O. karongae*.

Figure 70. Lake Ikapu: Female *Oreochromis spp.* The head shape, colour and melanic markings make it straightforward to identify the top specimen as *O. karongae* and the middle one as *O. shiranus*, but the lower specimen appears to show a mixture of features. All collected July 2011.

Lake Itamba

(-9.351, 33.844)

Lake Itamba was not easy to find. From the main road heading north from Kyela to Tukuyu via Ipinda and Kingiri, we needed to turn right at Mbambo and head East towards Itete, turning left at the faded sign for Ntapisi Primary School. Crossing the playing field (Fig. 71), we descended along a steep overgrown track to reach a small open beach, apparently mainly visited by children and cattle. The lake surface lies well below the level of the surrounding terrain. The lake is about 455 x 420m, and so is one of the smallest of the crater lakes. It lies at an elevation of about 825m. The water was relatively low in salinity, with conductivity of ~130-145 µS/cm, and clear, with a Secchi depth of 4.5m. The shores of the lake are steep and overgrown with trees, although there are a few patches of reeds too. No submerged macrophytes were seen. The lake is reported to be 17m deep, although we have only explored the shallow areas. The most obvious feature of the lake is the spectacular display of sponges growing on submerged reeds and dead wood (Figs. 76 & 77). In deeper water, large bivalves were numerous (Fig. 78), and occasional crabs (*Potamonautes*) were recorded, but no gastropods.

Fish Fauna

Lake Ilamba appears to contain only mouthbrooding cichlid fishes, but includes *Astatotilapia*, and 2-3 native *Oreochromis*. Juvenile Nile Tilapia were observed in 2011.

Astatotilapia sp. ‘Itamba’ (Fig. 80-81)

Haplochromine cichlids of the genus *Astatotilapia* were numerous along the shoreline, but were scarce over the open muddy plain of the lake. The largest male collected was only 72mm SL, which was far smaller than any other lake where mature males were obtained. Males varied in colour when collected in the field, ranging from brown, through pinkish to black. The brown/black differences persisted for several years in fish transferred to the aquarium at Bangor University, but eventually the older fish all turned dark grey. In the aquarium stock, 1st and 2nd generation males have tended to be yellowish when young, turn greyish with a prominent black eye-stripe, but eventually turn dark grey to black when older. This relationship between size and colour was not seen in wild fish, as many of the largest ones were brownish. Furthermore, body shape varied considerably, including head and jaw morphology. However, genome sequencing of a large number of individuals (Malinksy *et al.* 2015) did not reveal any population differentiation but indicated that they were closely related to *A. calliptera*. This appears to be a crater lake endemic species.

Oreochromis karongae and *O. cf. squamipinnis?* (Figs 82-84)

Juvenile *Oreochromis* of the ‘chambo’ complex were often observed in the shallows, but larger fish including males in breeding dress were only obtained by offshore fishing. The largest male (180mm SL) collected (in 2011) displayed the all-black breeding dress of *O. karongae*. This fish was in poor physical condition, with a rather emaciated body. Many of the smaller chambo collected also had large heads and short thin bodies, rather like the *O. cf. squamipinnis* found in Lakes Ilamba and Masoko and a few smaller (up to 134mm SL) males had an element of bluish colour on the head typical of that species. Intermediate-sized males in full breeding colour tended to have relatively smaller heads, well-nourished looking bodies and no trace of blue on their heads. Thus, it is possible that two chambo species co-occur in this lake: both species are endemic to the Lake Malawi, although it possible that one or more of the crater lake populations may deserve recognition at the species or subspecies level.

Oreochromis cf. shiranus (Fig. 85)

Numerous small individuals of this species were seen in shallow water on the open beach at site A. Several large males were usually seen among the reeds and roots in very shallow water (less than 1m depth). These were very skittish and fled to deep water. A few of these were obtained in gillnet catches. Males were black with a red dorsal fin margin and the larger specimens showed enlarged jaws and a concave head profile, as is typical of *O. shiranus*. The largest male was 28cm SL, much bigger than any other tilapiine cichlid found in any of the SW Tanzanian crater lakes. Females and immatures tended to be more grey-brown than usual for the species, and 3 out of 5 individuals showed 3 anal spines, with only 2 having the more usual 4 spines. This species is known from Lake Malawi, Lakes Chilwa and Chiuta, the Shire and Zambezi rivers, north to the Ruvuma system. The crater lake populations are the only ones known to have high frequencies of 3-spined fish.

Oreochromis niloticus (L. 1758) (Fig. 86)

Small specimens of Nile Tilapia were collected in both July and November 2011, from just off the beach at Site A. The species is not native to the Lake Malawi region: the nearest native population is in Lake Tanganyika. The local fishery officer, Mr Mwaibako, told us that he had personally stocked all of the crater lakes (including Lake Ngozi) with Nile Tilapia obtained from the government hatchery at Morogoro in 2010. This was an attempt to established productive fisheries in the lake. He admitted he had no idea what fish species were already present in the lakes. The small Nile Tilapia individuals we collected in 2011 were about the right size to have been part of the original introduction. No individuals of this species were seen during snorkelling in 2014 or diving in 2016, so it seems likely that this species did not establish a breeding population. We did not find Nile Tilapia in any of the other crater lakes.

Figure 71. Lake Itamba is inconspicuously concealed a short distance off the Mbambo-Itete road.

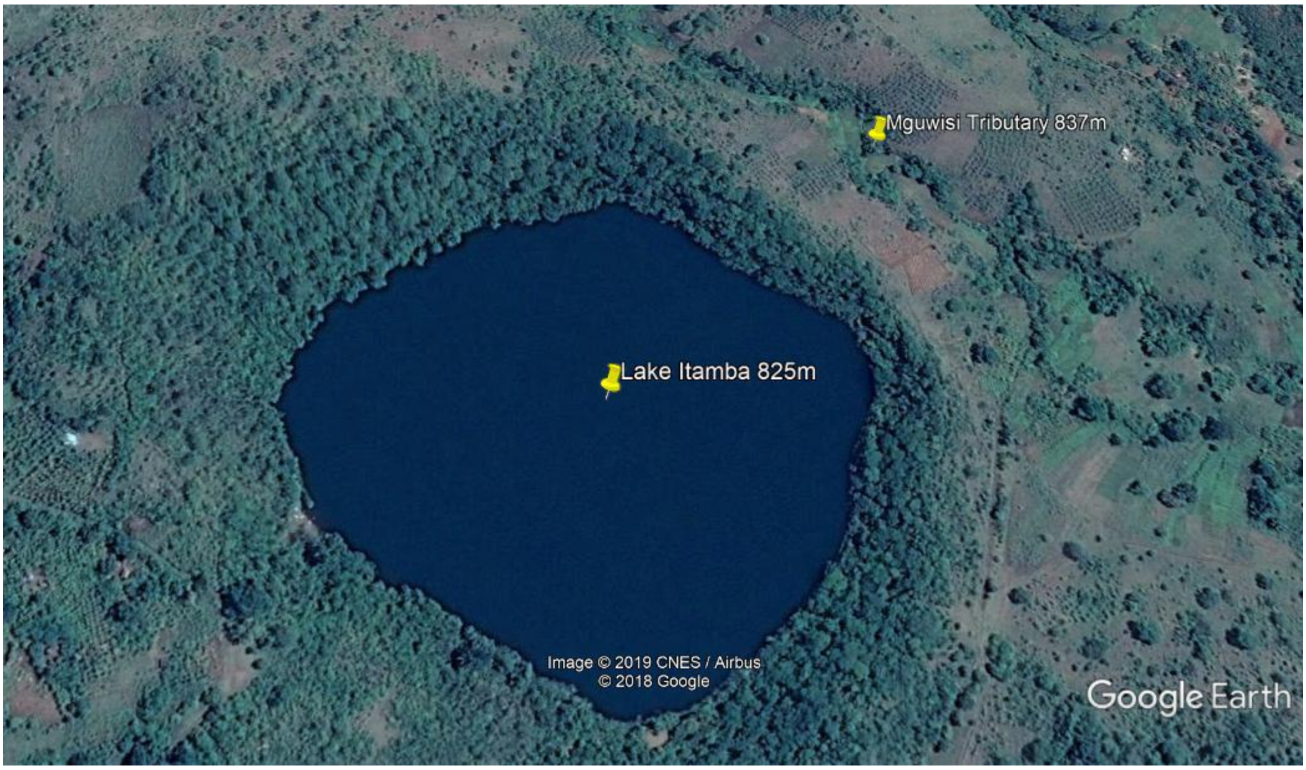

Figure 72. Lake Itamba lies mostly below the level of the surrounding terrain. The stream to the north joins the outflow of Lake Ilamba close to Lake Kingiri. We have yet to visit it and unaware of any faunal surveys.

Figure 73. Lake Itamba: (left) the beach at site A **-** the wooden boat belonged to the Tanzania Fisheries Research Institute; (right) the shoreline viewed from the boat was mainly overgrown with trees, but included substantial areas of reedbeds.

Figure 74. Lake Itamba: most of the shoreline is overgrown with trees, often extending far out over the water.

Figure 75. Lake Itamba. *Astatotilapia* among the rocks on the beach at site A, and on a sunken tree just offshore.

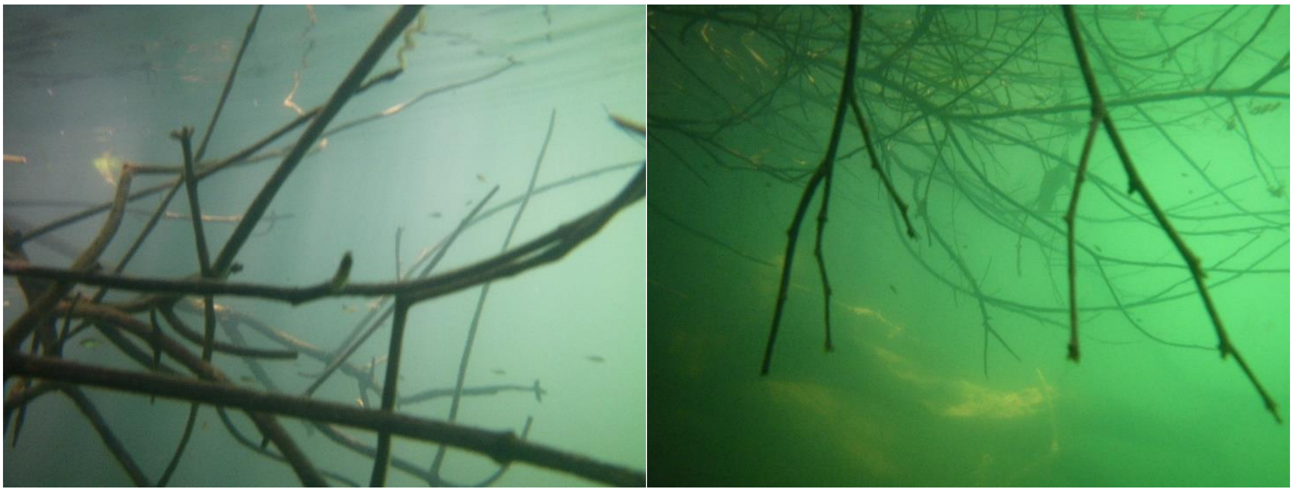

Figure 76. Lake Itamba: the roots and sunken branches of overhanging trees provide a substantial refuge for juvenile fish.

Figure 77. Lake Itamba: living tree roots and dead branches are covered in a range of sponge forms.

Figure 78. Some shallow areas of Lake Itamba were dominated by leaf-litter, with occasional patches of emergent vegetation.

Figure 79. Large bivalves were very common in the deeper water in Lake Itamba.

Figure 80. Lake Itamba: *Astatotilapia* spp. showed considerable variation in male colour and body shape.

Figure 81: *Astatotilapia sp.* ‘Itamba’ male in the aquarium at Bangor University.

Figure 82. Lake Itamba: Large male *Oreochromis karongae* in poor physical condition.

Figure 83. Lake Itamba: a small male *Oreochromis karongae* in good physical condition, but exhibiting unusual white vertical markings.

Figure 84. Lake Itamba: these small *Oreochromis* of the chambo complex have the large-headed appearance of *O. cf. squamipinnis* from Lakes Ilamba and Masoko.

Figure 85. Lake Itamba populations of *Oreochromis cf. shiranus* grow to a large size (male above). Females tend to be greyer than usual, but show the species-typical horizontal bands.

Figure 86. Juvenile Nile Tilapia (*Oreochromis niloticus*) collected from Lake Itamba in 2011.

Lake Masoko or Kisiba

(-9.334, 33.756)

In the scientific literature and in what little tourist information is available, this lake is referred to as Lake Masoko (e.g. Seegers 1996; Garcin *et al.* 2007; Delalande *et al.* 2008; Fonteijn *et al.* 2013) or sometimes Massoko (e.g. Williamson *et al*. 1999; Barker et al. 2000, 2003; Malinsky *et al.* 2015). The spelling with a double 's' seems to have been in use by the German colonial administration (e.g. von Lettow-Vorbeck 1920). However, the people we spoke to who lived near the lake called it Lake Kisiba and the nearby village and school are also called Kisiba. However, a recent archaeological and ethnographic study by a Tanzanian researcher called it Lake Masoko (Itambu 2016). So, we will refer to the lake as Masoko.

The lake is quite accessible, being close to the main (dirt) road from Ipinda to Tukuyu and there is a driveable path almost up to the lake. In 2011, it was possible to drive a 4WD car right up to the lakeshore, but this route has been fenced off, although the lake remains accessible to motorcycles, many of which are washed in the lake every day. The lake surface is about 861m above sea level, and it has a diameter of about 700m and a maximum depth of 36m. Our surveys indicated that the lake was oxygenated right to the bottom (Table 5) and indeed ROV footage showed fish living at depths of over 30m. Electrical conductivity was very low: measured as 34.9-35.9 µS/cm in 2017 and 37.6 µS/cm in 2018, with earlier published figures of 30-40 µS/cm measured in 1996 (Barker *et al.* 2000). The pH was mildly acidic, at around 6.5-6.7 in 2017, but reported at 6.7-8.0 in 1996 (Barker *et al.* 2000). In June 2017, we found temperatures were generally around 23-25C from the surface to 30m depth, with no sign of a thermocline. Barker *et al*. (2000) reported a thermocline at 15m in October 1996, with surface waters at 27C, and the hypolimnion at 24C.

About half of the lake shoreline is overgrown with trees but the other half is fairly open. The lake bottom can be divided into three zones: the littoral, the crater wall and the mudplain. The **littoral zone** extends to around 5-10m depth, with a relatively gentle slope. The shallowest part of the littoral has a few patches of reeds, and at some times of the year covers terrestrial vegetation such as grasses. These areas provide refuges for invertebrates and fish fry- both cichlids and clariids. The deeper part is more open with a muddy bottom (often with gravel just underneath), with occasional rocks or submerged tree trunks. The fish community is conspicuous and diverse, with many *Astatotilapia*, including large yellow males, numerous *Oreochromis* including fry in the shallows and large adult males defending territories, and occasional *Coptodon* and *Clarias*. The **crater wall** is a more steeply shelving area: largely gravelly with occasional outcrops of large rocks extending from 5-10m down to 20-25m. In the northern part of the lake, this zone is more muddy with sunken wood. *Astatotilapia* found here are often in large feeding schools, sometimes foraging well off the bottom. Towards the bottom of the habitat, large blue males *Astatotilapia* can be found defending territories on rocky outcrops or joining foraging schools. Occasional *Clarias* catfish can be seen here, usually lying up close to rocks or sunken trees. The lighting regime quickly alters through this zone, becoming dim and green. The **mudplain** occupies most of the lake bottom. The transition is abrupt, with the rocky slope suddenly giving way to a flat layer of silt, which is often very deep. There is very little light on the mudplain and the silt is easily disturbed, making observation difficult. The only fish seen here are *Astatotilapia*, with small groups of females or juveniles near the bottom, with the occasional large blue male. Tiny fry are occasionally observed swimming close to the bottom. The **open water** of the lake seems sparsely populated: the occasional school of large *Oreochromis* can be seen in the surface 10m or so, even above the deepest part of the lake, but the feeding schools of *Astatotilapia* have not been observed far from the bottom.

At present, there are no surface connections between Lake Masoko and any other water body. The Itupi stream passes close to the western side of the lake but at a much lower altitude, although it is higher up some distance to the north. A couple of small springs emerge from the base of the crater wall to the eastern side. These appear to be subterranean outflows from the lake: none of fish species known from the main lake have been found near the origin of these springs, although some stream catfish unknown from the lake have been found, suggesting there is currently no exchange of fish faunas. Although most of the lake is surrounded by high crater walls, there is a small section around sites A and C which lies below the level of the surrounding land and could have been flooded in the past by overflows from neighbouring streams.

Table 5. Limnological measurements for Lake Masoko.

Transect	Site	Depth (m)	Range (m)	Temp (C.)	O2 (mg/l)	pH	EC (uS/cm)
T1	A (men's beach)	8.8	38.0	24.6	7.3	NA	NA
T2	Cow path	8.8	48.0	24.6	*5.3	NA	NA
T3	Black rock	10.4	48.0	24.9	6.2	6.9	34.6
T4	B (orchid path)	10.4	36.0	24.8	5.9	6.6	33.4
T5	Reed gap 1	9.2	39.0	23.6	7.5	6.6	NA
T6	C (women's beach)	9.3	50.0	26.0	7.1	6.4	39.2
T7	White rock / fallen tree	11.0	35.0	*29.0	8.3	7.0	32.4
Mean		**9.7**	**42.0**	**24.8**	**7.1**	**6.7**	**34.9**

Transect	Site	Depth (m)	Range (m)	Temp (C.)	O2 (mg/l)	pH	EC (uS/cm)
T1	A (men's beach)	20.3	65.0	24.3	8.2	NA	NA
T2	Cow path	20.1	78.0	24.7	*4.5	NA	NA
T3	Black rock	21.8	74.0	24.8	8.7	6.5	35.3
T4	B (orchid path)	20.7	65.0	24.7	6.0	6.6	33.5
T5	Reed gap 1	20.1	62.0	24.8	7.3	6.2	36.5
T6	C (women's beach)	20.3	72.0	24.0	7.9	6.6	*29.3
T7	White rock / fallen tree	20.9	62.0	25.0	7.3	6.8	*29.1
Mean		**20.6**	**68.3**	**24.6**	**7.6**	**6.5**	**35.1**

Transect	Site	Depth (m)	Range (m)	Temp (C.)	O2 (mg/l)	pH	EC (uS/cm)
T1	A (men's beach)	28.6	114.0	23.7	8.5	NA	NA
T2	Cow path	29.2	173.0	24.6	*4.7	NA	NA
T3	Black rock	31.1	178.0	24.6	8.7	6.5	35.6
T4	B (orchid path)	29.8	152.0	24.1	*3.9	6.7	34.4
T5	Reed gap 1	31.0	157.0	25.3	7.1	7.0	37.8
T6	C (women's beach)	30.7	136.0	24.0	7.2	6.7	*28.0
T7	White rock / fallen tree	30.6	103.0	25.0	6.8	6.8	*28.9
Mean		**30.1**	**144.7**	**24.5**	**7.7**	**6.7**	**35.9**

Data collected by A. Ford July 2017. Range= distance from shoreline, EC= electrical conductivity. Asterisked values are considered errors and were not used in calculation of means.

Plants and Invertebrates.

No submerged or floating macrophytes have been seen in the lake, but there are some large patches of reeds (*Phragmites*) on the NW side. Sponges are common on hard substrates, including rocks, trees and reeds: in shallow water they are often green or orange, but tend to be white at greater depth. Bivalves (*Coelatura* spp.) are abundant down to the crater wall zone. Large crabs (*Potamonautes*) are occasionally seen. Gastropods are represented by *Melanoides* and *Biomphalaria* (a schistosome host): both appear to be most numerous at Site B. Most insects are found in the shallowest 10cm or so of the lake, although some large burrowing odonatan nymphs can be found a bit deeper. Most common are the larger predatory kinds, such as odonatan nymphs, dytiscid beetles, water scorpions (*Nepa* and *Ranatra*). Saucer bugs (naucoridae) are especially numerous. Mayfly nymphs and chironomids were occasionally found.

Fish Fauna

The lake has 4 fish species, although one of these has diverged into two distinct ecomorphs. The dominant species is the unique polymorphic *Astatotilapia*, while the brilliantly-coloured breeding males of the unique *Oreochromis* population are also conspicuous. The two much less abundant species, *Coptodon rendalli* and *Clarias gariepinus* might have been introduced to the lake.

Astatotilapia sp. 'Masoko' (Figs. 97-99)

Astatotilapia have been observed through the lake, generally within about 2-3m of the lake bed, but at all depths, although densities and overall numbers are much higher at depths of less than 20m (Table 6). The males are conspicuously colour-polymorphic and this is associated with water depth. Most males in the littoral zone are predominantly yellow, very similar to the yellow male of the closely-related *A. calliptera* found in most rivers and small lakes in the Lake Malawi catchment, as well as in the shallow weedy habitats of the main lake itself. In deeper water, all mature males seen have been blue. These have been known as 'Littoral' and 'Benthic' ecomorphs respectively (Malinsky *et al.* 2015). Relative to body length, Littoral males generally have heavier bodies, heavier lower pharyngeal bones and larger teeth on the lower pharyngeal bone. The largest specimen recorded was a 121 mm SL male littoral, far larger than any other crater lake *Astatotilapia*, but such large fish are rare and the lake was far more heavily sampled than any of the others. The ecomorphs have significantly different body shapes, as indicated by geometric morphometric analyses. Littoral fish have significantly enriched carbon^{13}/carbon^{12} isotope ratios, compared to Benthics, indicative of a greater influence of a planktonic-based food chain in the diet of the latter (Malinsky *et al.* 2015).

Underwater observations indicate that Massoko Littoral-morph fish are seasonal breeders, with observations of brooding females and courting males largely confined to the period March-May. Males do not seem to be strongly territorial. Receptive females have been observed moving rapidly over the bottom, being followed by very large colourful males who attempt to lead them into the shelter of a nearby rock (youtube: QKXEfl3Jcdw). Spawning has been observed to occur underneath the overhang of a rock, with one or two eggs laid at a time and rapidly picked up by the female (youtube: n3ICvDEfMs4). Although occasional courtship attempts by smaller males have been observed in deeper water, to date, all prolonged bouts of courtship involving circling with females, occurred with very large yellow males in shallow water (less than 2m depth). In the aquarium, brooding females guard fry for around one week after initial release, adopting dark eyes and striking dark markings on the head. This has not been observed in the lake: mouthbrooding females are generally seen in mobile schools of actively foraging fish of a similar size.

Foraging behaviour by *Astatotilapia* in shallow water has been observed frequently, and includes sediment feeding, rasping at hard surfaces such as rocks, wood and reeds, surface feeding, midwater feeding (generally in large schools), stalking the eggs/larvae of *Coptodon rendalli*, striking at juvenile schooling fish in shallow water and tearing flesh from open bivalve shells.

Large adult males (both blue and yellow) have occasionally been observed to school in company with similar-sized *Oreochromis* at depths of around 2-10m, and large yellow males occasionally flee from disturbance into deeper water, but generally they are concentrated in the shallowest part of the lake, around 5m depth or less. Depths of 5-15m are generally populated by schools of medium-sized fish, including small males that are developing breeding colour: both blue and yellow. These were initially suspected to represent additional ecomorphs, but in the aquarium they developed into large blue or yellow males. Occasionally intermediate-looking large males were observed at intermediate depths and occasionally large blue males have been seen in shallow water. It is not clear whether these are individuals of the Benthic ecomorph, blue Littoral fish or genetically intermediate fish.

Large blue males of the Benthic morph have mostly been observed deeper than 15m (youtube: 40hf5B38Gtw). Many have been observed over the mudplain, often singly or with groups of smaller fish, as deep as 36m. They have also been seen associated with mobile groups of small fish over the deeper part of the rock wall zone from around 15m deep (youtube: dVj7u2Hiipw). Rocky outcrops deeper than about 18m seem invariably to be occupied by large blue males. They seem to remain in a specific location and to threaten other approaching males (youtube: nbRpskdvjY0). It appears that at least some large blue males are territorial all year round. No yellow males have ever been observed at deeper than 15m or showing territorial behaviour. Mouthbrooding females have been observed over the rock wall and also out over the mudplain. Tiny fry have also been observed swimming low down over the mud far from the crater wall. In the aquarium Benthic morph fish, like Littoral morph fish, lay their eggs on the bottom. Any eggs laid over the mudplain would probably disappear into the silt before the female could collect them, so it seems most probable that the Benthic morph fish breed on the crater wall zone.

Over the deeper part of the crater wall, *Astatotilapia* are generally observed foraging in midwater, often in large groups, sometimes of hundreds of individuals. They tend to descend to the bottom when alarmed. Over the mudplain they are generally seen singly or in small loose groups foraging near the bottom.

Taxonomically, this population poses a problem, with the deep-water population with blue males appearing to merit the status of a distinct species, but yet it seems to continue to interbreed with the shallow water population, which retains the appearance of a typical riverine *A. calliptera*.

Table 6. Estimation of distributions of *Astatotilapia* on the bottom habitat in Lake Masoko. Despite the larger lake bottom area deeper than 20m (66.5%), most fish (>80%) are found shallower than 20m. This estimate does not account for fish swimming in midwater.

	Bottom Area		Fish Count					Assumed 2 densities		
Depth (m)	Area (x10^3 m$^{3)}$	% A	Mean	95% CI	Sample Counts	Relative # Fish	% Fish	Mean Count	Relative # Fish	% Fish
0-10	82.5	21.4	60.8	28.9	17	13.0	55.6	58.5	12.5	53.5
10-20	46.2	12.0	53.1	48.7	7	6.4	27.2	58.5	7.0	30.0
20-30	98.7	25.6	8.7	10.1	7	2.2	9.5	6.0	1.5	6.6
30+	154.5	40.9	4.4	3.3	12	1.8	7.7	6.0	2.5	10.5
Total	384.8				43	23.4			23.6	

NB: counts were estimated from 5 minute ROV transects or (at depths < 5m also 5 min static GoPro films; analysis indicated no significant different in counts at overlapping depths). Area at depths was estimated from 3 lakewide sonar transects, soundings taken every 10m. Contour boundaries were interpolated linearly and areas calculated assuming a circular lake. The second analysis (assumed 2 densities) was based on Anova using Log (X+1) counts which indicated an overall significant difference among the depth ranges, F =17.21, P<0.001 with posthoc LSD indicating no significant differences in densities between 0-10 v 10-20 and between 20-30 v 30+, so the analysis was re-run clustering all raw fish counts into 2 depth ranges, 0-20 and 20+m. Data from 2018 collected by R. Pinsonneault & H. Davey.

Oreochromis cf. squampinnis (Fig. 100-103)

A single species of *Oreochromis* is found in Lake Masoko. The wide head, long, branched genital tassel and characteristic bower shape mark it out as a member of the Lake Malawi chambo complex. The bright blue head of mature males is characteristic of *Oreochromis squamipinnis*. However, a number of features suggest that this is a unique population, perhaps deserving recognition as a distinct species. Males attain a relatively small size (150mm SL) and develop a 'big-headed' look very much at variance with that seen in *O. squamipinnis* in Lakes Malawi, Malombe and Kingiri. A single adult male brought back to the aquarium at Bangor in 2011 had not grown much larger at the time of writing in 2019 and retained this 'big headed' appearance, under conditions in which *O. karongae* from Lake Malawi have grown much larger and deeper-bodied. This suggests that the characteristic morphology of this population may have a genetic basis. Additionally, the blue area on the head is generally overlain with multiple spots and stripes, not normally seen in the typical populations of *O. squamipinnis*. Finally, females and juveniles are bright golden-yellow, with thin blotchy stripes quite unlike typical silvery, broad-barred Lake Malawi *O. squamipinnis*.

Adult males were seen on bowers for most of the year. The bowers were often in very shallow water (<2m deep), although some were found as deep as 10-15m if the bottom was muddy, as it is beyond site B. Males were energetic in territory defence and far less skittish than chambo in Lake Malawi, perhaps because they are not fished. Small fry were often found in large schools in very shallow water, particularly among vegetation, and seemed to feed in the water column. Larger individuals, around 2-5cm long, were often seen in loose groups near the bottom at depths of 2m or less, mostly feeding among the sediment or by rasping on hard substrates, such as rocks, wood or reeds. Individuals larger than 5cm seemed to spend most of their time offshore, presumably plankton-feeding. For example, a large group was filmed by ROV at 5-6.5m depth where the lake bottom was around 30m deep. On calm days, the surface of the lake far from shore could sometimes be disturbed by what looked like feeding actions of a large number of fish, almost certainly *Oreochromis*. Occasionally large schools could be seen feeding on large sunken trees at depths of 2-5m.

While *Oreochromis squamipinnis* is considered endemic to the Lake Malawi catchment (Trewavas 1983), this population may deserve to be recognised as a distinct species or subspecies.

Coptodon rendalli

Coptodon rendalli was relatively infrequently seen in the lake, mainly in shallow water (less than 2m). Larger specimens usually swam around in pairs. Occasionally adults were seen guarding a small pit dug in the mud, and eggs or wrigglers could be seen at the bottom. These pits were often close to a small rock. Parental adults were almost always kept busy chasing away stalking *Astatotilapia*. Free-swimming fry were never observed under parental care, and it seems likely that mortality of the offspring was very high. None of the individuals yet observed showed any sign of the bright red colour seen in many other populations of the species. *Coptodon rendalli* is native to Lake Malawi and its catchment, and it is found in some of the other crater lakes, so it may be native. However, it is also possible it was introduced for the purpose of fishery enhancement.

Clarias gariepinus (Fig. 104)

The African or sharptooth catfish (*Clarias gariepinus*) was occasionally seen in the littoral and crater wall zones, most usually resting on the bottom among rocks. It does not seem to grow very large in the lake, perhaps no more than 45-50cm long. Small juveniles (up to 6-7cm long) could be collected by handnetting in very shallow margins of the lake (<5cm deep) among flooded terrestrial vegetation. It is likely that the eggs and larvae suffer heavy mortality from *Astatotilapia* and predatory invertebrates. Local people suggested that the species was introduced, although it is native to the Lake Malawi catchment.

Figure 87. Lake Masoko. Contrary to the Google Earth label, the village is Kisiba, not Masoko.

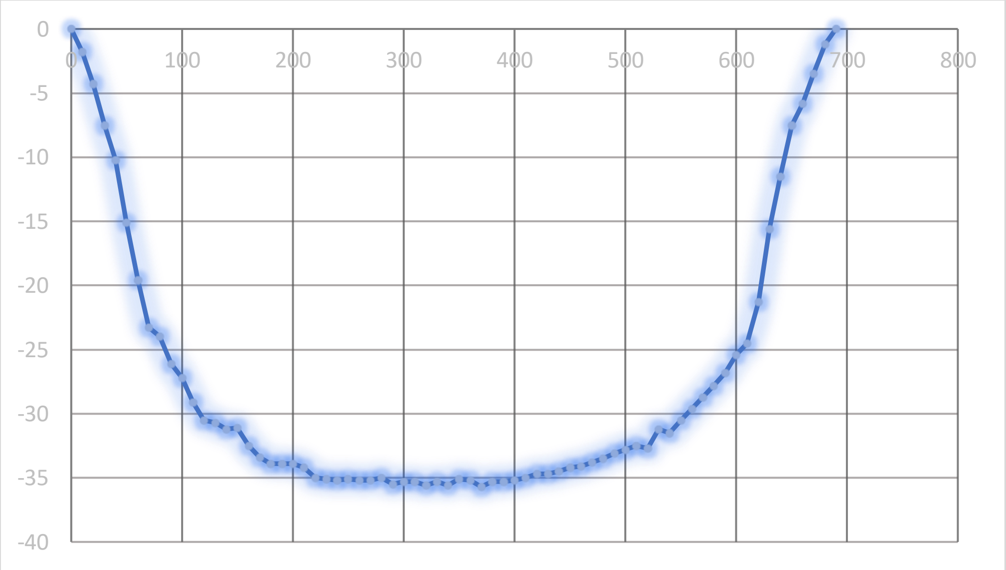

Figure 88. Bathymetric profile of Lake Massoko (2018 data), showing that most of the lake bottom is deeper than 30m.

Figure 89. Lake Masoko: (top left) panorama looking east; (top right) open grassy shoreline between sites A and B; (bottom left) open habitat with rocks on gravel near site A; (right) patch of *Phragmites* NE of Site B

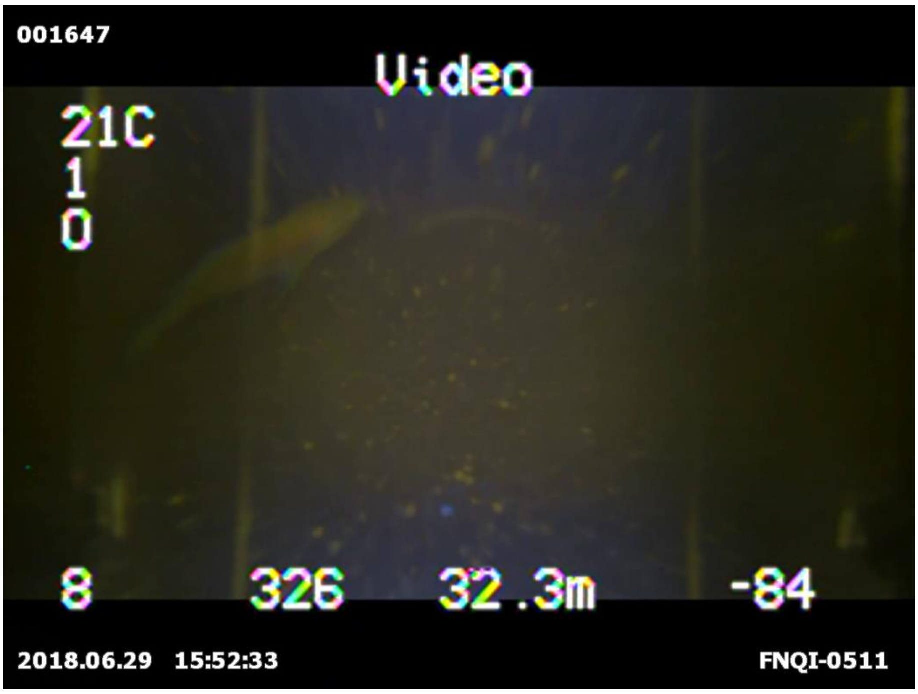

Figure 90. Lake Masoko: a cichlid fish observed over the mudplain at 32.3m depth (screengrab from video taken by ROV in June 2018).

Figure 91. Lake Masoko reedbeds (left) underwater stems heavily encrusted with sponges; (right) *Astatotilapia* among reed stems and debris.

Figure 92. Some of the diversity of sponge forms in the reedy habitat of Lake Masoko.

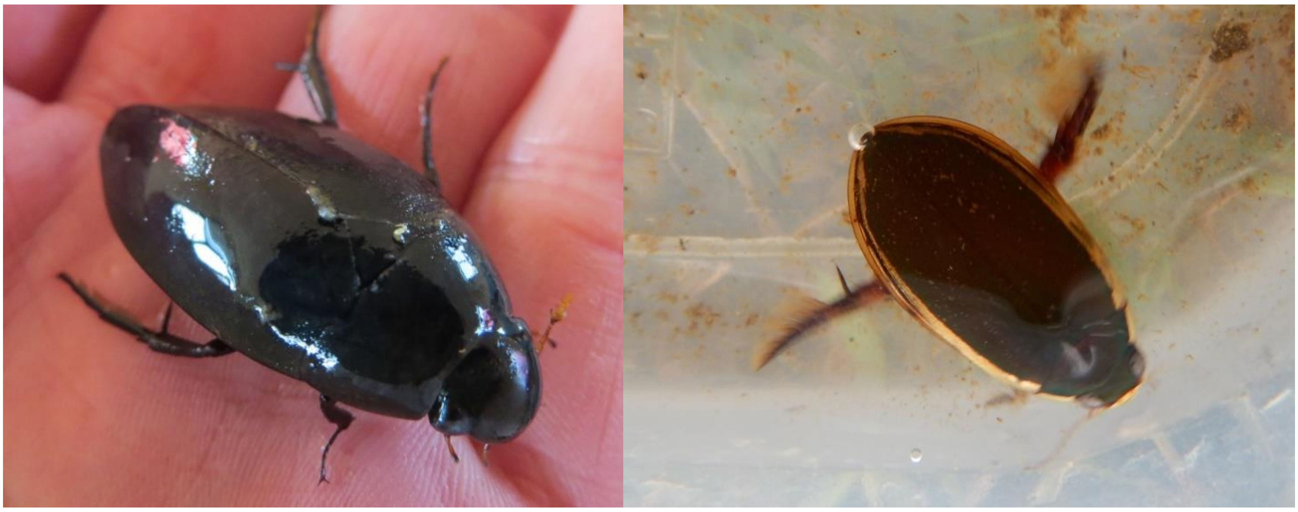

Figure 93. Lake Masoko: (left) Water beetles: scavenger *Hydrophilus* spp.; (right) predatory *Cybister* spp.

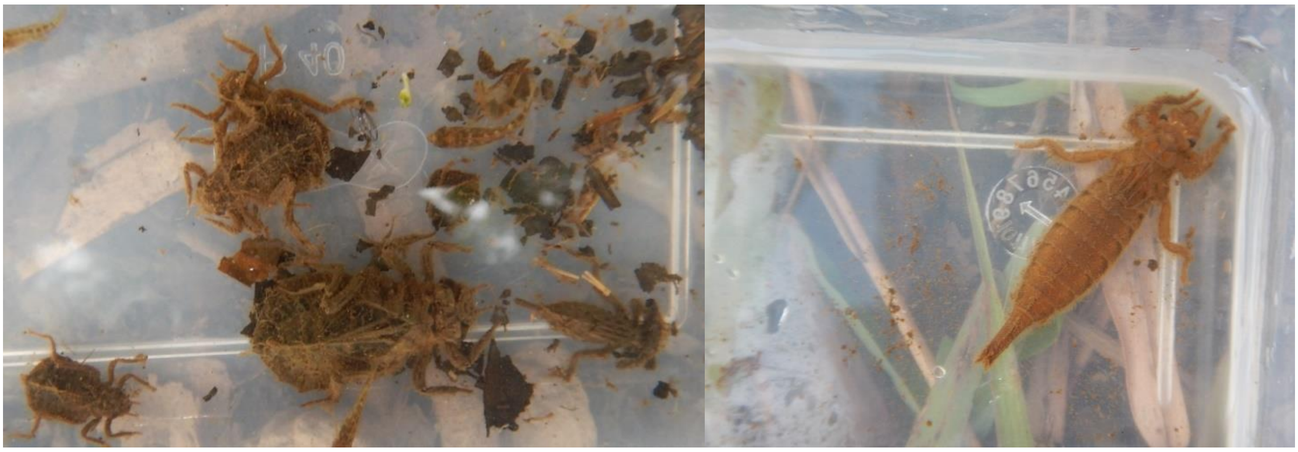

Figure 94. Lake Masoko dragonfly nymphs, Gomphidae.

Figure 95. Lake Masoko invertebrates: (left) water stick insect (*Ranatra* spp); (right) pale burrower- polymitarcyid ephemeropteran nymph (possibly *Povilla*).

Figure 96. Lake Masoko: Bivalve (*Coelatura* spp.).

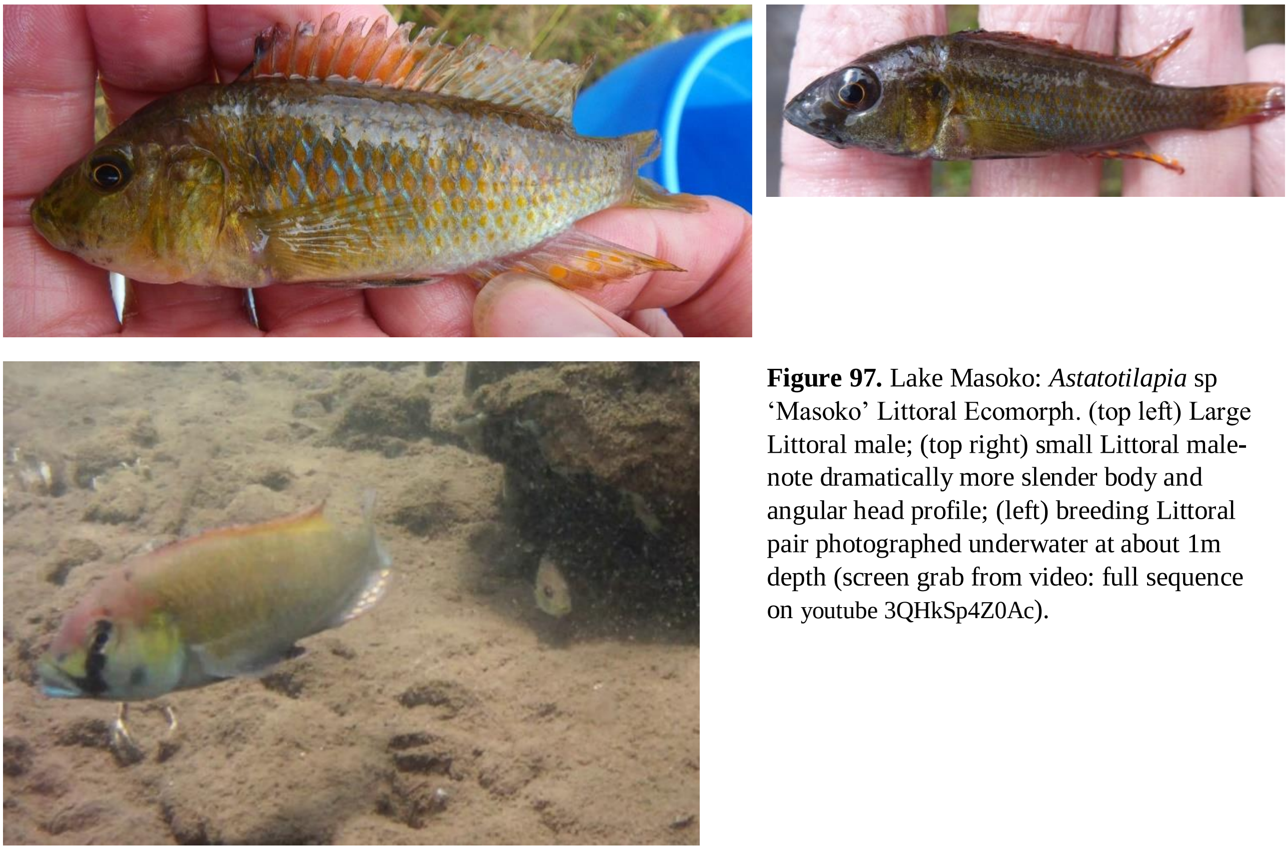

Figure 97. Lake Masoko: *Astatotilapia* sp 'Masoko' Littoral Ecomorph. (top left) Large Littoral male; (top right) small Littoral male- note dramatically more slender body and angular head profile; (left) breeding Littoral pair photographed underwater at about 1m depth (screen grab from video: full sequence on youtube 3QHkSp4Z0Ac).

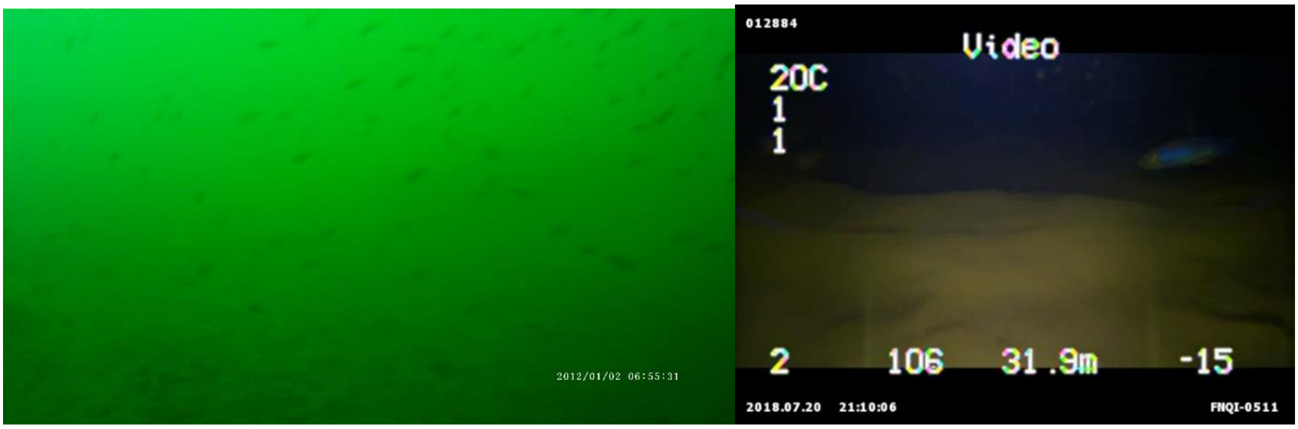

Figure 98. Lake Masoko: (left) a school of *Astatotilapia* descending to the crater wall at about 15m depth (screengrab from video); (right) blue Benthic male over the mudplain at 32m depth (screengrab from ROV footage).

Figure 99. Lake Masoko: *Astatotilapia* Benthic males **-** (top) freshly collected; (middle) underwater at around 20m, illuminated by artificial lighting; (bottom left) on territory among rocks at 18-20m depth in natural light; (bottom right) threatening a passing rival male, in natural light (middle and bottom are screen grabs from videos).

Figure 100. Lake Massoko *Oreochromis cf. squamipinnis.* (top left) adult male showing 'big headed' body morphology; (top right) male showing fresh breeding colour; (left) breeding male head colour; (below) juvenile showing the golden hue and narrow blotchy stripes that distinguish this population from *O. squamipinnis* from Lake Malawi and Kingiri.

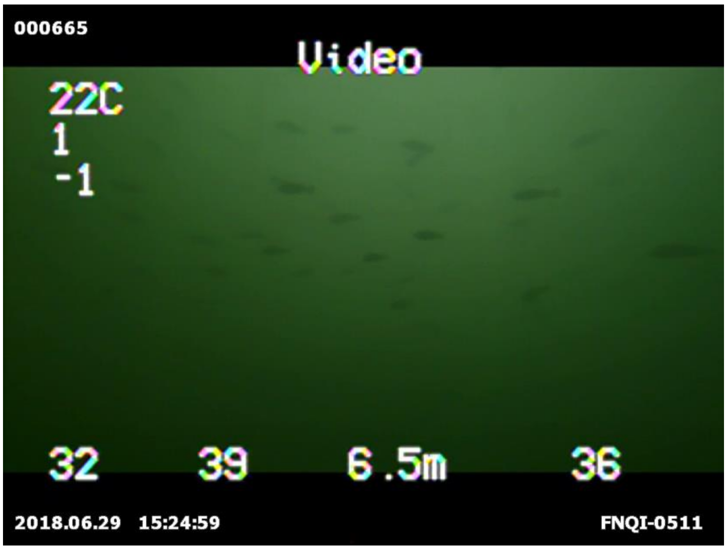

Figure 101. Lake Masoko: Feeding school almost certainly of *Oreochromis cf. squamipinnis* at 6.5m depth in the middle of the lake (screen grab from ROV footage).

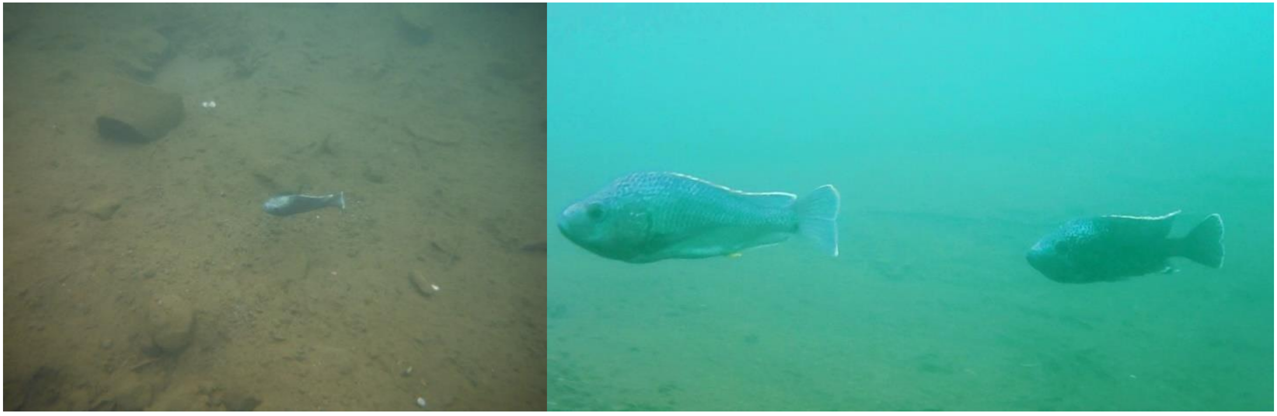

Figure 102. Lake Masoko: *Oreochromis cf. squamipinnis* (left) male over shallow muddy bottom (right) territorial defence in a lek at ~2m depth (screen grab from video: youtube: 4o-C4aBZwQM)

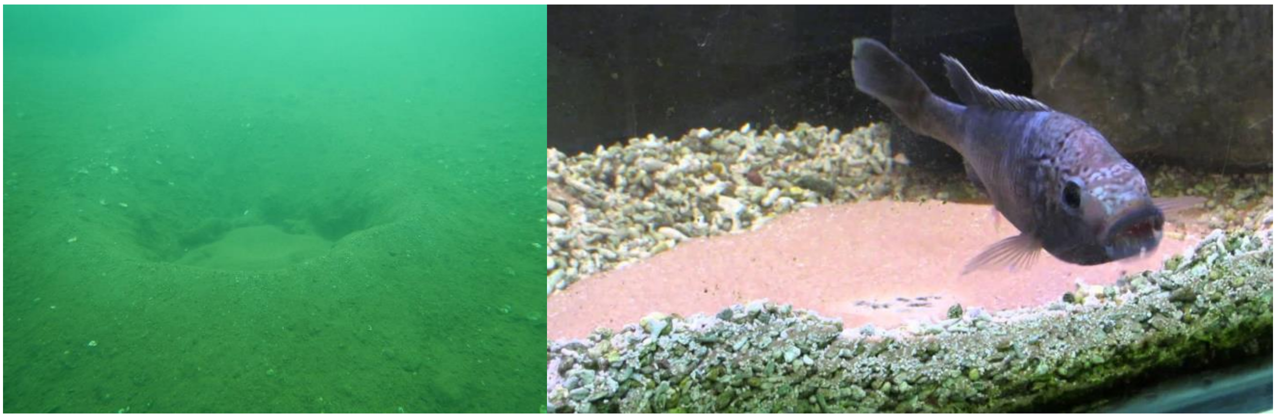

Figure 103. Lake Masoko: *Oreochromis cf. squamipinnis* bower building (left) a bower at ca 2m depth; (right) bower construction in the aquarium (screen grab from video youtube: v0uqaPkRpEA)

Figure 104. Lake Masoko: *Clarias gariepinus* (above left) juvenile caught by handnetting in shallow water; (above right) large individual underwater among rocks at around 15m depth (video screen grab); (left) in shallow water (~3m depth).

Lake Kyungululu

(-9.306, 33.864)

Lake Kyungululu is relatively distant from the other crater lakes, lying about 5km NE of Lake Itamba, close to the town and mission hospital of Itete. A tributary of the Lufilyo River (also known as Lufilio, Rufiryo and Rufilyo etc) runs about 3km away at the foot of the Kipingere Range (or Livingstone Mountains). The lake is at a relatively high altitude (924m above sea level). It is a small lake, no more than 420m in diameter but it is very deep: our sonar estimate was more than 45m in the centre. It seems a hostile environment for fish, with steeply sloping crater walls meaning there is little benthic production. The water is turbid, but this does not seem to be due to high primary production, rather it looks grey and inorganic. It is not known whether the bottom of the lake is oxygenated and habitable for fish. There is one small open beach (site A) accessed down a steep cattle track. It has a steep shore with rocks of various sizes mixed with gravel. The rest of the lake has precipitous walls, overgrown with trees. In all areas surveyed by snorkelling, the bottom drops off quickly. A single SCUBA dive to 22.5m indicated that light penetration was poor and the steep rocky/gravelly bottom extended beyond 20m. Few fish were seen deeper than 2m.

A few patches of emergent vegetation (*Phragmites*) were seen, but no floating or submerged macrophytes. Sponges were observed on rocks, but not on wood or reeds. Large crabs (*Potamonautes*) were occasionally seen, along with insects including dytiscids and pond skaters. No molluscs were recorded.

The lake was used for drinking by cattle which were sometimes accompanied by children and dogs. During the first visit in July 2011, we met a single gillnet fisherman, who had deployed a single very long net in middle of the lake. He said he was not native to the area, and reported he was salting his catch in a drum to export to the Democratic Republic of Congo. He claimed that catches were very poor (1-5 small bony fish per day) and we did not see any sign of fishing activity on subsequent visits. When we examined his catches, all of the fish he had caught were the endemic *Oreochromis chungruruensis* (Ahl 1924).

Fish Fauna

The lake was known for the endemic *Oreochromis chungruruensis*, but we also observed two other tilapiine species not previously recorded from the lake. It seems likely that there were introduced. There are unpublished records that ‘Black Bass’ was successfully introduced into the lake for control of snails that act as bilharzia (schistosomiasis) vectors. Black bass is usually employed as a common name of *Micropterus salmoides* (Lacépède 1802), also known as the largemouth bass, a large (up to 11kg) piscivorous species originally from North America. This highly invasive species is not known as a molluscivore (Weyl & Lewis 2006). However, neither black bass nor any species of snail were observed during our visits to the lake.

Oreochromis chungruruensis (Ahl 1924) (Figs. 111-117)

Juvenile *Oreochromis chungruruensis* were found to be common in shallow waters, where they seemed to feed on sediment and by scraping hard surfaces, such as rocks, wood and the stems of reeds. Schools of tiny fry were common among reeds and sunken branches during June 2017. During visits in July 2011 and June 2017, emaciated adult fish were seen swimming slowly in the shallows and could be picked up by hand. Other adult fish bought from a local gillnet fisherman were also in poor condition. At that time of the year, adults (apart from the emaciated fish) were not seen underwater by snorkelling, but ripples of surface feeding fish were seen in the middle of the lake, and the gillnetter had set his net at the surface across the middle of the lake, suggesting that the adult fish are largely pelagic midwater feeders. During the survey of November 2011, large black males (up to 137mm SL) were numerous in the shallows, usually on bowers close to reeds or overhanging vegetation at depths of 1m or less. A population of this species has been maintained in the research aquarium at Bangor University since 2011.

This species was described from specimens collected by Dr Friedrich Fülleborn and deposited at the Natural History Museum in Berlin, where they were eventually described by Ahl in 1924 as *Tilapia chungruruensis*. The original labels state that the specimens were collected in 1899, not 'about 1923' as stated by Trewavas (1983). The status of this species was rather confused by later studies by Trewavas (1976, 1983). She regarded some of the Berlin specimens as *Oreochromis lidole*, on the basis of their morphology, specifically their slender pharyngeal bones, lower number of tooth rows and large heads. Our investigations suggest that these are actually emaciated 'spent' specimens of *O. chungruruensis*. Before we visited Lake Kyungululu, the senior author had a suspicion that *O. chungruruensis* might well be merely a population of one of the Lake Malawi 'Chambo' speces, most likely *O. karongae*. We now feel that it is clearly a distinct species, possibly of hybrid origin. The following traits are distinctive: (i) males have never been found to develop the long branched genital tassel shown by chambo; (ii) females, juveniles and non-breeding males often show a uniformly dark body colour, or sometimes show a series of midlateral blotches, in contrast to the silvery body with dark vertical bars of chambo; (iii) the bower is a simple pit and lacks the central raised platform of fine sediment produced by chambo; (iv) in the aquarium, large males develop enlarged jaws more typical of *O. shiranus* than a chambo species; (v) aquarium specimens have not grown larger than 17cm SL, under conditions in which *O. karongae* has attained sizes of 30cm SL, suggesting a partly genetically-based smaller size at maturity; (vi) mitochondrial sequence analysis clustered *O. chungruruensis* with *O. shiranus* rather than the chambo, while microsatellite DNA indicated it was intermediate between the two groups (Shechonge 2013).

The occurrence of emaciated specimens in June-July suggests that at least some individuals are unable to recover at the end of the breeding season- such a semelparous breeding strategy has not previously been documented for cichlid fishes, although it is common in other fish groups, such as salmonids. Aquarium-held specimens have not become emaciated. Juveniles seem to be benthic feeders in shallow water, and are likely in competition with the substrate-spawning cichlids *Coptodon rendalli* and *Tilapia sparrmanii*, both of which are likely to have been stocked in the lake. All specimens labelled as *O. chungruruensis* (Ahl) were examined by GFT during a visited to the Museum für Naturkunde, Berlin: none appeared to be *Coptodon* or *Tilapia*. The Berlin collection contains no additional material from Lake Kyungululu deposited by Fülleborn (E. Aßel pers. comm.). It seems highly improbable that the collector would have missed specimens of these two species, which were extremely abundant in shallow waters in the 2010s, and so it seems most likely that they were stocked some time after 1899.

Coptodon rendalli (Fig. 118)

This large substrate-spawning cichlid was commonly seen in shallow water when snorkelling. Some of the specimens collected were large and appeared to be in good body condition.

Tilapia sparrmanii (Fig. 118)

Many small specimens of *T. sparrmanii* were observed from shallow waters down to depths of at least 10m. Pairs guarding eggs or wrigglers were seen on several occasions.

Figure 105. Lake Kyungululu, with the approximate location of the open beach marked as Site A.

Figure 106. Lake Kyungululu viewed from the playing field of a nearby school. The small accessible beach is directly opposite.

Figure 107. Lake Kyungululu. (left) The small accessible beach is steeply sloping, and rocky; (right) overgrown steep area of the crater wall**-** the height can be judged against the vehicle parked at the top.

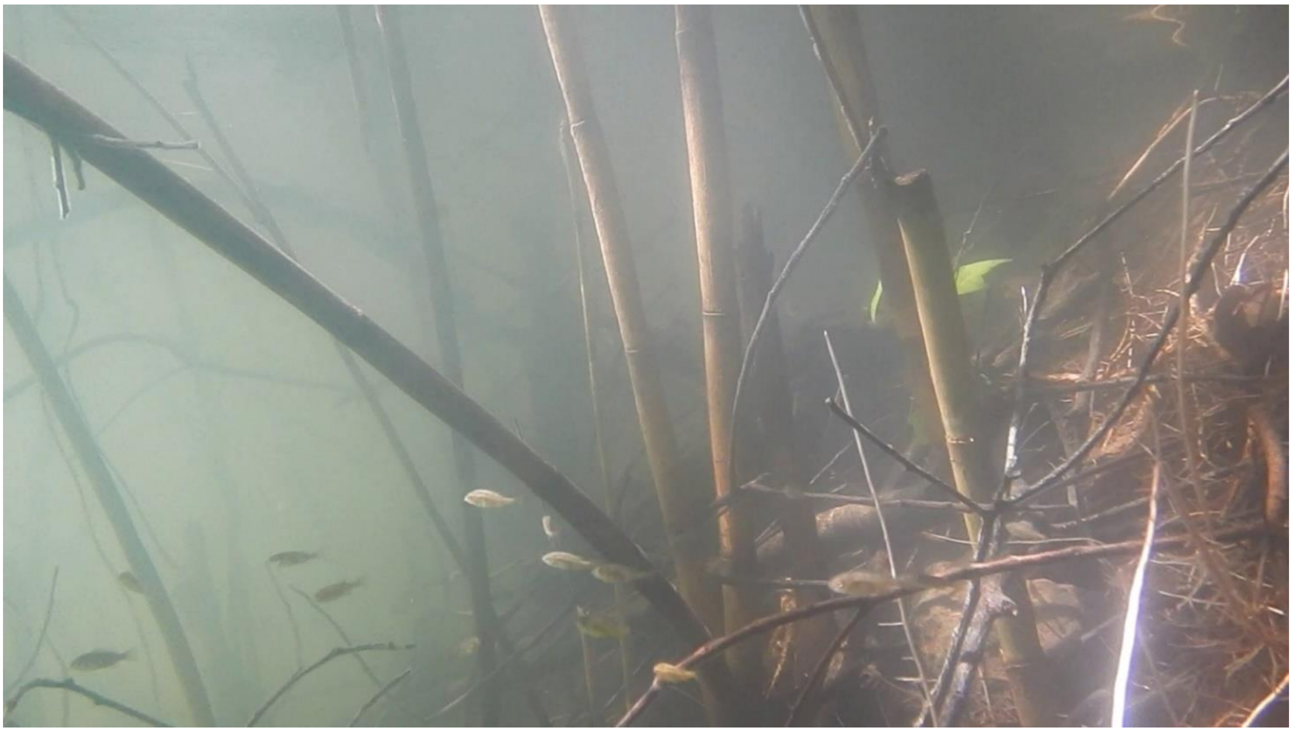

Figure 108. Lake Kyungululu: Juvenile *Oreochromis chungruruensis* among a patch of reeds.

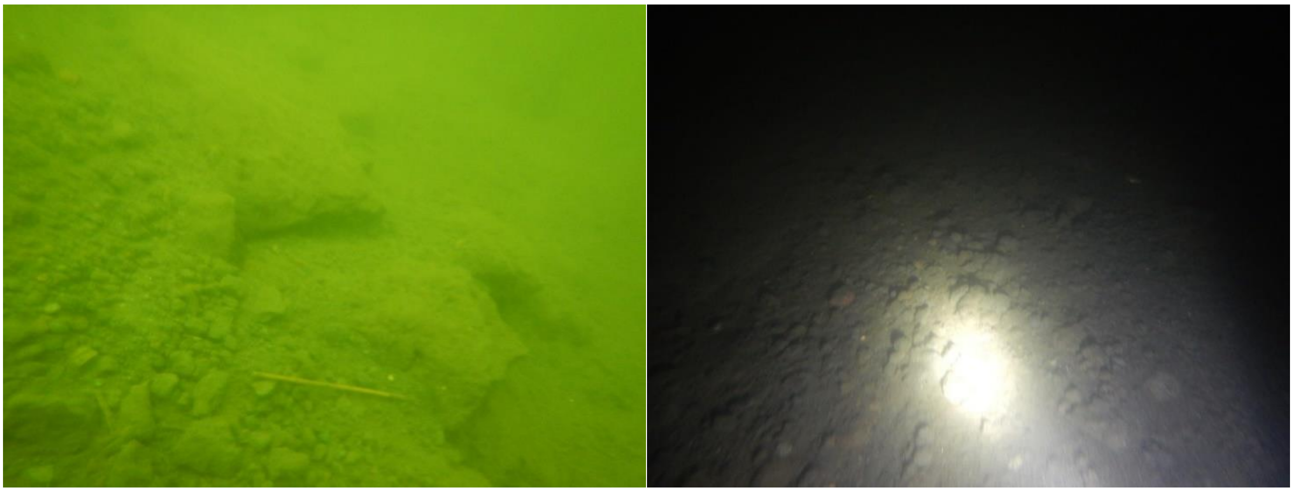

Figure 109. Lake Kyungululu: (left) crater wall at 3m, descending steeply; (right) at 20m depth, the crater wall is dark, barren and still descending steeply.

Figure 110. Lake Kyungululu: (left) large diving beetle (*Cybister cf. vicinus*) and (right) large crab, *Potamonautes montivagus* (Chace 1953).

Figure 111. Lake Kyungululu: adult male *Oreochromis chungruruensis* in breeding dress, November 2011.

Figure 112. Lake Kyungululu: *Oreochromis chungruruensis*: (left) adult in good body condition with undeveloped gonads (November 2011); (right) spent individuals (July 2011).

Figure 113. Lake Kyungululu. Emaciated adult *Oreochromis chungruruensis* in July 2011 (left) and June 2017 (right).

Figure 114. Lake Kyungululu: *Oreochromis chungruruensis* juveniles.

Figure 115. Lake Kyungululu: *Oreochromis chungruruensis* aquarium specimens: juvenile (left) and adult male (right)

Figure 116. Type specimens of *Oreochromis chungruruensis* (Ahl) at the Museum für Naturkunde, Berlin. (left) Holotype; (right) Paratype showing emaciation: such specimens were assigned to *Oreochromis lidole* by Trewavas (1983), erroneously in our view.

Figure 117. Specimens of *Oreochromis chungruruensis* (Ahl) at the Museum für Naturkunde, Berlin. (left) Adult male showing dark body colour and background midlateral melanic blotches; (right) juvenile non-type material, collected with the types.

Figure 118. Lake Kyungululu: (left) *Tilapia sparrmanii*; (right) *Coptodon rendalli*.

Lake Itende

(-9.322, 33.788)

Lake Itende lies high up to the east of the Mbaka River, at an elevation of 1027m. The lake has a peculiar shape with a rounded area on the eastern end, roughly 275m in diameter and an elongated ‘pan handle’ to the west, making the long axis of the lake about 540m. The lake is surrounded by very tall spiky reeds (*Phragmites*), and the open water is almost entirely filled with macrophytes: first rooted plants and then a deep layer of unrooted hornwort (*Ceratophyllum*). Over most of the lake, the hornwort layer comes up to the surface, leaving few open spaces where fish can be glimpsed at close range. In 2018, a small area of open water with a muddy bottom was found near the shore at Site C, with a bottom depth of less than 2m.

There is no close road access, even for 4WD vehicles. From the main Ipinda to Tukuyu road, there is a right turn just north of the market town of Mbambo: the road is steep and rough. Vehicles can be parked at the football field of the village of Msoso. The lake can be accessed by a hike, mostly uphill, of around 45 minutes, including a river crossing accomplished by wading or going over an exciting log bridge. There is a good view of Lake Ikapu on the left shortly before arriving in sight of Lake Itende. The only track to the open water of the lake (site C) involves a steep descent and (for an adult) crawling on all-fours under a patch of shrubs. In 2011, we used pangas (machetes) to cut a path through the *Phragmites* near the western end of the lake (site A), and this was still accessible in 2018, but access involves wading chest-deep through thick beds of macrophytes, followed by swimming through very resistant vegetation that reaches to the surface. It takes an additional hike of around 40 minutes to get to Site A, but there are spectacular views of Lake Masoko and the Mbaka River. Site B can be accessed via a reasonable cattle track, turning right as you arrive on the path from Msoso. Here, there is an open grassy area above a shallow pond which lies outside the ring of *Phragmites* that surrounds the main lake: fish from the lake can be collected here, along with a rich diversity of invertebrates, but the grasses in the pond are very sharp and bare arms and legs will receive numerous painful scratches. There is no access to the open water of the main lake. Site B is used for watering cattle and goats. Children have been seen to visit Sites B and C, possibly angling as well as bathing, but otherwise, it appears that no human use is made of the lake.

Physicochemical analyses were carried out in June 2018: giving electrical conductivity of 90-105.4 µS/cm, pH 7.5-8.7, TDS 65-77.5 mg/cm and temperatures of 22.2-25.4C. Dominant macrophytes included *Phragmites, Nymphaea caerulea* and *Ceratophyllum*, with smaller amounts of others including *Ammania* and *Urticularia*. Invertebrates were numerous and diverse in the pond at Site B, including dragonfly nymphs, dytiscid beetles and their larvae, as well as giant water bugs (Belostomatidae). Gastropods were numerous, including *Radix spp*. formerly *Lymnaea*, an intermediate host of *Fasciola*, a parasite of grazing mammals and occasionally humans, as well as *Bulinus*, an intermediate host of *Schistosoma*, a human parasite (Brown 1994).

Fish Fauna

The fish fauna was depauperate and appeared to consist of 2 mouthbrooding cichlid species.

Astatotilapia sp. ‘Itende’ (Figs 130-131)

Astatotilapia appeared to be easily the more numerous of the fish species, being found in all habitats surveyed. A pair of individuals were raised from fry brought to the aquarium at Bangor. Mature males and females had colouration typical of riverine/ Lake Malawi *Astatotilapia calliptera*. The male had a generally yellow breeding dress, with reddish upper part of the head, strong black head markings and iridescent blue lips. Eggspots were orange-yellow and arranged in single row. The female was sandy coloured, with horizontal melanin markings and thinner vertical markings on the flanks, with a yellow-orange anal fin and lower half of the caudal fin. A video of their spawning behaviour was made (youtube: cMnPB59wwy8).

Oreochromis spp. (Fig 132)

A single *Oreochromis* juvenile was collected in November 2011. The general body shape, predominantly vertical flank barring and count of 3 anal spines suggest that this is a ‘Chambo’ species rather than a population of *O. shiranus*. Other immature fish have been glimpsed underwater, but no males in breeding dress have been seen and so it is not possible to assign it to *O. karongae* or *O. squamipinnis*.

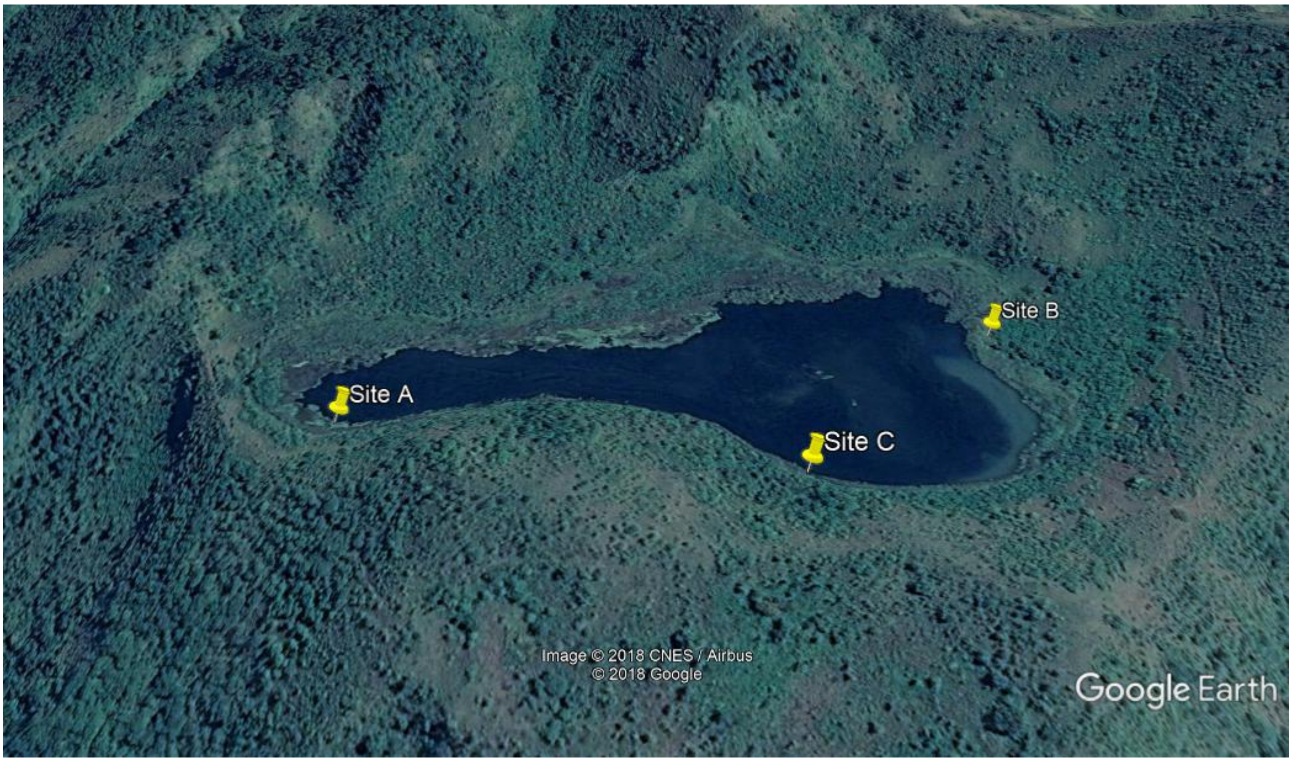

Figure 119. Lake Itende. The initial approach to the lake from Msoso is via the faint path on the far right of the image.

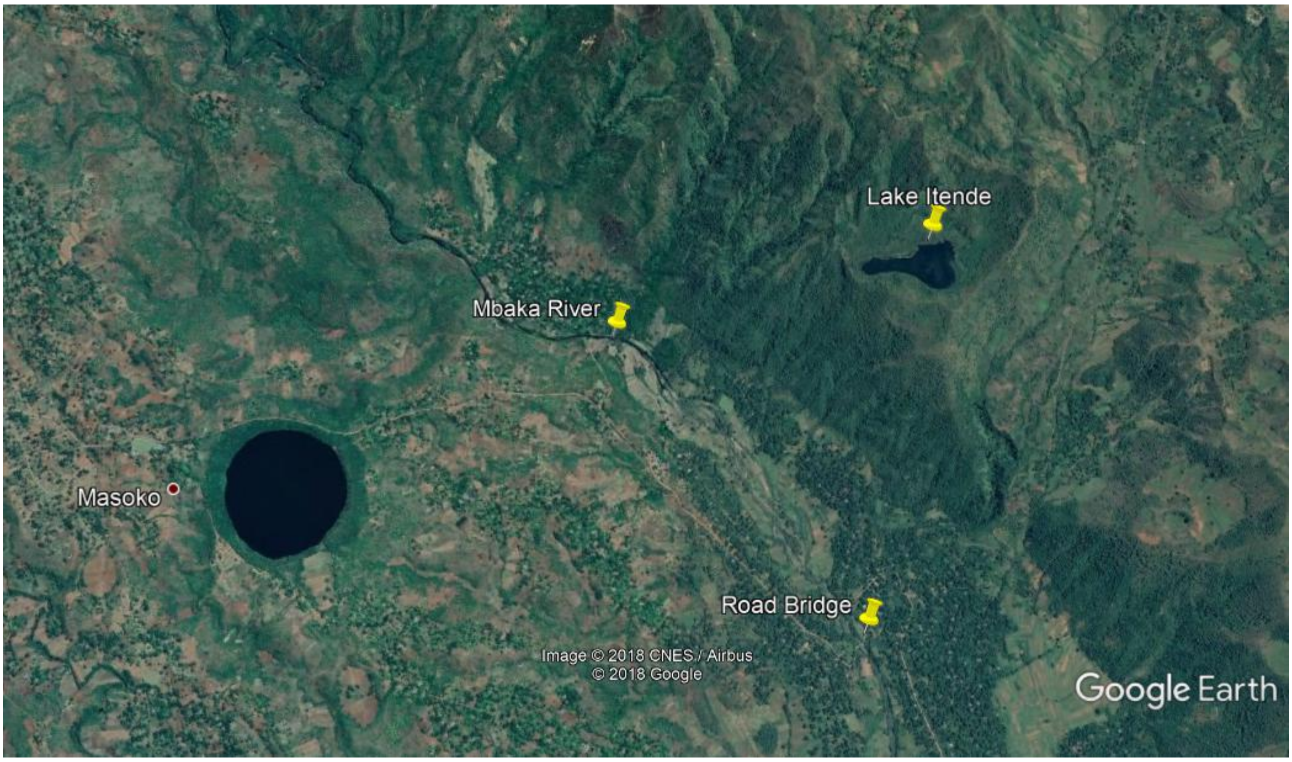

Figure 120. Location of Lake Itende relative to Lake Masoko and the Mbaka River. The stream closest to each lake is called the Itupi, although they each independently flow into the Mbaka River from opposite sides.

Figure 121. Lake Itende, viewed from the path at the eastern end.

Figure 122. Lake Itende (left) from the western end, near Site A; (right) the pool at Site B.

Figure 123. Lake Itende, open areas around site C.

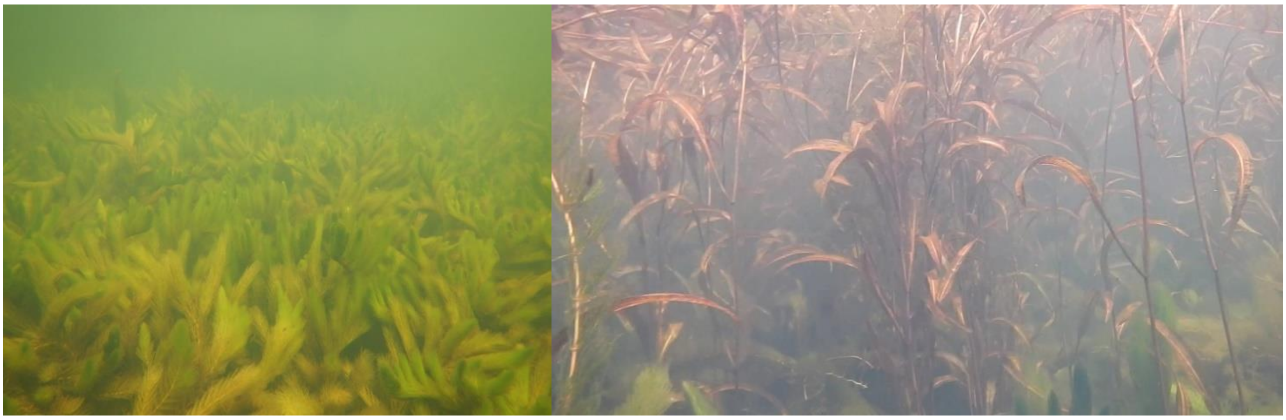

Figure 124. Lake Itende: (left) much of the bottom is carpeted with *Ceratophyllum*, with smaller patches of other species, such as *Ammania* near the shore (right).

Figure 125. Lake Itende: Dragonfly nymphs (odonata): (left) *Aeschna* spp.; (centre) *Anax* spp.; (right) libelulidae.

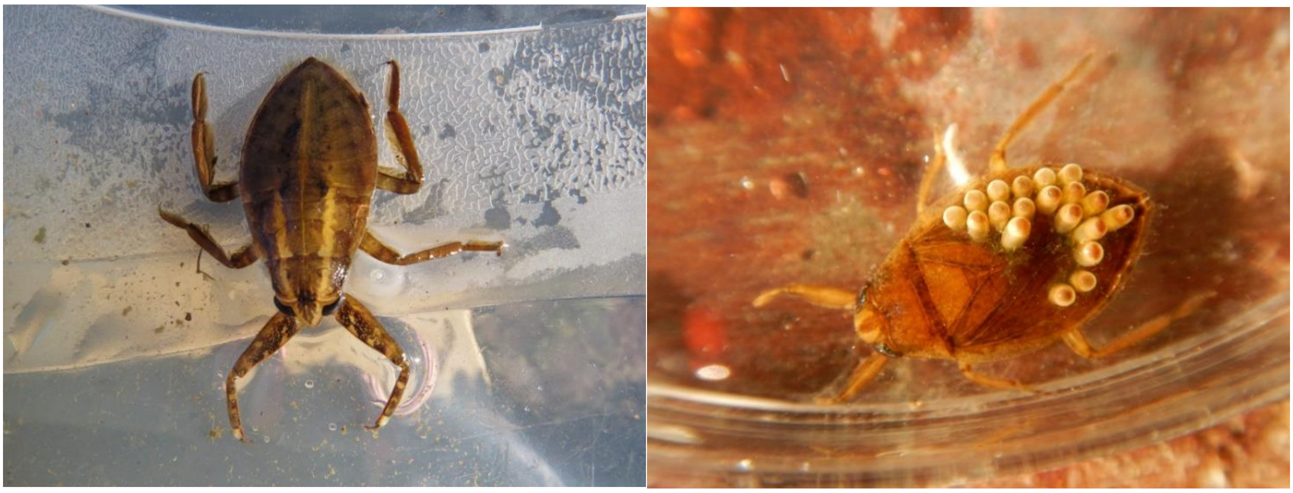

Figure 126. Lake Itende: Giant water bugs (belostomatidae): *Hydrocyrius* nymph; male *Appasus* with eggs.

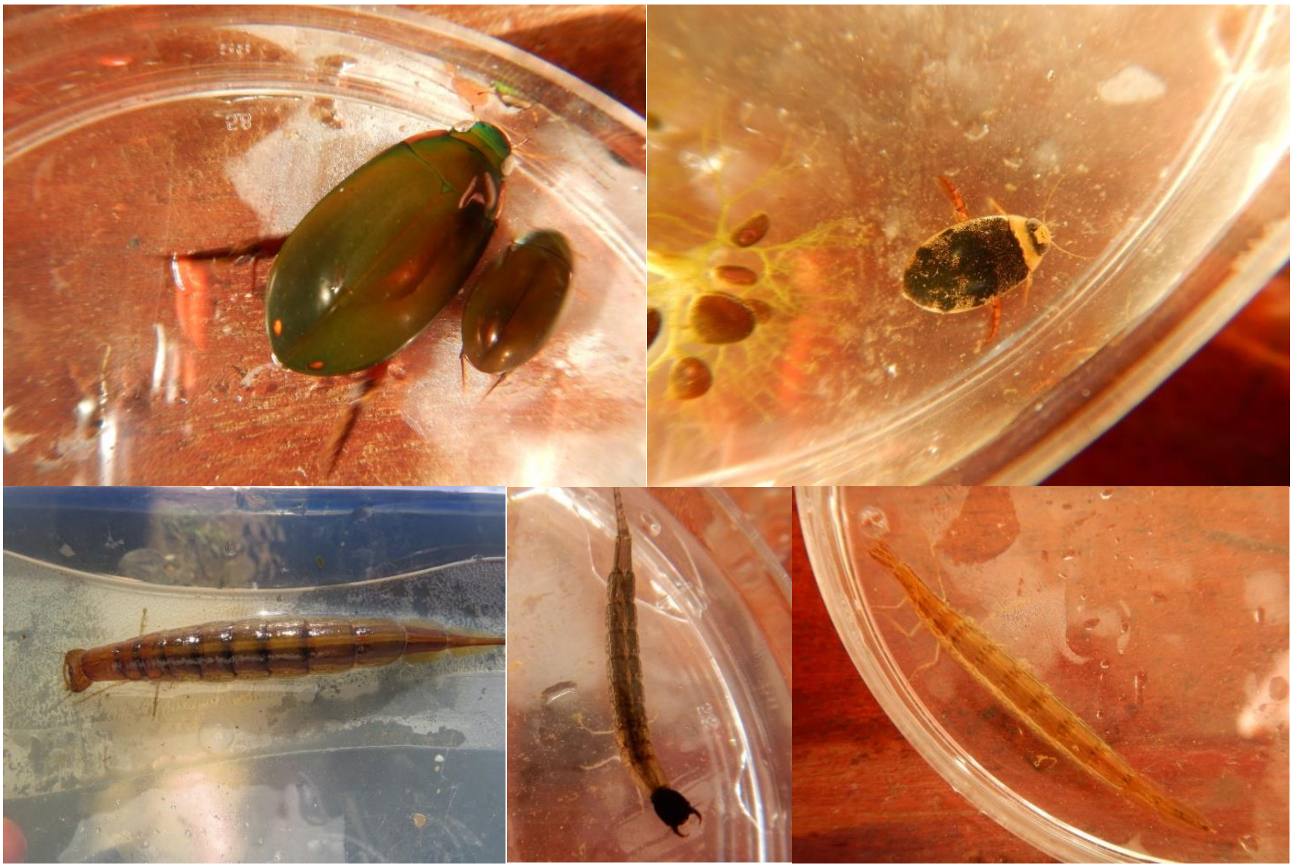

Figure 127. Lake Itende: dytiscid beetle adults and larvae: (Top left, larger individual) *Cybister cf. vulneratus.*

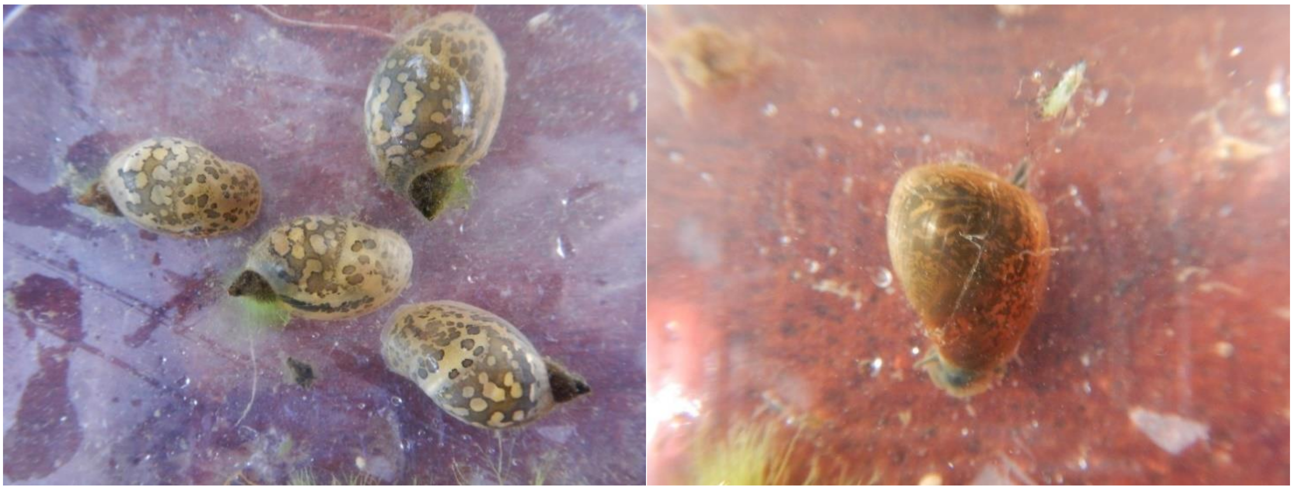

Figure 128. Lake Itende: Gastropods: *Radix* (formerly *Lymnaea) natalensis* (Krauss 1848) and *Bulinus* spp.

Figure 129. Lake Itende: *Astatotilapia* sp. ‘Itende’ among macrophytes.

Figure 130. *Astatotilapia* sp. 'Itende' in the aquarium: male (left) and female (right).

Figure 131. *Astatotilapia* sp. 'Itende' courting male (with female in background) in aquarium.

Figure 132. Lake Itende: *Oreochromis* spp. collected in November 2011. Dark spots on the pectoral fin and elsewhere appear to be digenic trematode cysts (Diplostomatidae), similar to *Crassiphiala* and *Uvulifer*. These have a complex life cycle involving snails, fish and birds (definitive host).

Lake Ngozi

(-9.175, 33.553)

Lake Ngozi is a huge lake (2.7 x 1.7km) in the caldera of Mount Ngozi, a volcano which has erupted as recently as 500 years ago. Mount Ngozi is publicised as a hike for adventurous tourists and guides can be hired from a booth at the turning off the main tarred road from the Malawi border to Mbeya. The ascent to the rim is over 300m in elevation. There is a rough track through dense rainforest suitable for a 4WD, but the majority of the ascent has to be on foot. The view from the crater rim is spectacular. The descent to the lake is over 120m and involves a lot of 'scrambling', which in this context often means lowering yourself down near vertical earthen descents by holding on to exposed tree roots. The lake surface is 2073m above sea level. The lake is reported to be 74m deep (Josephat 2016). There are no surface inlets or outlets. It is very saline with a TDS of 4490-5300 µS/cm, surface temperature of 19-21C and pH of 6.4-7.2 (Josephat 2016). The lake is believed to be fed by 3 submerged hot springs, bringing up liquids from deep in the mantle (Josephat 2016). The sulphur content of the water is high, and indeed a distinctly sulphurous odour could be noticed on arriving on the shoreline. On our visit in 2017, three snorkelers spent about 30 minutes in the water. Reeds and other emergent plants were observed, but no fully submerged macrophytes. Pondskaters (Gerridae) and a distant waterbird were seen on the surface, but the only animal seen underwater was a tiny dytiscid beetle- notably an airbreather capable of flight. It seems likely that the water is toxic to most aquatic life. It was reported that this almost completely inaccessible lake was stocked with Nile Tilapia in 2010, but there seems no reason to imagine that these have survived.

Figure 133. Lake Ngozi.

Figure 134. Lake Ngozi from the crater rim (left) and looking up from the lake at an unstable part of the crater wall (right).

Figure 135. Heavily vegetated trails leading to Lake Ngozi.

Figure 136. The shoreline of Lake Ngozi.

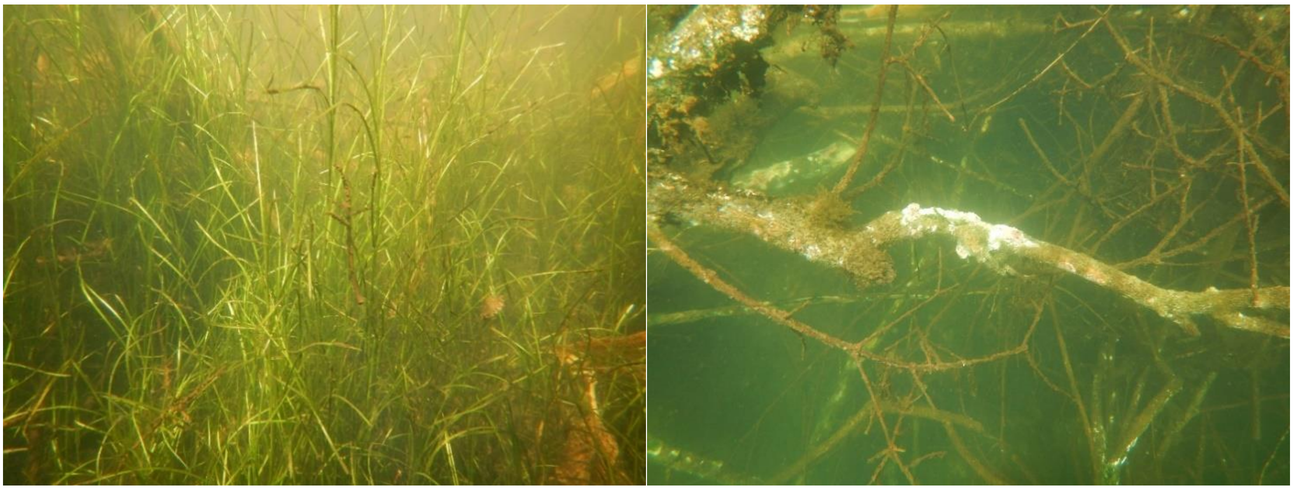

Figure 137. Lake Ngozi underwater: (left) submerged parts of emergent vegetation; (right) sunken branches covered with what appears to be fungal growth.

Lake Ndwati

(-9.049, 33.644)

Lake Ndwati is the most elevated of the crater lakes, at 2083m above sea level. It is largely marshland, although covering an area of about 500x400m. When visited in 2011, the water was extremely cold and no fish could be seen despite persistent attempts at snorkelling. It is thought that the lake may not contain water all year round. There are reports the lake had been stocked with *Clarias* catfish: this nocturnal species might not have been easy to see in the heavily vegetated areas visited, so it is not impossible that there are fish in the lake.

Figure 138. Lake Ndwati.

Kiwira River: Riverside Fish Farm

(-9.169, 33.559)

The Kiwira River is one of 3 major rivers running through the crater lake zone and emptying into Lake Malawi. It drains the area between Mt Ngozi and Mt Rungwe and passes to the West of the other crater lakes. We visited a fish farm near Kiwira Town, elevation 1366m. This large farm had been built on the Kipoke river, a tributary of the Kiwira, with numerous well-tended ponds, stocked with a variety of tilapia species: the farm manager said these were from Lake Malawi, local farm ponds, the Sokoine University of Agriculture and from Lake Victoria. Thus, many source populations were of species not native to the catchment. Species observed in culture included *Oreochromis niloticus* (invasive species not native to the catchment), an unidentifiable possible hybrid *Oreochromis*, *Coptodon rendalli* (native to the Malawi catchment) and probably *Coptodon zillii* (Gervais 1848), a species not native to Tanzania but likely to hybridise with *C. rendalli*. The farm made its own fish food, used hormone production to produce monosex fry and rotated breeders between hapas in ponds to attempt to minimise inbreeding. However, the owner reported that they had found relatively few outlets for the sale of fish beyond their own bar & restaurant and that the fish farm was unprofitable. Biosecurity was minimal. Drainage channels accommodated overflows from the ponds, and fed directly into the river, allowing for possible escape of fry of farmed species into the natural waters. At the time of visiting these channels housed large populations of *Astatotilapia cf calliptera* (presumably native), which probably consumed the majority of escaping fry. Non-native guppies, *Poecilia reticulata* (Peters 1859), were also extremely numerous. The river itself had been canalised for a long distance and an effort had been made to build a bathing pool, which had been rejected by local planning authorities. However, no authority had rejected the introduction of non-native fish species to the catchment of Lake Malawi. The farm also boasted accommodation, outdoor dining areas, and a well-outfitted bar.

Figure 139. The Riverside Fish Farm on the Kipoke River, a tributary of the Kiwira River.

Figure 140. Kiwira River: (Left) a canalised stretch of the Kipoke River flowing through the Riverside Fish Farm; (Right) a large aquaculture pond with nearby drainage ditch taking overflow from the pond into the river, which ultimately drains into Lake Malawi.

Figure 141. Kiwira River: *Astatotilapia cf calliptera* males (left) freshly caught and (right) post-mortem, showing range of colour and eggspots. All specimens observed had the rather short head and jaws typical of riverine *Astatotilapia* in the crater lake region.

Figure 142. Kiwira River: *Coptodon rendalli* (left) and *Coptodon zillii* from Riverside Fish Farm.

Figure 143: *Oreochromis niloticus* (left) and a possible hybrid *Oreochromis* (right) from Riverside Fish Farm.

Figure 144: Guppies, *Poecilia reticulata*, from the drainage channels at Riverside Fish Farm in 2017, representing the first known record of a non-African fish species breeding wild in the catchment of Lake Malawi.

Mbaka River System

The Mbaka River passes down through the crater lake region, east of Lake Masoko and west of Lakes Itende and Ikapu, discharging into Lake Malawi to the east of Kyela. The upper reaches of the river are shallow and rocky and supplied by tributaries, such as the (western) Itupi passing close to Lake Masoko. The lower reaches are deep and turbid, but seasonally have extensive floodplains, leaving pools populated by a diversity of fish species. Recent roadworks have been carried out to attempt to improve the roads in the floodplain and thus increase canalisation.

Itupi Stream

The (Western) Itupi stream is a small tributary of the Mbaka River. It arises a short distance north of the main Ipinda to Tukuyu Road, NW of Kisiba, passing through fields and homesteads. Augmented by several springs, it descends rapidly into a deep valley to the West of Lake Masoko and Kisiba school where it becomes progressively more overgrown by shrubs and trees. The channel thus varies in depth, water flow and cover. Many invertebrate species are found in the main channel, including dragonfly, damselfly and mayfly nymphs, fly larvae and crabs. Shallow weedy pools near the river accommodate dragonfly nymphs and dytiscid beetles. Fish collected in the faster flowing areas included hillstream catfish such as *Chiloglanis* and *Amphilius* spp. and the danionid *Opsaridium* spp. In slower flowing areas, the dominant species was *Astatotilapia calliptera*, with typical riverine yellow males. Occasional *Mastacembelus* spp. spiny eels were also found.

Figure 145. Itupi stream (left) passing through cultivated land near the main road; (right) a deeper section with grassy banks nearer to Lake Masoko.

Figure 146. Itupi Stream.

Figure 147. Itupi Stream: (left) Damselfly nymph (*Platycypha*); (right) Mayfly nymph.

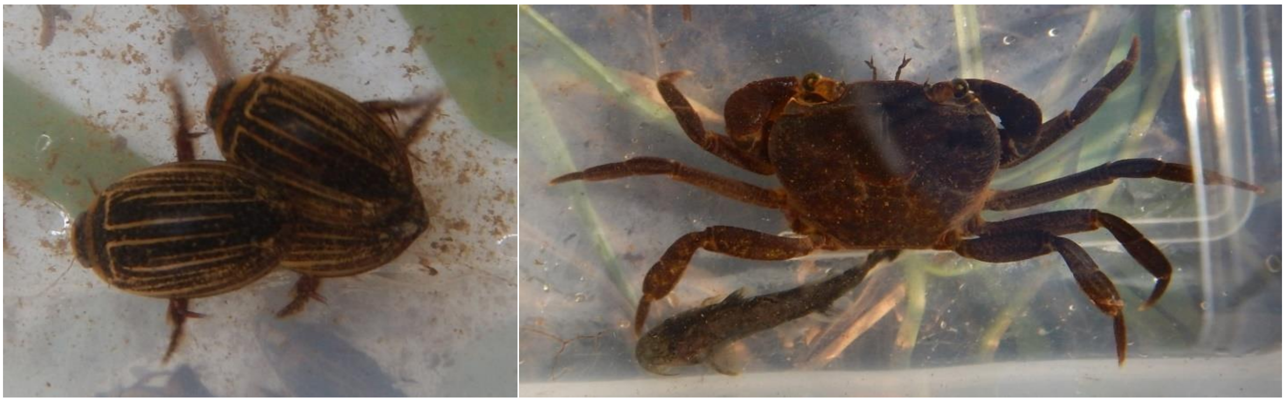

Figure 148. Itupi Stream: (left) Dytiscid beetles (*Hydaticus flavolineatus* Boheman 1848) from a pool at the edge of the stream; (right) a river crab *Potamonautes cf. montivagus*, with a small *Chiloglanis* catfish below.

Figure 149. Itupi Stream: *Astatotilapia calliptera* yellow male.

Figure 150. Itupi Stream: *Amphilius spp.*

Figure 151. Itupi Stream: Suckermouth Catfish. *Chiloglanis spp.*

Mbaka River - main channel between Lake Masoko and Mbamba

We sampled the Mbaka River in the vicinity of Lake Masoko, at a footbridge at -9.326, 33.771, at an elevation of 736m and also at the main road bridge at -9.340, 33.786, at an elevation of 711m. At the footbridge, the river was deep and lined with *Phragmites*, but at the roadbridge, the Mbaka was fast-flowing and rocky, with areas of white water, but with quiet pools at the margins. In the deep pools of the main river, crabs, odonate nymphs, fly larvae and belostomatid bugs were among the major invertebrates. Fish included mormyrids, danionids (*Opsaridium tweddleorum* and numerous small fry of indeterminate species) and cyprinids (*Enteromius kersteni, E. trimaculatus, Labeobarbus johnstonii* Boulenger 1907). Shallow springs near the main river contained numerous tadpoles, dytiscids, odonata nymphs and predatory bugs, along with many *Astatotilapia calliptera*: adult males exhibited the standard yellow breeding dress typical of riverine populations, and attained lengths of up to 105mm SL. Brooding females and juveniles were also collected in quieter pools near the roadbridge.

Figure 152. Mbaka River at the footbridge at -9.326, 33.771 (left) view from the footbridge; (right) a short distance upstream at the site of an old bridge.. The water was deep and turbid and the banks lined with *Phragmites*.

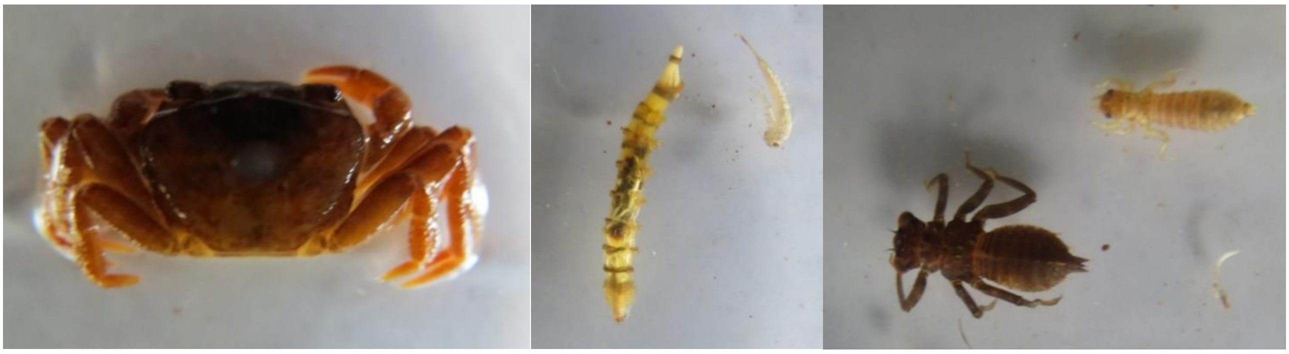

Figure 153. Mbaka River main channel upstream of the footbridge : (left) river crab (*Potamonautes*); (centre) fly larva and mayfly nymph (right) dragonfly nymphs.

Figure 154. Mbaka River main channel cypriniformes: (top left) *Labeobarbus johnstonii*; (top right) *Enteromius trimaculatus;* (bottom) *Opsaridium tweddleorum*: female above and mature male below. The white eyes are the result of these specimens having been placed in ethanol prior to being photographed.

Figure 155. Mbaka River, at the road bridge between Kisiba and Mbambo.

Figure 156. From the Mbaka River near the roadbridge: (top) *Astatotilapia calliptera* female; (bottom left) *Enteromius lineomaculatus* Boulenger 1903; (bottom right) *Enteromius kersteni*.

Figure 157. Mbaka River: large tadpole.

Mbaka River: Lower Reaches.

The lower reach of the Mbaka near Kyela is a deep, turbid fast-flowing permanent river, but during the rainy season major floods were common over a wide area. During the dry season, the floodplain was crossed by numerous shallow streams, some canalised in areas of rice production. Amongst these were scattered deep pools, sometimes the result of road-building activities. Emergent vegetation was common, including major stands of *Phragmites*. Angling by children was commonly seen and occasional fish fences were constructed to attempt to channel migratory fish into wicker fish traps. The main Kyela to Ipinda Road crosses the Mbaka River at -9.543, 33.888, which is approximately 7 km from Lake Malawi at an elevation of 496 m, only 19 m higher than the level of the lake and with no obvious barriers like cataracts or weirs. Despite this, surveys of pools near the main road yielded a typical riverine fauna, dominated by cyprinids. No Lake Malawi endemic haplochromines were recorded, and no *Oreochromis (Nyasalapia)* spp., despite their abundance in the crater lakes. However, samples included many individuals of *Pseudocrenilabrus philander* and a few *Tilapia sparrmanii*. Neither species has been recorded from Lake Malawi itself, although both have been found in rivers and satellite lakes near Nkhotakota. Other cichlids found included *Astatotilapia calliptera* and *Oreochromis shiranus*.

Figure 158. Lower Mbaka River: (left) Pool on a tributary of the Mbaka River near Kyela; (right) male *Pseudocrenilabrus philander*.

Figure 159. A diverse catch from a pool on the Mbaka floodplain, including *Astatotilapia calliptera, Pseudocrenilabrus philander, Oreochromis shiranus, Micropanchax johnstoni, Enteromius arcislongae* (Keilhack 1908) (most abundant), *Enteromius bifrenatus* (Fowler 1935), *Enteromius haasianus* (David 1936), *E. kersteni, E. paludinosus, Enteromius radiatus* (Peters 1853), and a characin, perhaps *Hemigrammopetersius barnardi*.

Figure 160. Sampling deep pools in the Mbaka floodplain, near the Kyela-Ipinda Road.

Figure 161. Lower Mbaka River: (left) *Tilapia sparrmanii*; (right) *Oreochromis shiranus*.

Figure 162. Lower Mbaka: (top left) *Brycinus imberi*; (top right) *Marcusenius* spp.; (bottom left) *Enteromius paludinosus*; (bottom right) *Enteromius trimaculatus*.

Figure 163. Lower Mbaka River: (top left) *Enteromius radiatus;* (top right) *Enteromius arcislongae*; (bottom left) *Enteromius haasianus;* (bottom right) *Enteromius* spp.

Kalambo Hot Springs (-9.551, 33.80)

The Kalambo Hot Springs lies about 9.5km NW of Kyela, not far from the main Kyela-Tukuyu Road. They lie at an elevation of approximately 575m, which is about 100m higher than Lake Malawi, which is about 16.6 km away. We visited the site on 18 August 2015, opportunistically and lacking most sampling equipment. At the time of visiting, the springs emerged at several locations, and felt hot to the touch. They ran as narrow streams across an open muddy area, and not far downstream of the emerging springwater, small cichlids were seen. These were skittish and we were unable to catch any. Further downstream, the water accumulated in a large deeper pool, with waterlilies and fringing emergent vegetation, including *Phragmites*. The use of small hand nets on marginal vegetation yielded a number of cichlid fishes, including *Astatotilapia calliptera* (typical riverine yellow males) and *Pseudocrenilabrus philander*. It seems this pool drains into a stream which runs north and east to join the Mbaka River, rather than south to the closer Kiwira system.

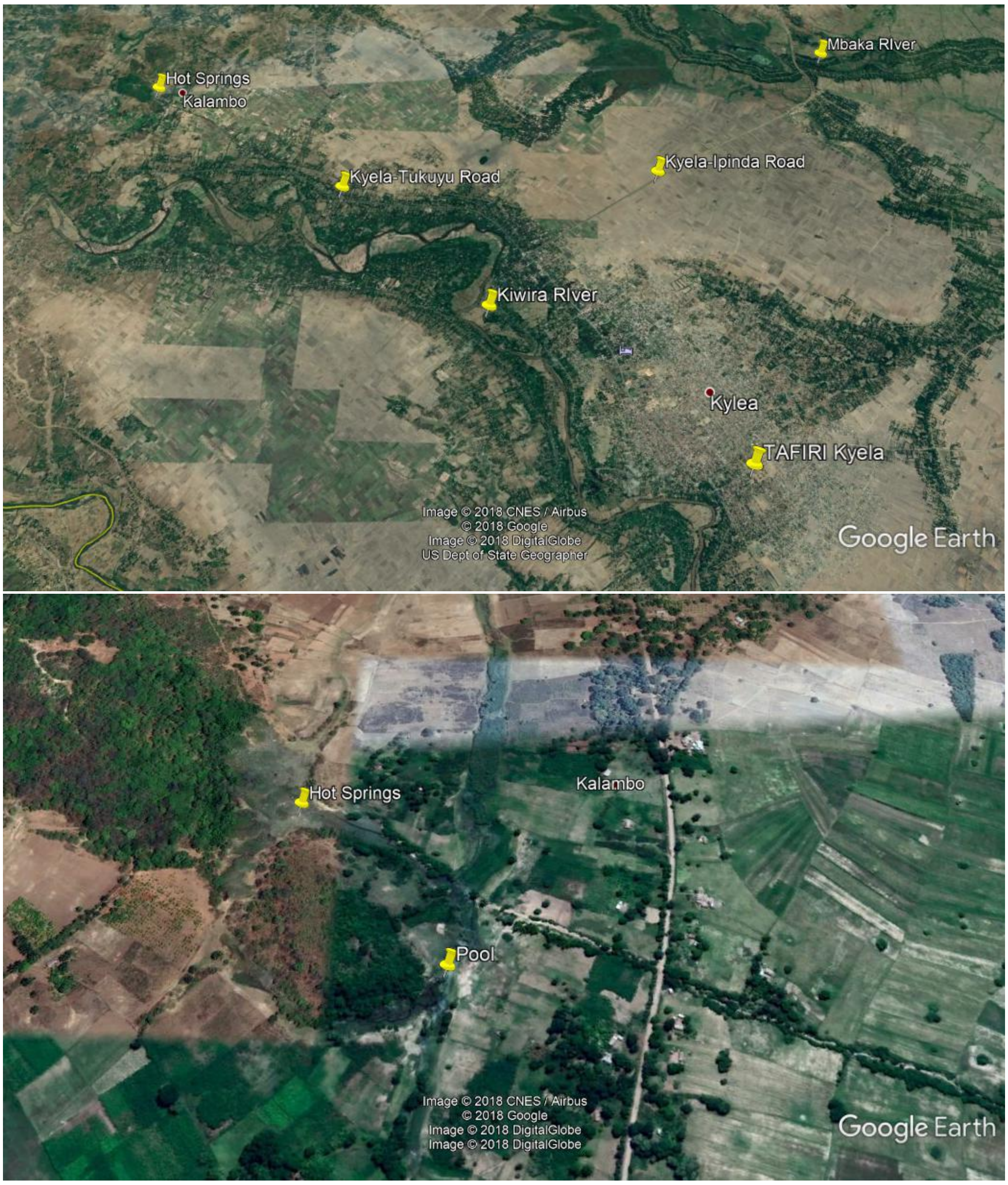

Figure 164. (Above) Location of Kalambo Hot Springs, between the Kiwira and Mbaka Rivers, just north-west of Kyela (erroneously marked as Kylea on Google Earth); (below) Kalambo Hot Springs, illustrating the main area of springs and the deep pool.

Figure 165. Kalambo Hot Springs: (top left) view of a source springs; (top right) brown coloration suggesting extremophile micro-organisms; (bottom left) shallow open stream reaches containing cichlid fishes; (bottom right) deeper vegetated pools were larger cichlid specimens were obtained with handnets.

Mguwisi River System

The Mguwisi River flows to the East of the Mbaka. It is a tributary of the Lufilyo River which discharges into Lake Malawi about 4.5km NE of the mouth of the Mbaka (at -9.519, 33.985). In relation to the evolution of the cichlids of the crater lakes, a significant feature of the Mguwisi is that one of its tributaries is the outflow of Lake Ilamba: although the Mguwisi passes very close to Lake Ilamba, the outflowing Ilamba stream does not join it until about 2.8 km away, just north of Lake Kingiri. A key imperative of sampling was to study the relationships between the river fauna, in particular the *Astatotilapia*, and that of the neighbouring lakes. We focussed on three sites spread over a distance of ~4km (Figure 166).

Mguwisi Site 1 was in the vicinity of the roadbridge on the track from the Ipinda-Tukuyu Road in the direction of Lake Ilamba (Figure 167): -9.395, 33.827; elevation 568m. This site was visited in July 2011, June 2017 and July 2018. The river was about 4m wide and comprised shallow riffles with smooth cobbles interspersed with deep pools with muddy bottoms and shallow muddy backwaters. In places, there was considerable overhanging vegetation (*Phragmites* or terrestrial plants) and substantially undercut banks. Much of the river was shaded by trees and bamboo. A small shallow tributary joined the main channel just upstream from the bridge. Invertebrates were numerous, including crabs and shrimps, damselfly and dragonfly nymphs (odonata). Tadpoles were common and several adult clawed frogs (*Xenopus* spp.) were caught. Of the fish species, *Chiloglanis* spp. was abundant, particularly in the small tributary and riffle areas. Cyprinids included juvenile *Labeobarbus johnstonii*. A shallow muddy backwater with floating bamboo poles contained a high density of small *Astatotilapia* spp., while an area under an overhanging thicket of branches was a hotspot for mouthbrooding females. No mature males were collected on any of the visits, but immature fish returned to the aquarium at Bangor developed into typical riverine yellow male *Astatotilapia calliptera* (Figure 168).

Mguwisi 2 was a pool at the base of a natural waterfall a little downstream from the roadbridge (Figure 168: -9.400, 38.829; elevation 564m), visited in June 2017. The pool was deep (~2m) with a sandy bank and several large boulders. Fish collected were all cypriniformes: *Enteromius paludinosus* and *Opsaridium microcephalum* (Günther 1894) and *O. tweddleorum* (Figure 169). No fish at all were found in the area just downstream of the pool.

Mguwisi 3 was around the roadbridge on the track from Kingili to Itete (Figure 170; -9.414, 33.858; elevation 520m), visited in July 2011 and June 2017. This site is downstream of the junction of the Ilamba stream and the main Mguwisi channel. *Astatotilapia* collected here included some large males that looked like they would probably be yellow when fully coloured.

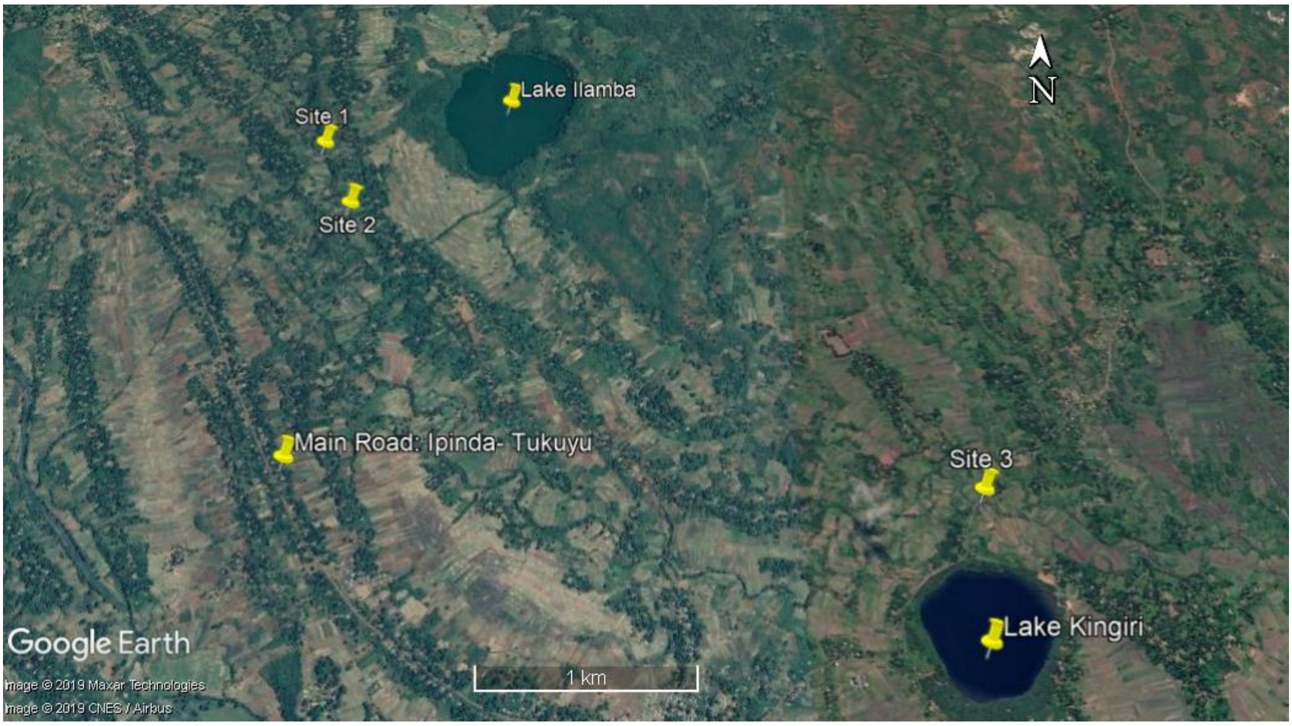

Figure 166. Mguwisi River sampling sites.

Figure 167. Mguwisi River Site 1, at road bridge near Lake Ilamba: (left) main channel; (right) inflowing tributary.

Figure 168. Mguwisi River Site 1: (top) *Astatotilapia cf calliptera* yellow male and females in aquarium; (middle) *Astatotilapia cf calliptera* brooding female; (bottom left) *Labeobarbus johnstonii*; (bottom right) *Chiloglanis* spp.

Figure 169. Mguwisi River Site 2, near Lake Ilamba: (left) footbridge and weir, (right) natural waterfall.

Figure 170. Mguwisi River Site 2, pool below waterfall: (top) mature sanjika, *Opsaridium microcephalum*; (bottom left) *Opsaridium tweddleorum;* (bottom right) *Enteromius paludinosus*.

Figure 171. Mguwisi River Site 3, near Lake Kingiri: (left) habitat; (right) male *Astatotilapia cf calliptera*.

Discussion

Overview of the Satellite Lake Fish Faunas

Lake Malawi's satellite lakes have proved to be surprisingly diverse in their physical and chemical composition, with depths ranging from less than 3m (Itende) to around 40m (Kyungululu). Most are inhabited by fish, and most of these seem to be native to the lakes. Overall, they are collectively home to a large number of fish species. Furthermore, many of these appear to be unique and represent evolutionarily significant units that would almost certainly merit recognition as full species in a better-studied system. This represents a marked advance on previous knowledge, given that that prior to our visits beginning in 2004, the only unique population known was *Oreochromis chungruruensis* which itself had never been studied in the field since the original collection in the 1800s.

The satellite lake faunas show a remarkable contrast with the faunas of neighbouring river systems, particularly in the dominance of cichlid fishes. Only the three lakes at the lowest elevation (Chilingali, Kingiri and Ilamba) were found to contain cyprinid fish, which are dominant in most riverine habitats. All three of these lakes also contained populations of Lake Malawi endemic haplochromine genera (*Lethrinops, Otopharynx, Rhamphochromis*). This suggests that these lakes may have been colonised directly from Lake Malawi at higher lake level stands.

Strikingly, all of the lakes contained *Oreochromis (Nyasalapia)* of the 'chambo' complex endemic to the Lake Malawi catchment. We did not find a single specimen of chambo in any of the river systems we sampled, although they are abundant in the main lake. Furthermore, we found *Oreochromis (Oreochromis) shiranus* in most lakes, yet this species only occurred in our samples from the floodplain areas far downstream from the crater lakes.

Satellite Lake Endemics

During the surveys of the Lake Malawi satellite lakes, 11 distinctive cichlid taxa were identified, four of which were found in more than one lake. Should these phenotypically similar forms in different lakes be independently derived, then the total number of evolutionarily significant units would be at least 18.

Direct tests of assortative mating have been carried out with *Rhamphochromis* sp. 'chilingali' v *R. longiceps* (Genner *et al.* 2007) and *Lethrinops* sp. 'chilingali' v *L. lethrinus* (Tyers *et al.* 2014). Both studies revealed a high level of assortative mating, consistent with biological species status for the satellite lake taxa. However, a similar trial with *Astatotilapia* from Lake Chilingali v Senga Bay (from a swamp near Lake Malawi) did not show significant assortative mating (Tyers & Turner 2013). Notably, in the latter test, the male breeding dress of the two populations was very similar, and a reasonably high level of assortative mating was shown against a population from Chisumulu Island within Lake Malawi where the males were blue rather than yellow (Tyers & Turner 2013). Thus, as a rule of thumb, we have assumed that it is appropriate to grant species status to satellite lake populations of cichlids of Malawian endemic haplochromine genera and to populations of *Astatotilapia* with strongly divergent male breeding colours. On that basis, we would conservatively identify the following 7 taxa as satellite lake endemic haplochromine species: *Astatotilapia* sp. 'masoko' (because of the blue deepwater ecomorph), *Astatotilapia* sp. 'black' (populations in the Mguwisi lakes: Kingiri, Ilamba, Itamba & Ikapu), *Lethrinops* sp. 'chilingali', *Otopharynx* sp.

‘tetrastigma Ilamba’, *Rhamphochromis* sp. ‘chilingali’, *R.* sp. ‘kingiri dwarf’ and *R.* sp. ‘kingiri large’.

Table 7. Candidate Endemic Species and Evolutionarily Significant Units from Malawi’s Satellite Lakes.

Taxon	Lake(s)	Distinctive traits
Astatotilapia sp. ‘kingiri’/ ‘ilamba’	Lake Kingiri, Ilamba	Black Males
Astatotilapia sp. ‘ikapu’/ ‘itamba’	Lake Ikapu, Itamba	Dark Males
Astatotilapia sp. ‘masoko’	Lake Masoko	Deep-water adapted Benthics/ Blue Males (as well as Yellow)
Lethrinops sp.’chilingali’	Lake Chilingali	Assortative mating, morphological & colour differences
Oreochromis chungruruensis	Lake Kyungululu	Morphology, colour, bower form
Oreochromis cf. shiranus	Lakes Kingiri, Ikapu, Ilamba, Itamba	Polymorphism in anal spine count
Oreochromis cf. squamipinnis	Lakes Ilamba, Masoko, Itamba?	Small size at maturity & ‘hunger form’
Otopharynx cf. tetrastigma	Lake Ilamba	Genetics indicating hybrid origins
Rhamphochromis sp. ‘chilingali’	Lake Chilingali	Small size, assortative mating
Rhamphochromis sp ‘kingiri dwarf’	Lake Kingiri	Small size, anal fin markings
Rhamphochromis sp. ‘kingiri large’	Lake Kingiri	Large size v sympatric congener

The situation with *Oreochromis* is more problematic, as no assortative mating trials have been reported. *Oreochromis chungruruensis* seems to be clearly distinct, exhibiting a mosaic of traits typical of the ‘chambo’ group (*O. karongae, O. squamipinnis* and the probably extinct *O. lidole*) and *O. shiranus*. The black breeding dress is common to *O. shiranus* and *O. karongae*, but of these two, the white fin margins, wide head and possession of 3 anal fin spines are consistent only with *O. karongae*, while the enlarged mouth of the larger breeding males, simple bower and lack of elongated genital tassel are consistent only with *O. shiranus*. However, the breeding male’s genital papilla is not the simple conical structure seen in *O. shiranus*, but can be comprised of several lobes and branches (Trewavas 1983). Contrary to suggestions based on morphology, both nuclear and mitochondrial DNA analyses place the Lake Malawi *Oreochromis (Nyasalapia)* ‘chambo’ group (which includes *O. karongae*) as close to a group containing *Oreochromis shiranus* and *O. placidus ruvumae*, with *O. chungruruensis* not clearly resolved into either group (Ford *et al.* 2019). It is possible that *O. chungruruensis* is a taxon of hybrid origin.

The *Oreochromis (Nyasalapia)* ‘chambo’ populations in the crater lakes can generally be assigned to one of two species from Lake Malawi: *Oreochromis karongae* or *O. squamipinnis*, based on male breeding dress. Blue-headed *O. squampinnis*-types are found in Lakes Kingiri, Ilamba and Masoko, but all-black *O. karongae*-types in Lakes Ikapu and Itamba, although in the latter case there may also be some *O. squamipinnis*-types or intermediates. To date, there are no records of the male breeding dress of the Lake Itende chambo.

In contrast to Trewavas (1983), we do not assign any crater lake populations to *Oreochromis lidole* (Trewavas 1941). This species, which was once abundant in southern Lake Malawi but has not been seen alive since 2004, was a specialised offshore planktivorous form, which was seldom encountered in shallow muddy habitats (Trewavas 1983). The morphological similarities of the ‘hunger forms’ of *O. chungruruensis* and other crater lake chambo populations (big-headed appearance, reduced oral and pharyngeal dentition) are unlikely to be indicative of recent common ancestry. Trewavas (1983) was unaware of other key features of the crater lake taxa that distinguish them from *O. lidole,* such as the blue-headed breeding dress of the males of the populations in Lakes Kingiri and Masoko (*O. lidole* males were all-black) or the lack of elongated genital tassels in *O. chungruruensis*.

Among the crater lake chambo populations, two phenotypic traits differentiate many of them from the Lake Malawi populations. Firstly, many of the populations exhibit a much smaller size at maturity, undergoing a transition of body proportions to a bony big-headed ‘hunger form’. A single mature male from Lake Masoko has maintained this form for many years in captivity, suggesting a genetic basis to this trait. Secondly, the females and juveniles of many populations exhibit a bright golden body colour with irregular slender bars, whereas those from Lake Malawi are generally silvery-grey with wide bars or sometimes dull brownish with faint bars, the latter particularly in *O. karongae* (Turner 1996). Exceptions to this are the Lake Kingiri and Lake Chilingali *O. squamipinnis* populations, where mature adults appeared to attain relatively large sizes and had a robust well-fed appearance: females and juveniles are silvery grey, like in Lake Malawi. These two lakes are the ones at the lowest altitudes of all the studied satellite lakes and have diverse faunas including cyprinids and species of the Lake Malawi endemic genus *Rhamphochromis* and in the case of Chilingali, *Lethrinops*. It is not surprising then that the populations of *O. squamipinnis* might be less differentiated from those of Lake Malawi. For the other crater lake populations, there might be grounds for considering them to represent distinct ‘crater lake’ species or subspecies of *O. karongae* and *O. squamipinnis*. It is unclear whether the derived traits of the crater lake populations arose independently in each lake, or whether they evolved once in an ancestor that may have inhabited the rivers in the area prior to colonisation of the craters. It is hard to judge this, as so far no riverine populations of chambo have been detected in the area. To avoid over-proliferation of names, we would tentatively suggest recognising single crater lake endemics of each male colour form.

The crater lake populations of *Oreochromis cf. shiranus* might also warrant formal taxonomic recognition. At present, the taxonomy of this group is confused, but the most obvious comparison would be with the Lake Malawi population of *O. shiranus,* currently placed in the nominate subspecies, *O. shiranus shiranus*. Mature male *O. s. shiranus* exhibit a number of characteristic traits, including a black breeding dress, with orange to red dorsal and caudal fin margins, a simple unbranched white genital papilla, narrow head with enlarged jaws and a concave head profile. Males build bowers in the form of a simple pit without the raised central platform produced by the ‘chambo’. Females and juvenile have a golden-yellow body colour with brownish horizontal bands on the flanks. Currently, a distinct subspecies is recognised from Lake Chilwa: *O. shiranus chilwae* has silvery-coloured females and immatures (Trewavas 1983), and males have extensive patches of white scales on their flanks (G.F.Turner pers. obs.). However, Lake Chilwa is about 650km away from the Tanzanian crater lakes and the distinctive colouration of both sexes has not been reported in the crater lake populations.

In the field, a very useful diagnostic trait is the anal fin spine count, which is generally 4 in *O. shiranus* species and 3 in all the other cichlid fishes of Lake Malawi (Trewavas 1983, Turner 1996). There are a few reports of 3-spined *O. shiranus*, but at very low frequency in natural populations (see Trewavas 1983). By contrast, the frequency of 3-spined individuals seems relatively high in the populations in Lakes Ilamba and Itamba (Table 8). Perhaps this might justify recognition of subspecific status? Certainly, these populations seem more distinct than those from the Rovuma, which are presently classed as belonging to *O. placidus ruvumae*. The explanation for anal spine variation in the higher altitude crater lakes is unclear. Typically, this trait seems relatively invariant within species and populations of *Oreochromis*, often providing a good diagnostic trait (Trewavas 1983). Within Kenya, populations with variable spine counts are suggested to be hybrids between the upstream 4-5 spined *O. spilurus niger* (Günther 1894) with the downstream 3-spined *O. spilurus spilurus* (Günther 1894) (Trewavas 1983). Could hybridization also explain variation in crater lake populations? Notably all lakes containing *O. shiranus* also contain *Oreochromis* of the 'chambo' group that generally have 3 anal spines. Perhaps the lower altitude lakes, such as Kingiri and Chilingali are less isolated and have been subject to gene flow from nearby Lake Malawi or river populations, leading to greater genetic similarity. The populations in the higher altitude lakes may reflect a history of introgression, perhaps during past periods of population contraction following founding or environmental pressures such as lake level falls. Genomic analysis could shed light on these issues.

To date, we have not noticed any features that would suggest unique satellite lake diversity among substrate-spawning cichlids (*Tilapia, Coptodon*) nor fishes of other families. It is not clear whether this represents the lower diversification tendencies of these taxa, their confinement to relatively low altitude lakes (apart from possible cases of stocking) or the interest and expertise of researchers.

Table 8. Comparison of Diagnostic Traits of Populations of *O. shiranus* and Related Species.

Location	Male Colour	Male Jaws	Female Colour	Anal Spines	Current Classification
L. Malawi	Black	Enlarged	Golden	Usually 4	*O. shiranus shiranus*[1]
L. Chilwa	Black with white patches	Enlarged	Silvery	Usually 4	*O. shiranus chilwae*[1]
Ruvuma	Black	Enlarged	Golden	Usually 4	*O. placidus ruvumae*[1]
L. Chilingali	Black	Enlarged	Golden	4	*O. shiranus shiranus*
L. Kingiri	Black	??	Golden	6% 3; 94% 4 (N=18)	*O. shiranus shiranus*
L. Ilamba	Black	??	??	60% 3; 40% 4 (N=10)	*O. cf shiranus*
L. Ikapu	Black	??	Golden	36% 3; 64% 4 (N=11)	*O. cf shiranus*
L. Itamba	Black	Enlarged	Grey-Brown	60% 3; 40% 4 (N=10)	*O. cf shiranus*

1. From Trewavas 1983

Origin and Affinities of the Fish Faunas.

We found clear evidence of introductions of non-native fish species in the form of the Nile Tilapia (*Oreochromis niloticus*) collected in Lake Itamba in 2011, and several non-native species found in the fish farm on the Kiwira River, including Nile Tilapia, *Coptodon zillii* and guppies (*Poecilia reticulata*). Apart from the guppies, whose origins are unclear, all of these introductions appear to have been carried out in the 21st Century and none appear to have become established in the wild.

All of the other fish species collected in these lakes have affinities to taxa known from the Lake Malawi catchment. Three other species do not seem to be closely related to anything found in Lake Malawi itself: *Engraulicypris cf. ngalala*, *Pseudocrenilabrus philander* and *Tilapia sparrmanii*. However, both *P. philander* and *T. sparrmanii* are known from the inflowing rivers around Kyela area north of Lake Malawi, as well as near Nkhotakota (Tweddle *et al.* 1979): just where the satellite lakes occur. Seegers (1995, 1996) also reported a species of *Mesobola* (now considered a junior synonym of *Engraulicypris*: Riddin *et al.* 2016) from the area between Ipinda and Kyela. This seems likely to be in the Mbaka River. So, all three species appear to be native to the catchment, even though they do not seem to be established in Lake Malawi. All the other species seem to be native to Lake Malawi, or else plausibly endemic sister taxa to them.

However, just because they are native to the catchment need not necessarily mean that they are all native to the lake where they are currently found. There is good circumstantial evidence that neither *Coptodon rendalli* nor *Tilapia sparrmanii* were present in Lake Kyungululu in the 19th Century when the types of *Oreochromis chungruruensis* were collected. Other introductions seem possible, but the presence of clearly unique cichlid phenotypes indicates that many populations are naturally occurring.

How do fish get into isolated lakes? A recent review by Hisrch *et al.* (2018) indicated that many people believe that fish eggs are commonly transported accidentally by birds, but that in fact there is little evidence for this. Moreover, the majority of the Malawi satellite lakes are populated by mouthbrooding cichlid fishes, which do not leave adhesive eggs lying around on the bottom. Species with demersal eggs, such as cyprinids would be better candidates for this kind of dispersal, but they are under-represented in lakes compared to rivers. Another possibility mentioned by respondents to Hirsch *et al.* was of ‘fish rain’ where tornadoes or water spouts carry fish across land and there is at least one plausible-sounding report of this happening (Bajkov 1949), although the frequency of this might not be very high. Furthermore, there is recent evidence that surface-living fishes can move between water bodies via underground aquifers, although it is unclear whether this process happens often outside of the particularly permeable limestone karstic environments where it was demonstrated (Palandačić *et al.* 2012).

In all probability, the likeliest explanation is direct transfer in water, whether through current or past stream flows, occasional flood events or past high level stands of Lake Malawi. The whole area is very tectonically active and areas of land can rise and fall. There is considerable evidence that Lake Malawi’s water level was much higher in the past and this could have an impact on the access of fish directly into the lower-lying lakes (Genner *et al.* 2007). A geological map shown by Fontijn *et al.* (2012) indicates that ‘new lake bed’ rocks extend to about 20km north of the current shoreline of Lake Malawi, dating them to Pleistocene-Holocene, so within the last 2.5My. This distance would encompass Lake Kingiri and possibly Lake Ilamba, suggesting that these lakes might have been directly inundated by the waters of Lake Malawi in the past. Genner *et al.* (2007) suggest that Lake Chilingali might also have been directly connected to Lake Malawi, as it is only about 30m above the present level of the larger lake, less than Lake Kingiri at 50m. All three of these lakes contain populations of cichlid fishes belonging to genera endemic to Lake Malawi catchment and rarely found far upstream from the main lake: *Rhamphochromis* in Lakes Chilingali and Kingiri, *Lethrinops* in Lake Chilingali and *Otopharynx* in Lake Ilamba. Full phylogenetic resolution of these genera has yet to be attempted, but the satellite lake species show clear morphological similarities to Lake Malawi species that frequent shallow muddy habitats. *Lethrinops* sp. ‘chilingali’ closely resembles *Lethrinops lethrinus*, while *Otopharynx* sp. ‘tetrastigma Ilamba’ resembles *O. tetrastigma*. Both of the Lake Malawi species are commonly encountered in shallow weedy habitats, such as Lake Malombe (Turner 1996). *Rhamphochromis* species are generally offshore-living pelagic predators, so they might seem less plausible candidates for finding their way into satellite lakes. However, juveniles of two species are routinely found in shallow habitats: *Rhamphochromis esox* (Boulenger 1908) and *Rhamphochromis longiceps* (Günther 1864). The former attains very large sizes and has a distinctive head shape, with a deep, smooth blade-like lower jaw. However, *R. longiceps* is a relatively small species, with small teeth, resembling the small satellite lake forms. Mouthbrooding females of this species are known to enter shallow muddy lagoons to release their fry (Genner *et al.* 2008). However, the satellite lake *Rhamphochromis* males have plain orange anal fins, lacking the 'eggspots' which both *R. esox* and *R. longiceps* possess. It may be that this trait is relatively easily lost or indeed may be selected against in the conditions in satellite lakes. Alternatively, or it may indicate affinities with other *Rhamphochromis* species, few of which have eggspots (Genner *et al*. 2007). Mitochondrial DNA sequence analysis of the Lake Malawi and Chilingali species shed little light on this, indicating trans-species polymorphisms and little cladistic resolution, suggesting considerable incomplete lineage sorting or rampant introgression (Genner *et al.* 2007).

In addition to the presence of cichlids of Lake Malawi endemic genera, the three lowest altitude lakes also had by far the largest number of species recorded: at least 25 in 'large' Chilingali, 11 in Kingiri and 10 in Ilamba. These three lakes were also the only ones to contain cyprinid fishes or indeed fish of any family other than cichlids and clariids. Our surveys of the 5 lakes at higher elevation reported no more than 4 species per lake: 4 species in Masoko, Ikapu and Itamba, 3 in Kyungululu and 2 in Itende, with only Masoko and Ikapu containing a single clariid species, the rest being cichlids. Tilapiine cichlids and clariids, of course, are widely cultivated as food fishes and we know that attempts have been made to stock all these lakes, so the natural species richness of these high elevation lakes may be even lower. However, among the cichlids, there are clearly endemics in both high and low elevation lakes, indicating that most if not all were colonised naturally.

Surveys of the neighbouring rivers have shown that *Astatotilapia* are common throughout, and it is plausible that they could have accessed the lakes in the relatively recent past. Lake Ilamba and Lake Chilingali have surface water connections, ultimately to Lake Malawi, but the other crater lakes are presently entirely isolated. However, in a tectonically active area, surface topography is subject to change including elevation of ground level. None of the lakes that are presently known to be inhabited by fish are surrounded by a complete crater wall that rises above the surrounding ground level: all are 'downhill' at least in part from a substantial area of terrain, often including some kind of seasonal water course, suggesting the possibility of access by fish through flooding events. For example, it is possible to trace a path going continually downhill from the source of the Itupi stream into Lake Masoko (Figure 172). Even the high-altitude Lake Itende has evidence of a stream bed nearby at an even higher altitude (Figure 172). Although these routes may not currently serve to connect these streams to the current lakes, these analyses indicate that such connections may have existed in the past if we can assume relatively minor topographical changes.

Figure 172: (left) Lake Masoko, showing possible downhill route from the Itupi Stream into the lake; (right) Lake Itende showing a nearby possible stream bed at higher altitude (1208m marker).

Sympatric Divergence

There is a clear case of intralacustrine divergence in the *Astatotilapia* from Lake Masoko, where genome sequencing indicates that the deep-water 'benthic' morph with blue males is derived from the shallow-water 'littoral' morph with (mostly) yellow males, in turn derived from neighbouring riverine populations (Malinsky *et al.* 2015). This makes sense, because *Astatotilapia calliptera* is a species confined to shallow weedy habitats within Lake Malawi: Ribbink *et al.* (1983) report it being occasionally seen as deep as 9m, but most common shallower than 4m. In rivers too, it tends to thrive in shallow pools, backwaters and floodplain ponds. It would seem plausible that when it initially colonised Lake Masoko, *A. calliptera* would have kept to its normally preferred habitat of the shallow margins. However, it seems likely that populations would have built up to carrying capacity in the shallows, making competition for food severe. As the species is an opportunistic omnivore, including fish fry in its diet, cannibalism also seems likely. The deepwater habitat seems hostile: dark, with little food and no shelter, but at some point it is likely that while it remained unoccupied, it is likely to have become easier to find food there than in the over-populated shallows. This, then, might have led to selection favouring those individuals that were inclined to occupy this habitat. Can this kind of local adaptation lead to the production of genetically divergent 'ecomorphs' or incipient species?

Classical population genetic theory (reviewed by Coyne & Orr 2004) suggested that local adaption and progress towards speciation would be inhibited by gene exchange, but an increasing number of case studies have emerged of organisms diverging into 'ecomorphs' in the face of substantial gene flow with their sister taxa. This appears to be the case in Lake Masoko (Malinsky *et al.* 2015). While some studies had suggested that secondary gene flow from outside a crater lake might be essential to trigger full speciation (Martin *et al.* 2015), and there is some evidence for a functional role for external gene flow in olfactory-based assortative mating in a Cameroonian crater lake cichlid (Poelstra *et al.* 2018). However, while analysis of populations of full genome sequences indicated some gene flow from nearby rivers into the littoral ecomorph in Lake Masoko, this was not associated with the signals of divergence between the lacustrine forms, suggesting that the key drivers of divergence were sympatric and likely driven by microhabitat preferences and adaptations (Malinsky et al. 2015). So far, we have not found any evidence for sympatric divergence outside of the Masoko *Astatotilapia* and it may be that particular features of the lake and this species were key to facilitating divergence. Lake Masoko is relatively deep and has an extensive oxygenated silt bottom separated from a productive shallow habitat by relatively steep crater wall: this may serve to create two divergent microhabitats separated by a relatively small area of intermediate habitat that is less suitable for maintenance of a breeding population. The only other really deep lakes are Kyungululu (which lacks haplochromine cichlids) and Kingiri (where all the male *Astatotilapia* seem to be black). It is not yet known whether there is an extensive deep-water oxygenated bottom in the latter, nor indeed whether there are genetically divergent ecomorphs specialised for different depths but not readily distinguishable on male breeding colours.

Conservation and Human Use

Prior to the dam collapse, Lake Chilingali was heavily fished, supporting almost 300 fishermen (Changadeya *et al.* 2001). During our visits, a diversity of fishing operations was observed including static gillnets, active beach seines and low intensity angling, mostly by children. A government-supported cage culture programme for tilapias had been started prior to 2009, but when we visited the cages were in a state of disrepair with netting used to make beach seines. Local fishermen reported that they didn't think it was worth going to all the trouble and expense of feeding fish for months, when they could be caught from the lake immediately. The lake was also used for drinking water, watering livestock, bathing, washing clothes and it was occasionally visited by tourists. It was not clear if it was being used for the original purpose envisaged when the dam was constructed, irrigation of downstream rice plantations. Following the collapse of the dam, the remaining smaller lakes were quite remote from roads and tracks. A single gillnetter was seen on Lake Chikukutu, but his net was small and full of holes and his catch poor. Large piles of green mosquito netting were seen near the larger lakes and there were a few canoes. When asked to fish, there was a lot of enthusiasm, but little ability and catches were poor, consisting mostly of tadpoles and invertebrates. It seemed that the skilled, productive fisheries from the pre-collapse period had fallen away: perhaps the fishers had moved elsewhere.

Fishing activities were very variable around the Tanzanian crater lakes. When interviewed, district fishery officer Mr Mwaibako justified the introduction of Nile Tilapia to the lakes on the basis of poor fishery yields. However, we found thriving populations of native tilapias in all the lakes except Ndwati and Ngozi, which seemed hostile to their survival. Despite this, active fisheries were confined to Lakes Kingiri and Ilamba. These lakes were at the lowest altitudes and were closest to Lake Malawi. Lakes Masoko and Ikapu are both accessible by road and had substantial tilapia populations as well as some catfish, but had no active fisheries, beyond small-scale angling by children. Interviews suggested there was little interest in eating fish or in fishing activities in the area.

Following the dam collapse, it appears that the endemic *Rhamphochromis* and *Lethrinops* in Lake Chilingali may have gone extinct. It is always hard to prove the extinction of an aquatic species. Lakes Chilingali and Chikukutu are not crater lakes but lie on a tributary of the Kaombe River near Nkhotakota (Genner *et al.* 2007). There are numerous small swampy lakes in area around Nkhotakota – but no published records or collections in international museums have been found. The large Chia Lagoon is presently connected to Lake Malawi by a narrow channel and appears to contain Lake Malawi taxa, although again collections are scarce. There are also pools and swamps around the mouth of the Bua River just to the north of Chilingali. It would seem appropriate to survey these areas to see if there are any relict populations of either species. There are captive breeding populations of both Chilingali endemic species in Europe. It has been reported that the Chilingali Dam is to be rebuilt. If so, it may be that these species could be reintroduced.

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