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*Review*

# A review of the farming of common carp (*Cyprinus carpio* L.) in Malawi: Policy research directions for aquaculture development in Malawi

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**The lack of better performing native fish species for aquaculture led the government of Malawi to import the exotic common carp (*Cyprinus carpio* L.) from Israel in 1976. Growth trials at Domasi and Kasinthula Experimental Stations had shown that common carp grew faster and to a larger size than the indigenous fish species. The government decided to distribute the fish to farmers for grow-out. Barely five years into common carp distribution to farmers, the government reversed its policy and banned the use of the species in aquaculture. The government not only became unpopular but also lost the confidence of the farmers who had begun to see positive impacts of common carp to their livelihoods. The farmers are as unconvinced today as they were before with the reasons behind the banning of common carp. This paper explores the background to common carp farming in Malawi, why the fish was later banned, and the impacts of the fish's ban on the status of Malawi's aquaculture. The paper further highlights the farmers' call for a return of common carp to Malawi's aquaculture and the research needed to be undertaken to inform government's policy for the development of a sustainable aquaculture industry in Malawi.**

**Key words:** Aquaculture, common carp, fish introduction, exotic fish, Malawi.

## INTRODUCTION

Fish is the most affordable source of animal protein in Malawi, contributing over 70% of animal protein to the diet of Malawians (Mahony et al., 2014; Chidammodzi et al., 2015; Sanudi et al., 2015). Most of the fish consumed by Malawians come from capture fisheries. Aquaculture contributes about 2% to the total fish supply in Malawi. Over the past decades, fish production from capture fisheries has plateaued, with little or no prospect for further expansion (Weyl et al., 2010). Overfishing and weak enforcement of fisheries regulations have been blamed for dwindling catch rates from lakes and rivers. With the increasing human population (growing at 3% p.a.), the scarcity of fish in Malawi has had many ramifications.

Foremost is the increase in demand and prices of fish (GoM, 2011). As 65% of the people in Malawi are poor,

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living on less than 1 US $ per day, many people may not afford to buy fish. This is notwithstanding that compared with other animal products, fish still remains relatively cheap. Consequently, many Malawians may lack sufficient animal protein in their diets, leading to stunting and other protein-deficiency problems (IFFRI, 2012). Further, fish availability has declined, resulting in decreasing per capita fish consumption from 14.7 kg/person/year in 1970 to 4.9 kg/person/year in 2011 (Russell et al., 2008; Nagoli et al., 2009; Sanudi et al., 2015), and is projected to reach zero by 2034 (GoM, 2011) (Figure 1).

As fish is important to people's health and the economy of Malawi, the government has been considering various options of increasing fish supply in the country. Aquaculture is seen as the most viable option (Sanudi et al., 2015). However, the main constraint in Malawi's aquaculture is the slow growing and small-sized native fish species cultured (GoM, 2011, 2012). This problem has been observed since the 1960s, but efforts to identify more suitable indigenous fish species have been unsuccessful. This led the government of Malawi to import the common carp (*Cyprinus carpio* Linnaeus, 1758) (Figure 2) from Israel in 1976.

Test trials for growth showed that the common carp grew fast and to a large marketable size. The government distributed the fish to farmers in southern Malawi from 1985 to 1990. Further importation and distribution of the fish was stopped in 1991 and a ban imposed on its culture in 1992. But farmers wanted a reversal on carp ban to promote growth in the aquaculture sector (GoM, 2011). Details on the history of aquaculture development in Malawi are covered in Pruginin (1976), Balarin (1987) and ICLARM/GTZ (1990). This paper reviews the origin and status of carp farming in Malawi, the issues surrounding the ban of the fish, and research areas to inform policy on common carp farming in Malawi are suggested.

## METHODS OF INVESTIGATION

Information on the farming of common carp in Malawi was obtained from the following sources:

(1) A compilation of existing literature on the origin and status of common carp farming in Malawi. Since farming of this fish in Malawi has been restricted, some of the literature on the subject is admittedly quite old (Betram et al., 1942; Pruginin, 1976; Balarin, 1987; Welcomme, 1988; Vanden Bossche and Bernacsek, 1990; Msiska and Costa-Pierce, 1993).
(2) Personal involvement as a research assistant in Zomba district in 1989/1990 under the International Center for the Living Aquatic Resources Management[1] (ICLARM/GTZ Africa Project).

Further information was obtained through attendance of meetings organized by ICLARM in 19891990 and in later years by the Department of Fisheries[2].

## RESULTS

### History of common carp farming in Malawi

The farming of fish in Malawi started in 1906 with the introduction of rainbow trout (*Onchorhynchus mykiss* Walbaum, 1792) for angling (Balarin, 1987). As the human population at this time was low, fish stocks in the capture fisheries were considered adequate and in healthy state. A nutritional survey following the League of Nations (1935), Report on the Psychological Basis of Nutrition recommended that the farming of fish for food in upland areas of Malawi needed consideration to redress the nutritional deficiency in the diet of people living far from lakes (Betram et al., 1942). Thus, fish farming for food began in 1956/1957 using the indigenous tilapias *Oreochromis shiranus* Boulenger, 1897 and *Tilapia rendalli* Boulenger, 1897 (Pruginin, 1976). In 1969, a joint Malawi Fisheries Department (FD)/FAO survey of fish yields of Malawian species was carried out to assess the performance of these fishes. Results indicated slow growth rate (< 1 g/day), leading to low fish yields from ponds and dams of 0.1 to 0.2 t/ha/year for Northern Malawi and 0.5 to 1.0 t/ha/year for Southern Malawi (Msiska, 1993).

Presently, there are five main indigenous fish species used in Malawi's aquaculture, the tilapias *O. shiranus*, *Oreochromis karongae* Trewavas, 1941, *Oreochromis mossambicus* Peters, 1852, *T. rendalli*, and the catfish *Clarias gariepinus* Burchell, 1822 (Figure 3). Tilapias and catfish make up 93 and 5% of aquaculture production, respectively. *Oreochromis shiranus* is the most widely cultured fish in Malawi, followed by *T. rendalli*. *O. mosambicus* is cultured in the Lower Shire river basin. These tilapias grow slowly and to small sizes, with *O. shiranus* and *O. mosambicus* reaching sexual maturity as small as 6 g and breed precociously (M'balaka et al., 2012).

The perceived absence of a fast-growing local species and the need to provide animal protein and farm employment to rural people prompted the government of Malawi, as suggested by a consultant named Pruginin, to decide importing common carp, from Israel in 1976, for aquacultural purpose (Mkoko, 1993). Five hundred common carp of both scaled and mirror carp were imported and acclimated at the Kasinthula Experimental Station (Moreau and Costa-Pierce, 1997). Common carp is native in the piedmont zone of the Danube River to the Black, Caspian and Aral Sea basins, with western dispersants in central Asia and eastern dispersants in Siberia (Kirpitchnikov, 1999). However, the fish has been

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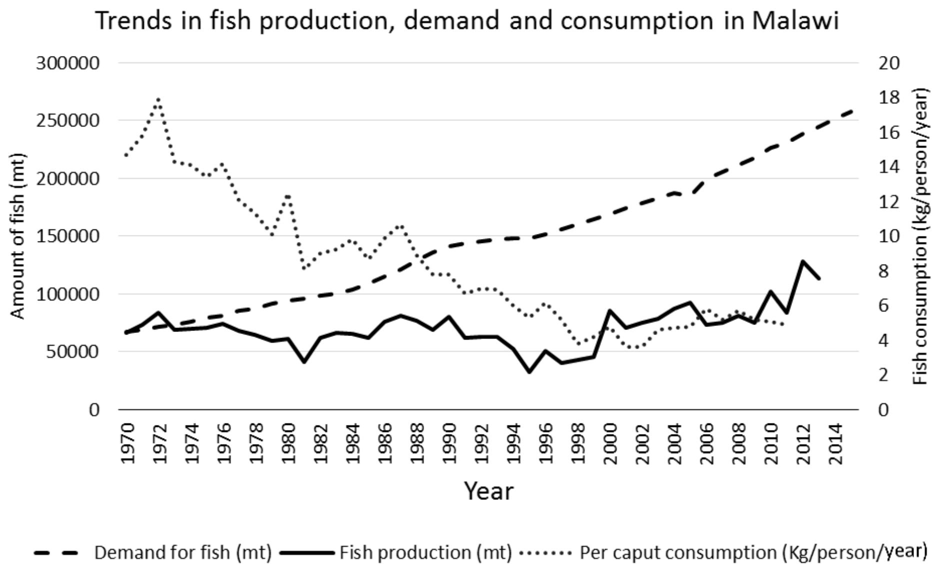


**Figure 1.** Trends in fish supply, demand and consumption in Malawi (Department of Fisheries, Lilongwe and National Statistical Office, Zomba)

**Figure 2.** Common carp (Donkers, 2004).

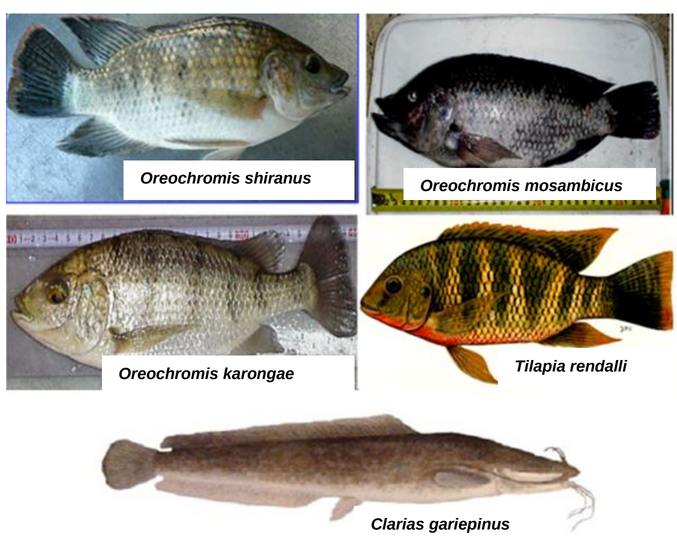


**Figure 3.** Native fish species used in Malawi's aquaculture (National Aquaculture Center and Atlas of Southern African Fresh water fishes).

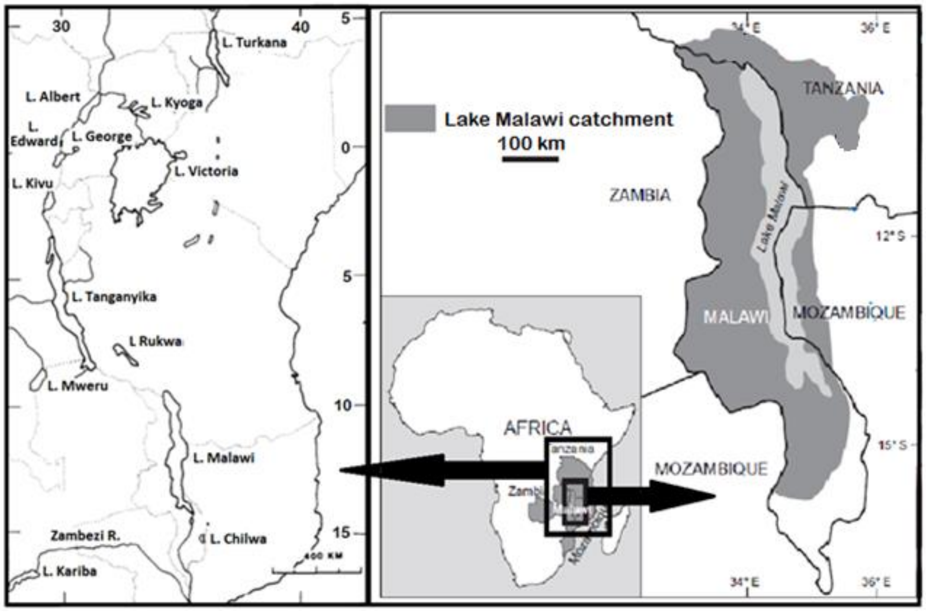


**Figure 4.** Catchment area of Lake Malawi, southern Africa (ILEC, 2005). Carp was distributed to farmers outside the catchment (not shaded).

translocated and introduced to non-native regions since Roman times (Balon, 1995). The fish is regarded as one of the best growing aquaculture species in the world, and has been referred to as a “biological miracle” for its excellent growth and production performance in aquaculture systems (Msiska and Costa-Pierce, 1993). Thus, the common carp was the first to be introduced outside its natural range for aquaculture farming (Balon, 1995; Alves et al., 1999) and remains the most widely distributed fish in the world (ISSG, 2000; Zhou et al., 2003; Casal, 2006). In 2010, the fish accounted for 9% of the total fish production in freshwater aquaculture (Rahman, 2015). Some European countries obtain as much as 80% of their freshwater aquaculture production from common carp alone (Woynarovich et al., 2010; Rahman, 2015).

During test trials from 1976 to 1983 at the Domasi and Kasinthula Experimental Stations in Malawi, the carp performed well in ponds with growth increments averaging 4 g/day, leading to yields of 5 t/ha/year (Msiska, 1993). For example, in the Chingale area of Zomba district of Malawi, common carp was able to grow up to 9 kg in 2.5 years (Moreau and Costa-Pierce, 1997). Average weights for carp were 400 g; *O. shiranus*, 57 g and *T. rendalli*, 78 g (Noble, 1993). Following encouraging performance of carp in test trials, the government considered distributing the fish to farmers.

Before the distribution of carp to farmers, the Fisheries Department of Malawi formulated conditions for the distribution: (1) only farmers outside the Lake Malawi catchment area would be allowed to raise common carp; (2) no farmer would be allowed to breed the fish; (3) all carp fingerlings were to be supplied from government fisheries stations (Domasi and Kasinthula) at a nominal fee; (4) farm ponds must have screens on inlets and outlets to prevent carp escapes; (5) at harvest all fish must be killed and sold in the presence of a Fisheries Officer; (6) all farmers growing carp must submit records on their carp stocks and possible information on carp transfers to neighbors (Mkoko and Mutambo, 1993).

The distribution, carried out between 1985 and 1990, was largely confined to the southern region, outside the Lake Malawi catchment area (Figure 4), except for a small population of carp stocked in experimental ponds at Bunda College of Agriculture (now LUANAR) for experimental purposes (Moreau and Costa-Pierce, 1997). The fish was distributed to 36 individual farmers in southern Malawi, mainly in Zomba district, and two estates (Satemwa Tea Estate in Mulanje district and SUCOMA Sugar Estate (now Illovo) in the Lower Shire) (Msiska, 1993). Because of its fast growth rate and large market size, common carp was raised mainly for commercial purposes (NRCM, 1999). A fuller utilization of this fish was realized when raised in association with other fish like *T. rendalli*, *O. shiranus* and *O. mossambicus* or *C. gariepinus*. The ease with which this species could be cultured, fast growth under poor input conditions and breeding without slowing down growth, and adaptability to wide environmental conditions made this species attractive to farmers (Kapeleta, 2001). Consumers also liked the fish for its flavor, and the large harvest size made a lot of farmers realize income they never had before (Andrew et al., 2003).

By 1989, two incidences were reported that would change the course of carp farming in Malawi. Firstly, escapes were reported into Likangala stream in the Lake Chilwa basin and in the Lower Shire system. This implied that escapement of common carp was possible even with the best trained and well-experienced farmers. Secondly, the fish was reported to reproduce in the weedy margins of some of the farmers' ponds, contrary to the belief that the fish would not spawn under natural conditions. The Fisheries Department had never thought that these incidences would occur (Msiska and Costa-Pierce, 1996; Andrew et al., 2003). These two incidences heightened the concerns about the potential impacts of the fish on native fish biodiversity, particularly, in Lake Malawi, the world's most species-rich freshwater lake. Malawi has been particularly concerned about the possible negative impacts of carp on Lake Malawi fish biodiversity (Vanden Bossche and Bernacsek, 1990).

In 1990, the government of Malawi stopped further distribution of common carp fingerlings, pending a decision on the future of carp farming. This, coupled with drought in that year that dried up more than 50% of farmers' ponds, drastically reduced the number of carp farms to just about four or five in the country (Moreau and Costa-Pierce, 1997). In 1991/1992, carp withdrawn from farmers and the remaining stocks in ponds were eradicated in Malawi. All exotic fishes, including carp and even *Oreochromis niloticus,* were prohibited in the Lake Malawi catchment area by the Malawi Government, in order to conserve the lake's unique assemblage of native species (Msiska and Costa Pierce, 1993; Moreau and Costa-Pierce, 1997). The restriction of exotic fish farming became legalized in the 1997 Fisheries Conservation and Management Act [Part XI section 41(1) c] (Hecht and Maluwa, 2003). However, the farming of common carp was still carried out (although negligibly) in some parts of the Lower Shire and other areas in Southern Malawi (Msiska and Costa-Pierce, 1996; Andrew et al., 2003).

## Reasons for banning common carp in Malawi

The decision to import common carp did not consider the ecological effects of the fish on aquatic ecosystems (Costa-Pierce et al., 1993). When reports of devastating ecological impacts of the Nile perch introduced into Lake Victoria in the 1950s began to spread in the early 1990s, scientists in Malawi were awakened to the negative effects that introduced fish species can have on native biota. Although, common carp was highly valued and already being distributed to farmers, scientists began to ponder about the potential negative impacts of this species on the unique Lake Malawi fish biodiversity. Fortunately, the fish had already been introduced elsewhere in the world and to more than 21 countries in Africa (Table 1 and Figure 5) from which lessons of its ecological effects could be learned.

Lessons from other countries in Africa suggested that carp's habit of digging up lake's sediment could destroy tilapia breeding areas, thereby lowering tilapia recruitment due to disruption of nesting. The stirring of sediment by carp also hasten eutrophication by mobilizing sediment-bound nutrients (mostly phosphorus) into the water column (Costa-Pierce and Pullin, 1989; Breukelaar et al., 1994). However, considering the high economic value of carp farming, no country in Africa, beside Malawi, has rejected the fish on account of its ecological effects. The Malawi government was concerned about the potential threat of carp to the unique fish biodiversity of Lake Malawi if it escaped into the lake (Vanden Bossche and Bernacsek, 1990; Costa-Pierce et al., 1993).

## Impacts of common carp ban in Malawi

### *Declining contribution of carp to fish supply and continued slowing of aquaculture growth*

The contribution of common carp to aquaculture production declined from about 9% of total aquaculture production in the early 1990s to less than 0.5% by the early 2000s (Figure 6). During the same period, the contribution of common carp to global aquaculture production increased from 5.4% of global aquaculture production to 5.9%.

In Malawi, fish farming became less profitable for most of the farmers who were used to carp, prompting over 80% of them to quit fish farming altogether. Farmers' trust and confidence in the Malawian Fisheries Department declined sharply, setting the government on frantic but futile confidence rebuilding campaigns (Msiska and Costa-Pierce, 1993). Growth in Malawi's aquaculture has slowed. For instance the contribution of aquaculture to total fish supplies in Malawi has remained low, estimated at 2% (Sanudi et al., 2015). It is widely believed that if Malawi were to adopt common carp farming, aquaculture development would accelerate (GoM, 2011).

### *Search for indigenous aquaculture species*

Aquacultural farmers demanded a replacement of the common carp to maintain profitable fish farming in Malawi. The search for suitable native aquaculture species had already proved difficult when such efforts began in the 1960s. However, the scientists believed a lack of success in this direction was attributable to an absence of sustained project commitment to screen and test indigenous fish species (Msiska and Costa-Pierce, 1993). Such a project came along in late 1999 with funding from Japan International Cooperation Agency (JICA). A number of indigenous fish species were assessed. By the end of the 5-year project period (1999-2004), no suitable indigenous fish species was identified

**Table 1.** Common carp introductions in Africa (Welcomme, 1988; Moreau and Costa-Pierce, 1997; FAO Inland Water Resources and Aquaculture Service, 2003).

| Country | Origin | Year | Established? | Ecological effects? |
|---|---|---|---|---|
| South Africa | Germany | 1859 | Yes (Some reservoirs) | Yes |
| Kenya | South Africa | 1910 | Yes | Probably |
| Kenya | Uganda | 1910 | Yes | Probably |
| Madagascar | Unknown | 1914 | Yes (Lakes) | Probably |
| Zimbabwe | South Africa | 1925; 1963 | Yes (Some reservoirs) | Unknown |
| Morocco | France | 1925 | Yes | Yes |
| Egypt | Indonesia | 1934 | Yes | Unknown |
| Ethiopia | Italy | 1940 | Yes | Unknown |
| Zambia | Israel | 1980 | No | Unknown |
| Zambia | South Africa | 1946 | No | Unknown |
| Nigeria | Austria | 1954 | Probably | Unknown |
| Rwanda | Israel | 1960 | Yes | Unknown |
| Uganda | Israel | 1962 | Yes | Unknown |
| Ghana | Unknown | 1962 | Probably | Unknown |
| Tunisia | Germany/France | 1965 | Probably | Probably |
| C.A.R. | Israel | 1966 | Yes | Unknown |
| Cameroon | Israel | 1970 | Yes | Unknown |
| Malawi | Israel | 1976 | No | Improbable |
| Sudan | India | 1975 | No | Unknown |
| Mauritius | India | 1976 | Yes | Unknown |
| Cote d'Ivoire | Italy | 1976 | Yes | Unknown |
| Burundi | Rwanda | 1980-1989 | Unknown | Unknown |
| Algeria | Hungary | 1985 | Yes (Lakes) | Yes |
| Togo | Israel | 1965; 1971 | No | Unknown |
| Tanzania | India | 1981 | Unknown | Unknown |
| Mozambique | South Africa | 1988 | Yes (Limpopo R) | Unknown |
| Namibia | South Africa | Unknown | Yes | Unknown |
| Swaziland | South Africa | Unknown | Unknown | Unknown |
| Lesotho | South Africa | 1965 | Yes (Orange R) | Unknown |

**Figure 5.** Main producer countries of *Cyprinus carpio* (FAO, 2004-2017).

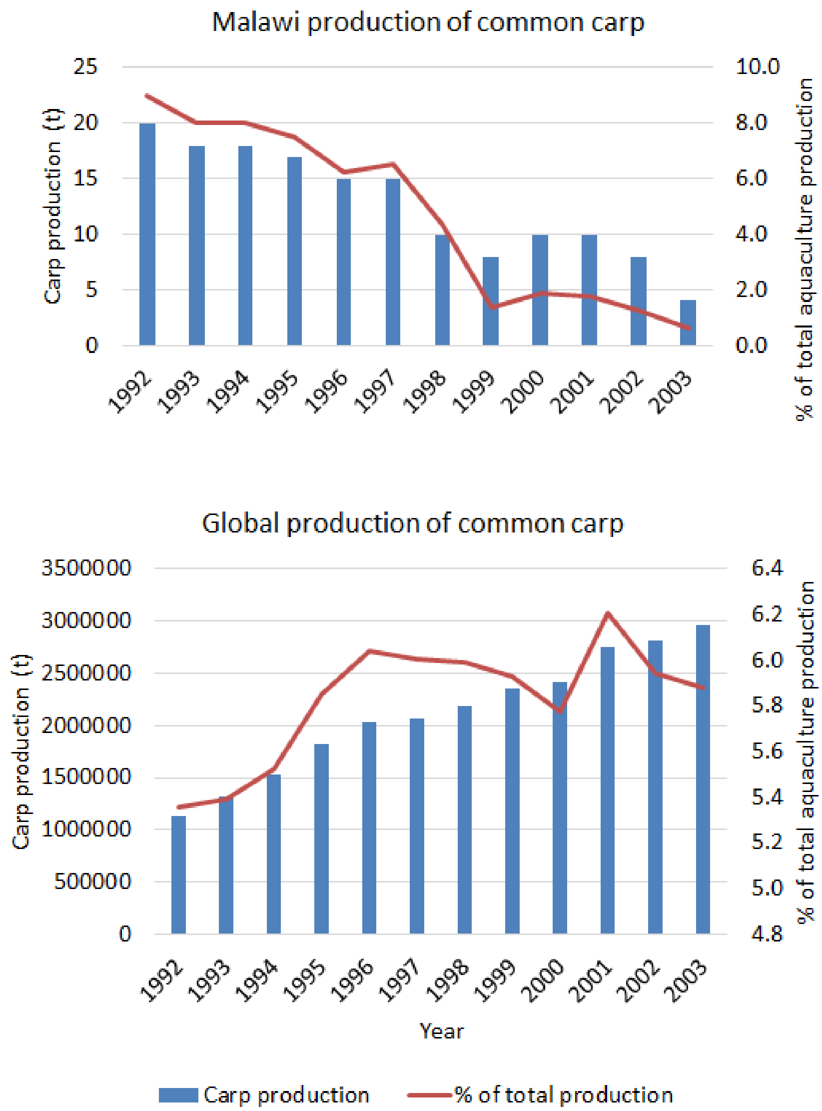


**Figure 6.** Impact of carp ban on carp production in Malawi (FAO, 2005-2016; NAC, 2003).

that could replace carp (SSC, 2005).

### *Pressure on policy review*

Failure by government to identify a better-performing native aquaculture species has attracted widespread calls from farmers for a reversal on common carp ban (GoM, 2011). Slow-growing and stunting native fish species have been cited as a major impediment to aquaculture growth in Malawi (GoM, 2011, 2012). The National Aquaculture Strategic Plan (NASP) (2005-2015) calls for impact studies to provide information that would form the basis for policy review on the use of carp in Malawi's aquaculture. The National Biodiversity Strategy and Plan (NBSP) also calls for impact assessment of alien species as potential candidates for aquaculture development in Malawi (Environmental Affairs Department, 2006). The government has emphasized the need to do more research on the ecological impacts of carp before it can consider reviewing its policy (Msiska and Costa-Pierce, 1993; Bandula, 1997; SSC, 2005).

### *Research directions related to policy on common carp farming*

Government insistence on judicious research on common carp before policy review is understandable and logical. However, government has not suggested any potential policy research direction on the issue. This paper suggests the following possible research avenues:

(1) Comparison of ecological impacts between common carp and *C. gariepinus*: Both of these species are benthivorous (Koekemoer and Steyn, 2002; Rahman, 2015). Anecdotal field observations of the impacts of these fishes in Malawi suggest they may impact on ecosystems in the same way. These observations contradict Msiska and Costa-Pierce (1993) who opined that common carp occupies a niche that no other farmed fish occupies in Malawi. Reports of common carp displacing *C. gariepinus* from its benthic niche in Zimbabwean reservoirs (Costa-Pierce et al., 1993) corroborate observations of similarity of niche occupation by the two species. If these observations are true, the introduction of one of them into a system already containing the other may not significantly alter the ecosystem.

(2) Assessment of colonization and establishment of common carp and its environmental impacts in the Lake Chilwa and Lower Shire drainage systems: Common carp is reported to have escaped from fish ponds into natural waters in these ecosystems in the 1988-1990 period (Msiska and Costa-Pierce, 1993). The escapees have not been followed to determine if they are established and what impacts, if any, they cause.

(3) Evaluation of common carp farming in the Lake Malawi catchment area in Tanzania and Mozambique: These riparian countries are reported to be farming common carp in their side of the lake's catchment (Costa-Pierce et al., 1993; Chirindza, 2010). Mozambique is one of the main African producer countries of common carp (Figure 5). If the species is already in the lake's watershed, the questions of what impacts the common carp is causing and what justification Malawi has for its unilateral rejection of the fish when other countries in the same watershed are farming it will need addressing.

(4) Invasion history of common carp in lakes of similar morphometry and physico-chemical conditions to Lake Malawi: Across-ecoregion analysis has shown that the invasivity of common carp is regulated by a number of ecological filters such as depth and trophic status of a water body (Bajer et al., 2015). However, no studies have been conducted to establish invasion history of common carp farmed in catchment areas of lakes with depth and trophic status similar to Lake Malawi. Lessons learned in these ecosystems can be used to make inference about the potential vulnerability or invasion potential of Lake Malawi to common carp.

## Conclusions

Common carp was introduced in Malawi to complement tilapia aquaculture production with an aim of increasing overall production from the fish farming industry. The indigenous tilapias were slow-growing, stunting and breeding precociously. The catfish *C. gariepinus* was economically a difficult fish for the majority of farmers as the species' protein requirements made it costly to feed. The species was also difficult to breed under prevailing pond conditions. Thus, these species had received farmers' disapproval as early as the 1960s. With common carp (1985-1991), the farmers' interest in fish farming surged as profits from fish farming began to increase. Government's withdrawal of common carp and its ultimate ban left many farmers disillusioned and wondering what the real justification was. The government insisted it was concerned with the effects the fish would have on Lake Malawi once the species found its way to the lake's catchment. Farmers were promised that a more suitable indigenous aquaculture species would be identified for use in Malawi's aquaculture sector.

To date, a more suitable native aquaculture species has not been identified in Malawi, despite the existence of well-resourced project investments in this effort. Lack of better performing indigenous fish species is continually being cited as a major constraint in the growth of aquaculture industry in Malawi. The Malawi government has persistently resisted calls to reverse its ban of common carp until it could be shown that carp's farming in the Lake Malawi catchment would not negatively affect the lake's unique fish biodiversity. This paper has outlined potential research areas that are relevant to policy decision-makers on the question of whether common carp would harm Lake Malawi.

Due to inconsistent and fragmentary documentation of the farmers involved in carp farming, this study has not been able to chronicle the trends of carp farmers in Malawi from the time of distribution of the fish to farmers to the time the fish was withdrawn from the farmers. Although it is recorded that carp was still being farmed after banning it (Andrew et al., 2003), the farmers could not make public declaration of the activity for fear of government reprisals. The study has therefore not been able to provide up-to-date records of carp production in Malawi. In addition, there are unconfirmed reports that farmer-to-farmer distribution of carp has occurred in Malawi, and that the fish is illicitly farmed in the Lake Malawi catchment area. This study has not been able verify these reports as the farmers fear to provide information.

## CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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*Full Length Research Paper*

# Morphological and genetic variability among Mpasa (*Opsaridium microlepis* Günther, 1864) populations from the inflow rivers of Lake Malawi

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**Fisheries management continues to be a nightmare due to over exploitation of fish stocks and various anthropogenic activities resulting in a reduction of genetic resources. *Opsaridium microlepis*, a commercially exploited fish species from Lake Malawi, is no exception, hence it is listed as endangered. *Opsaridium microlepis* stocks from four different rivers were analyzed using 13 geometric morphometric landmarks and 20 microsatellite loci, to determine if the stocks were morphologically and/or genetically different. AMOVA performed on DNA data revealed a significant ($P < 0.001$) genetic differentiation with 16.4% of the total genetic variance ascribed to differences among populations, and 83.6% due to differences within population. This finding was supported by higher pairwise FST values (FST = 0.17). MANOVA of morphological data showed significant body shape variation among the stocks (Wilk's $\lambda = 0.0913$; $P < 0.0001$). Pairwise comparisons using both methods indicated that all pairs were significantly different, except morphologically for Bua and Linthipe ($P$=0.3311). The morphological differences consisted of shorter gape and shorter head of the Bua/Linthipe stock was seen in the North Rukuru and Dwangwa stocks. The morpho-genetic differentiation revealed in this study implies that the populations are distinct and should be considered as separate management and conservation units.**

**Key words:** Lake Malawi, Mpasa, procrustes distance, genetic differentiation, endangered species, fish stocks, conservation.

## INTRODUCTION

Lake Malawi, a global biodiversity asset, has attracted worldwide attention amongst evolutionary biologists, due to the fastest large-scale adaptive radiation ever recorded in evolutionary history (Ribbink, 2001). It is estimated that

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the lake harbors over 800 species of cichlids, of which 99% are endemic (Snoeks, 2000), as well as about 50 other fish species, of which 50% are endemic (Ribbink, 1994). The lake's fish population also supports a multi-species fishery (Weyl et al., 2004, 2005), being both a source of income to the local people and a basis of national food security (Ribbink 2001; Weyl et al., 2005). In the multi-species fishery, *Opsaridium microlepis* (Günther, 1864) is one of the major species that is commercially exploited in this lake. It is endemic to Lake Malawi and its affluents where it is commonly known as lake salmon and locally known as Mpasa. Mpasa is commonly caught in the northern and central regions of Malawi, where it ascends rivers to breed. It has been known that catches have been on the decline (Tweddle, 1981; GoM, 2016). During their spawning migrations, Mpasa are heavily exploited by gillnets set near river mouths, and numerous fishing methods in the rivers themselves. Though, Mpasa is known to inhabit the Lake Malawi and its in-flows, it has disappeared in some in-flows where it used to be abundant due to ecosystem degradation, overfishing during migration (Ndamala, 2006), and a surge in human population density in the areas surrounding the in-flow rivers (Kingdon et al., 1999). Mpasa stocks have drastically declined by not less than 50% such that the species was listed in IUCN 2006 as endangered species (Kazembe et al., 2005), and still remains in that status until the time this study was conducted.The fact that this species remains endangered is a valid reason for immediate action to ensure the survival of this important commercial/food resource. Management procedures must be put in place in order to conserve the species; however, such management procedures require information on whether different affluent rivers inhabit different stocks or one panmictic population in the lake whose individual fish are free to go up into any river. Tweddle (1981) suggested that each river has got its own Mpasa stock, with little or no intermingling, however, such conclusion can only be confirmed through some quantitative analysis. Population studies need to address both genetic and phenotypic divergence because population structure can result in restricted gene flow, color variation and local adaptation in particular morphological features that indicate population divergence. Geometric morphometrics, a landmark-based approach for investigating body shape changes, has been shown to detect fine-scale morphological differences (Kassam et al., 2003a, b; Adams et al., 2004; Maderbacher et al., 2008). In combination with neutral genetic markers, such as microsatellites, changes in the phenotype of an organism can be used to assess the intensity and direction of natural selection (Raeymaekers et al., 2007; Maquia et al., 2013). Hence, this study aimed at unraveling whether stocks from different rivers were morphologically and/or genetically similar or not, since such information is crucial in the management of stocks/species.

## MATERIALS AND METHODS

### Sampling

For geometric morphometrics, the four major rivers, three in the central region {Bua (n = 49), Linthipe (n = 40) and Dwangwa (n = 20)}, and one in the northern region (North Rukuru, n = 30) were sampled. The samples were preserved in 10% formalin, and transported to Lilongwe University of Agriculture and Natural Resources (LUANAR) Bunda Campus where image acquisition was done within the same month since long preservation affects shape of any fish. For genetic analysis, 50 fish from each of the four rivers were sampled in February and April, 2010. Tissue samples (fin clips and muscle) were extracted from individual fish and preserved in vials with 95% ethanol and later kept at 4°C in the laboratory at Chancellor College, University of Malawi.

### DNA extraction and amplification

Genomic DNA was extracted following a standard SDS- proteinase K/phenol-chloroform procedure (Hillis et al., 1996). Twenty polymorphic microsatellite loci (Table 1) (Changadeya et al., 2013) were used for genotyping. The polymerase chain reaction (PCR) was carried out in a Mastercycler gradient 5331 Eppendorf (Version 2.30.31-09) with the following PCR conditions: initial denaturing at 94°C for 2 min, then 30 amplification cycles of denaturing at 94°C for 30 s, annealing at an optimal temperature for a specific primer pair for 15 s and elongation at 72°C for 30 s. The final extension was at 72°C for 20 min followed by a soaking temperature of 4°C. Finally, the amplified products of PCR were run on 6% polyacrylamide gel in BIORAD Sequi-Gen® GT Nucleic Acid Electrophoresis Cell where pGem DNA marker (Promega, 2000 USA) and $\phi$ X174 DNA/*Hinf* 1 (Promega, 2000 (USA) were used as band size standard markers.

### Analysis of molecular data

Genetic differentiation among populations was assessed by analysis of molecular variance (AMOVA, in ARLEQUIN version 3.1, Excoffier et al., 2006) followed by a computation of pair wise $F_{ST}$ values using GENEPOP (Raymond and Rousset, 1995). Mantel' test was performed to test if a correlation existed between the genetic and geographical distances, genetic and morphological distances and finally morphological and geographical distances. Unweighted Paired Group with Arithmetic Average (UPGMA) algorithm, based on Nei's (1973) genetic distance, was used to analyze population clustering in NTSYS (Rohlf, 1998).

### Geometric morphometrics

TPSDIG32 program (Rohlf, 2004) was used to digitize 13 landmarks (Figure 1) on all specimens. Procrustes superimposition was performed in CoordGen (IMP 6 package, Sheets, 2004). The superimposition translates all specimens to a common location and rotates them so that corresponding landmarks align as close to each other as possible and separates the two components of form, namely, size and shape. Separation of shape and size enables one to analyze each component separately depending on questions addressed (Bruner and Manzi, 2004; Kassam et al., 2004). The weight matrix of partial warp scores, representing shape variables, was generated from the overall procrustes superimposition and subsequent conventional statistics was applied to this weight matrix.

**Table 1.** Total number of alleles (A), allele size range (SR) in base pairs and microsatellite primer polymorphic information content (PIC).

| Locus | A | Gene Bank accession | $T_A$ | Allele Size Range (SR) | Repeat Motif | PIC |
|---|---|---|---|---|---|---|
| CypG49 | 12 | AY349167 | 53.6 | 170-192 | $(TA)_{11-21}$ | 0.74 |
| CypG3 | 11 | AY349122 | 56.4 | 150-202 | $(CAGA)_2$ | 0.76 |
| CypG13 | 13 | AY349132 | 53.4 | 140-172 | $(TAGA)_{10}$ | 0.73 |
| Ca3 | 10 | AF277575 | 54.5 | 162-182 | | 0.78 |
| CypG5 | 12 | AY349124 | 54.3 | 114-172 | $(TAGA)_{12}$ | 0.76 |
| CypG4 | 17 | AY349123 | 54.3 | 134-202 | $(TAGA)_{12}$ | 0.79 |
| CypG30 | 22 | AY349148 | 54.3 | 118-182 | $(TAGA)_7$ | 0.77 |
| Lid1 | 17 | | 55.3 | 140-194 | (TTTC)7 | 0.75 |
| CypG48 | 16 | AY349166 | 55.3 | 126-158 | | 0.80 |
| MFW | 11 | EF144124 | 55.3 | 106-126 | | 0.76 |
| CypG22 | 12 | AY349140 | 55.7 | 202-224 | | 0.70 |
| CypG6 | 12 | AY349125 | 52.5 | 192-218 | $(TAGA)_7$ | 0.71 |
| CypG8 | 18 | AY349127 | 52.5 | 132-166 | $(CAGA)_6$ | 0.73 |
| CypG21 | 14 | AY349139 | 52.7 | 158-184 | $(CAGA)_6$ $(TAGA)_7$ | 0.75 |
| CypG27 | 14 | AY349145 | 52.7 | 104-188 | $(TAGA)_8$ | 0.76 |
| Lid11 | 16 | | 53.7 | 200-228 | (TTTG)8 | 0.77 |
| AP1 | 13 | AJ428582 | 53.4 | 158-182 | $(TA)_{11-21}$ | 0.74 |
| AP2 | 18 | AJ428583 | 55.0 | 110-188 | $(AC)_{18-20}$ | 0.78 |
| Ru2 | 17 | | 53.6 | 142-174 | | 0.75 |
| CypG15 | 20 | AY349134 | 53.8 | 116-158 | | 0.82 |
| Mean | 14.75 | | | | | **0.76** |

$T_A$ annealing temperature.

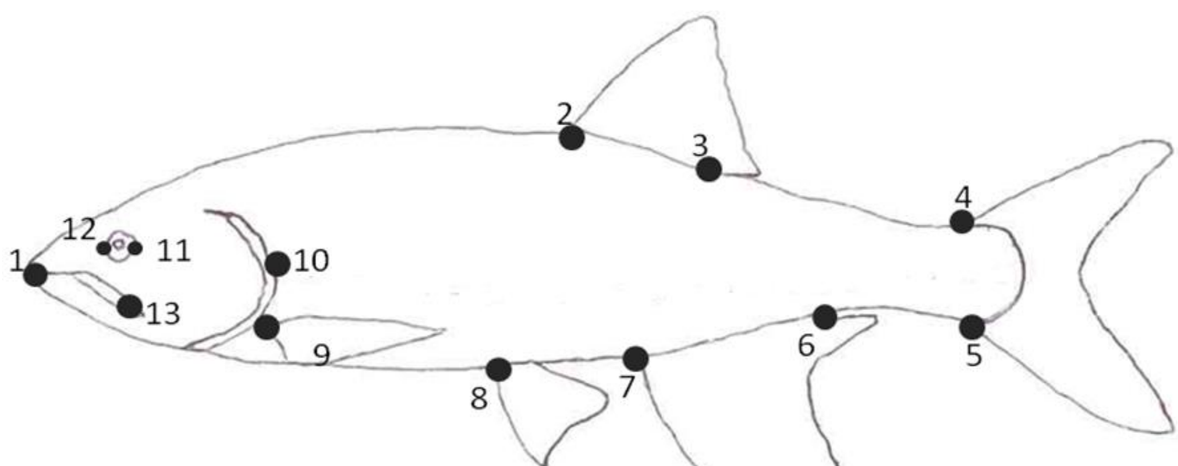


**Figure 1.** Landmarks digitized on every Mpasa specimen. 1: snout tip; 2-3:anterior and posterior insertion of dorsal fin; 4-5: caudal fin base; 6-7: posterior and anterior insertion of anal fin; 8: insertion of pelvic fin; 9: insertion of pectoral fin; 10: end tip of operculum: 11-12: eye diameter; 13: posterior end of gape.

**Analysis of morphometry data**

A canonical variate analysis (CVA) was performed on the weight matrix in order to determine differences in body shape among stocks through multivariate analysis of variance (MANOVA). If MANOVA revealed significant differences among stocks, pairwise multiple comparisons using Goodall’s F-test on Procrustes Distance was performed to determine which groups differ from one another.

**Table 2.** Pairwise comparison among all the four populations of Mpasa on morphological and genetic parameters.

| Population pair | Parameter | | | | | |
|---|---|---|---|---|---|---|
| | Geographical distance (km) | Procrustes distance | ***P* -values** | Nm | $F_{ST}$ | Genic and genotypic differentiation ***P* -values** |
| NR& BWA | 335.9 | 0.0225 | 0.0044 | 0.67 | 0.16 | 0.0000 |
| NR & LTP | 451.9 | 0.0234 | 0.0056 | 0.49 | 0.16 | 0.0000 |
| BWA& LTP | 122.11 | 0.0123 | 0.3311 | 0.70 | 0.14 | 0.0000 |
| NR & DWA | 294.24 | 0.0302 | 0.0011 | 0.38 | 0.19 | 0.0000 |
| BWA& DWA | 43.98 | 0.0287 | 0.0031 | 0.56 | 0.16 | 0.0000 |
| LTP & DWA | 158.85 | 0.0321 | 0.0022 | 0.45 | 0.19 | 0.0000 |

NR, North Rukuru river ; BWA, Bua river; DWA, Dwangwa river ; LTP; Linthipe river; Nm, gene flow; $F_{ST,}$ population fixation index

These statistical analyses were done in IMP software and CVA analysis was executed by CVAGen6, while pairwise comparisons were done by TwoGroup6 (Sheets, 2004). To determine population clustering due to morphological similarity, a UPGMA algorithm, based on Procrustes distance, was done using NTSYS (Rohlf, 1998).

## RESULTS

### Genetic population differentiation

AMOVA revealed a significant (P < 0.001) genetic variation with 16.4% of the total genetic variance attributed to differences among populations and 83.6% was due to differences within population. In this study, the average number of migrants per generation was *Nm* = 0.91, and the highest number of migrants were between the Linthipe and Bua (*Nm* = 0.70), while the lowest was between North Rukuru and Dwangwa (*Nm* = 0.38) populations (Table 2). The overall genetic differentiation ($F_{ST}$ = 0.17) signified high genetic variation among populations with the highest variation between North Rukuru and Dwangwa, Linthipe and Dwangwa population pairs ($F_{ST}$ = 0.19), while the lowest was between Linthipe and Bua population pair ($F_{ST}$ = 0.14) (Table 2).

### Morphological differentiation

MANOVA revealed significant body shape differences among stocks (Wilk's λ = 0.0913; p< 0.0001). Pairwise comparisons indicated that all pairs were different except the stock from Bua which was not significantly different from Linthipe stock (Table 2). From the deformation grids generated (Figure 2), the subtle morphological differences observed consisted of shorter gape of the Bua/Linthipe stocks as evidenced by the posterior and anterior displacements of landmarks 1 and 13, respectively, as opposed to the other 2 stocks. The anterior displacement of landmark 10 against posterior displacement of landmark 1 signified that the Bua/Linthipe stock had a shorter head than the North Rukuru and Dwangwa stocks. The Dwangwa stock had wider caudal peduncle than the North Rukuru stock as evidenced by displacements of landmarks 4 and 5.

### Morpho-genetic cluster analysis among populations

Both dendrograms (Figures 2 and 3) indicated that Bua stock was closely related (morpho-genetically) to Linthipe stock, despite Bua is geographically closer to Dwangwa than Linthipe (Table 2). However, the morphological dendrogram (Figure 2) unlike the genetic dendrogram (Figure 3) correlates with geographical distance differences by depicting a Bua-Linthipe-Dwangwa cluster that is clearly delineated from North Rukuru cluster. Mantel' tests revealed that there were no significant correlations between geographical distance and genetic distance (r = 0.18; *p* = 0.6369), geographical distance and morphological distance (r = -0.01900; *p* = 0.4856) and also between genetic and morphological distances (r = 0.72; *p* = 0.9328) among the stocks. This indicates that the morphological and genetic structuring observed among these stocks, is not necessarily due to geographical isolation.

## DISCUSSION

### Genetic differentiation

Pair-wise comparison amongst the four populations revealed significant genetic differentiation in *O. microlepis*. This suggests partitioning of the breeding population, limitation in migration between different areas and the existence of a distinct stock structure among populations. The high overall value of $F_{ST}$ (0.17) of microsatellite loci in *O. microlepis* was significantly different from zero (P < 0.001) suggesting great genetic differentiation among the populations. Wright (1978)

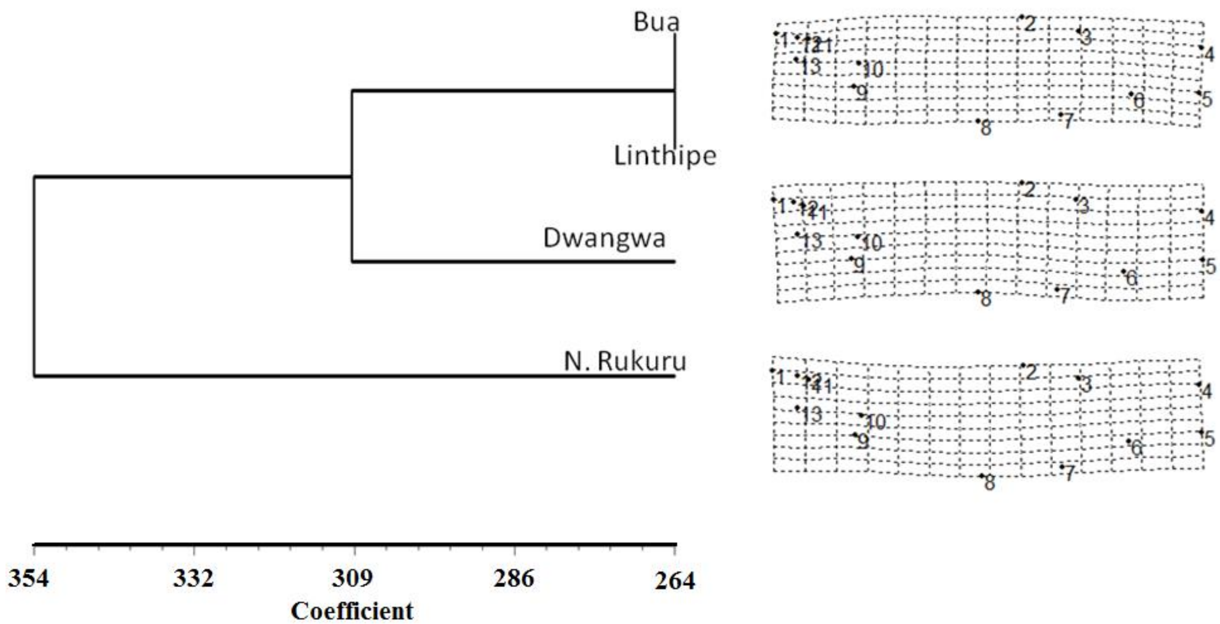


**Figure 2.** UPGMA phenogram based on Procrustes distances for the four populations of *Opsaridium mucrolepis* with consensus configurations representing the stocks at the tips of the phenogram.

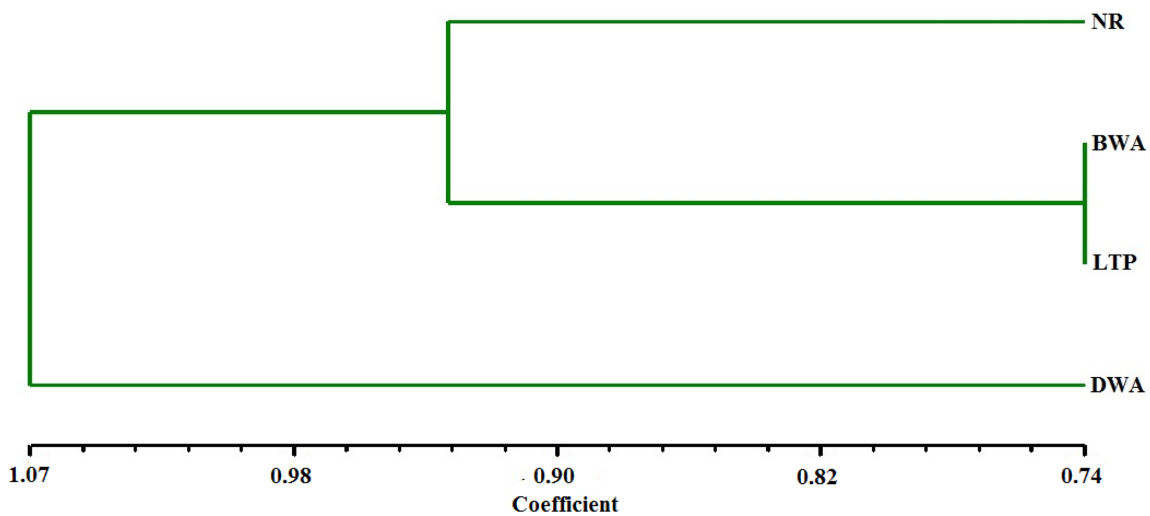


**Figure 3.** UPGMA phenogram based on Nei's genetic distances for the four populations of *Opsaridium mucrolepis*.

explained that any genetic differentiation ≥15% signifies high genetic differentiation and is associated with very low gene flow among populations. Level of genetic differentiation demonstrated by Mpasa in this study is higher than values seen in Pacific herring ($F_{ST}$ = 0.023), Atlantic herring ($F_{ST}$ = 0.035) and widespread anadromous fish like Atlantic salmon ($F_{ST}$ = 0.054) (McConnell et al., 1995). The plausible reasons for the observed high genetic differentiation among the populations are low gene flow among populations (Nm=0.91) and an absence of recent genetic bottlenecks as indicated by Bottleneck tests entailing that despite heavy exploitation, the populations are outbreed due to possible presence of large numbers of fish. The high $F_{ST}$ obtained in this study hence signify that the populations are distinct requiring independent conservation management for each river system. Mills and Allendorf (1996) concluded that the rate of migration of *Nm*≥1 leads to considerable homogeneity among populations but population divergence and structuring occurs when *Nm*≤ 1. The populations in the present study have an overall migration rate of *Nm*≤ 1 rendering them to structuring and divergence.

## Morphological diversity

Geometric morphometrics as used in this study has proved more robust than the traditional morphometric approach which could not clearly distinguish these stocks according to Chigamba et al. (2012). The morphological differences though subtle, are important because they clearly indicated that stocks from different rivers are not the same in body shape. These findings confirm Tweddle (1981) suggestion that the stocks of Mpasa are specific to each river system with little or no intermingling. Additionally, Chigamba et al. (2012) found that water quality in these rivers was also different, revealing different usage and status of environmental degradation of the rivers' water and air sheds. Therefore, the management and conservation measures of each fish population and its specific river should be independent and targeted because loss of one river' fish stock would mean extermination of a morphologically unique fish stock.

Kassam et al. (2003a) found a strong link in gape size with the feeding habit of some cichlid species. Gape size of a predator and body depth of the prey are the main factors determining whether a gape-limited piscivore can ingest a potential prey. Consequently, gape size governs predator-prey relationships. Magnhagen and Hiebo (2001) reported that a smaller Pike with relatively bigger gapes was observed surrounded by lowest prey availability, while a larger Pike with smaller gapes had the highest prey density. On the other hand, size of caudal peduncle has been related to sex and homing behavior. Beachan (1984) found that in Chum salmon, males had larger caudal peduncles than females, while Chum salmon from larger rivers had larger peduncles than those from smaller rivers. From the above, it seems probable than the differences in body shapes between the different stocks of Mpasa could be a reflection of many factors including size of the rivers, feeding behavior and availability of prey. More studies are required to determine the factors that have led to such differences in body shape. Nevertheless, the differences in body shapes as detected by this study infer that these stocks are different, and should be considered as separate entities in every aspect conservation and management.

In the present investigation, Mantel' tests showed no significant correlation between geographical, morphological and molecular distances among the populations studied. Low association between genetic and morphological distances is due to the fact that SSR loci are non-coding DNA which is not expressed hence not subjected to the same forces of selection which shape morphological characters (Kjaer et al., 2004; Vieira et al., 2007). Therefore, morphological and molecular differences observed among the populations may be due to local selection pressures imposed on the stocks since there is no evidence of isolation-by-distance effect. This revelation concurs with other studies of *Lenthrinops* species flock (Duponchelle et al., 1999; Changadeya et al., 2001), which reported fish flocks not fitting the isolation by distance model though in those studies, the fish populations exhibited high gene flow.

## Conclusions

The genetic and morphological differentiation revealed in this study underscores the need for separate monitoring and conservation strategies for each of the four populations. The study revealed closely comparable results between geometric morphometric and genetic analysis; therefore, geometric morphometric techniques can reliably be used in similar studies where DNA analysis is not possible due to high running costs and lack of specialized equipment. Thus, this study recommends that the management and conservation measures of each fish population and its specific river should be independent and targeted because loss of one river' fish stock would mean extermination of a morphologically unique fish stock.

## CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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