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REVIEW

Nile Tilapia, *Oreochromis niloticus* (Teleostei: Cichlidae): a threat to native fishes of Lake Malawi?

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Abstract The Nile Tilapia, *Oreochromis niloticus*, is a freshwater cichlid indigenous to the tropical and subtropical parts of the eastern and western Africa and is being cultured in the Lake Malawi catchment on the Tanzanian side. Historically, the Nile Tilapia has been successful in dispersing once it has been introduced into a catchment area. The probability of the Nile Tilapia successfully colonizing Lake Malawi is enhanced by many of its life history attributes including its fast growth rate, large size relative to native *Oreochromis* spp., and its diverse repertoire of feeding options. Where introduced, Nile Tilapia has had devastating impacts through competition or hybridization with native congenerics. We contend that the Nile Tilapia is a significant threat to the native fishes of Lake Malawi. With Lake Malawi harboring more species of fishes than any other freshwater lake in the world, a loss of species diversity due to the introduction of Nile Tilapia would be catastrophic for this unique system. Native fishes that in recent years provided 70% of the animal protein consumed in the country would be threatened by the colonization of the Nile Tilapia. We are convinced that should the Nile Tilapia become established in Lake Malawi it would (1) Cause the extirpation/extinction of native fishes, (2) Hybridize with endemic *Oreochromis* spp., and (3) Damage the livelihoods of existing artisanal fishermen.

Keywords Nile tilapia · Cichlidae · Fishing industry · Tilapia

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Introduction

The introduction of non-native fish species is a practice, dating back to the Middle Ages, with the common carp (*Cyprinus carpio* Linnaeus) being one of the earliest fish to be introduced outside its natural range (Alves et al. 1999). Species introduction is a human mediated transfer of organisms into an area out of their native range. Fishes have been introduced both purposefully (Garcia-Berthou et al. 2005) and unintentionally (Copp et al. 2005). Unintentional fish introductions often occur because of movement of fishes by humans or changes in the physical and/or

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chemical conditions of the environment, which facilitate fish movement (e.g., construction of the Welland Canal around Niagara Falls) without any linkage to human desires. More often, however, fishes are introduced deliberately to satisfy human intents (Welcomme 1988). After introductions, the non-native fishes may establish viable populations and expand their range of establishment either through vicariance or dispersal.

Intentional fish introductions have been initiated for many reasons, including enhancing capture fisheries, responding to aesthetic and ornamental demands such as aquarium trade, recreational angling, enhancing food supply through aquaculture, filling unoccupied habitat, and for biocontrol of undesirable species (Kerr and Grant 2000; Gozlan 2008). In some cases, tremendous socio-economic gains have accrued from fish introductions, including increased catches and associated economic activity (Reynolds et al. 1995; Ogutu-Ohwayo and Hecky 1991). This has made introductions globally enticing, increasing, and difficult to restrain (Blanchet et al. 2009; Gozlan et al. 2010). The purpose of this paper is to discuss the vulnerability and potential consequences of introduced fishes in Lake Malawi.

Overview of the biodiversity of fishes in Lake Malawi

Cichlids of the Great Lakes of Africa have speciated rapidly (Fryer and Iles 1972; Owen et al. 1990; Stauffer et al. 2007), with Lake Malawi harboring more than 850 (approximately 480 described) species (Konings 2016). Lake Malawi harbors more species and more endemic species of fish than any other lake in the world. As early as 1893, the unique diversity of the fishes inhabiting Lake Malawi was recognized by Günther (1893 in: Eccles and Trewavas 1989) and subsequent taxonomic studies of the fishes of Lake Malawi were well documented in the early literature (e.g., Boulenger 1901; Regan 1922). Regan's (1922) revision of the fishes of Lake Malawi encouraged several collecting expeditions, which provided the material for Trewavas' (1935) classic synopsis of the fauna, which was expanded by Eccles and Trewavas (1989). Since then, other surveys of the cichlids in Lake Malawi include Ribbink et al. (1983), Lewis et al. (1986), Turner (1996), Snoeks (ed 2004), and Konings (2016). Since 1984, there have been some 850–900 papers published on the cichlids of Lake Malawi.

Situated in one of the world's poorest regions, the fishes of Lake Malawi contribute significantly towards the food security, livelihoods, and economy of lakeshore communities. The lake is bordered by three countries (Malawi, Tanzania, and Mozambique) which together harvest some 80,000 tonnes of fish from the lake, predominantly via artisanal fishers (Weyl et al. 2010). Recently, the total fish-catch has been increasing due to the Lake Sardine, *Engraulicypris sardella* (Günther), and is currently the most important fishery species (Kanyerere et al. 2019). In 2018, Malawi reported a total catch of 221,849 metric tonnes (Government of Malawi 2019).

In Malawi, 23% of land is covered with water (Government of Malawi 2016). Thus, fish and the fisheries sector play a vital role in providing employment, nutrition, and income to Malawians. In addition to a large and vibrant artisanal fishery, there is also a trawl fishery which supply fish directly to urban centers and focuses mainly on offshore demersal and pelagic cichlids (Weyl et al. 2010). Fishes provide the least expensive source of animal proteins for the majority of Malawians and also provide economic support for about 14% of Malawians. Historically, the fishing industry provided 70% of animal protein consumed in the country (Government of Malawi 2019). The staple diet is dominated by maize and cassava, while fish supplements vitamins, minerals, micronutrients, and essential fatty acids (Jamu et al. 2011). The lakeshore area supports more than two million people in activities such as agriculture, fishing, tourism, and transportation. The fishing sector employs ~60,000 fishers and ~500,000 people in fisheries-related industries such as fish processing and marketing, net making, boat building, and engine repair and further supports the livelihoods of over 1.6 million people (Government of Malawi 2016). Malawian fisheries are classified into the small-scale commercial sector (traditional or artisanal) and the large-scale commercial sector (large capital investment). Data for catch rates are difficult to determine, but estimates are provided by the government of Malawi. Fish landings from small-scale fishing are ~45,000 tonnes per year, that consist predominantly of *usipa* and *utaka* (plankton-feeding rock-dwelling fish). The large-scale sector accounts for ~ 5600 tonnes of fish per year (Government of Malawi 2009).

The aquaculture sector produced 9014 metric tonnes in 2019, which was a decrease from 12,217 metric tonnes in 2017. The decline was attributed to low rainfall in 2019. The sector has about 15,000 fish farmers (Government of Malawi 2019). Fish farming mainly uses indigenous species like *Clarias gariepinus* (Burchell), *Coptodon rendalli* (Boulenger), *Oreochromis karongae* (Trewavas), and *Oreochromis shiranus* (Boulenger). The government bans the use of exotic species in Malawi (Government of Malawi 2016), but Nile Tilapia, *Oreochromis niloticus* (Linnaeus) is being cultured in the Lake Malawi catchment on the Tanzanian side (Kanyerere et al. 2019).

History of introductions of fishes in Lake Malawi

Despite the introductions of *Oncorhynchus mykiss* (Walbaum) into Nyika Highland streams in 1908 (Snoeks, 2004), *Micropterus salmoides* (Lacepéde) in the 1920s, *C. carpio* in 1976, and the lungfish *Protopterus annectens brieni* Poll by an ornamental fish trader (Tweddle 1989; Weyl et al. 2010; Snoeks 2004) the Malawian government remains opposed to fish introductions and has put in place legislation against introducing fishes (Government of Malawi 1997: Part XI Sect. 41(1) c; pubs.iclarm/.net/wfcms/file/bmz/Malawi_policy.pdf). For example, the suggestion in the 1950s and 1980s to introduce the clupeid *Limnothrissa miodon* (Boulenger) (Kapenta) from Lake Tanganyika into Lake Malawi was rejected (Jackson 2000). The common carp, which was introduced for aquaculture from Israel into Malawi in 1976 was restricted and later banned from the Lake Malawi catchment to protect the endemic fishes of the lake (Bandula 1997). Similar protection is not provided by the other countries where no legislation currently exists to prevent the use of non-native species in the catchment basin of Lake Malawi. As a result, *O. niloticus*, alongside another invasive tilapia *Oreochromis leucostictus* (Trewavas), has recently (2010) been introduced into the Lake Malawi catchment on the Tanzanian side from Morogoro to develop a new fishery at Lake Itamba and aquaculture near Songea (Genner et al. 2013). We could not find information on the spread of these introductions.

With the above exceptions, the knowledge we have of the impact of introduced fishes in Lake Malawi is based on within lake transfers. The vast majority of fishes native to Lake Malawi are endemic. Additionally, endemism to rock outcroppings, islands, and isolated shorelines within the lake is extremely high (Fryer and Iles 1972; Ribbink et al. 1983; Stauffer 1988). For example, some species of cichlids were introduced in the 1970s at Thumbi West Island in the southern part of Lake Malawi, from areas where they were endemic (e.g., Likoma Island) by the sole exporter (at that time) of ornamental fishes (Ribbink et al. 1983; Trendall 1988). Hert (1990) discussed the coexistence of an introduced species, *Metriaclima aurora* (Burgess) in a very species-rich community. She showed that when territorial males of *M. aurora* were removed, the territories were re-occupied by conspecifics. *Metriaclima aurora* would home from distances of 2.5 km (Hert 1992). Stauffer and Hert (1992) demonstrated morphological divergence between the transplanted and native populations of both *Metriaclima callainos* (Stauffer and Hert) and *M. aurora* and hypothesized that such divergence may have resulted from a founder effect (Mayr 1963), random drift, selection pressures, or ecologically mediated phenotypic plasticity (Chernoff 1982; Meyer 1987; Stauffer and Gray 2004). Stauffer et al. (1996) further showed that the transplanted population of *Cynotilapia zebroides* (Johnson) (referred to as *C. afra*) to Thumbi West Island, hybridized with the resident *Metriaclima zebra* (Boulenger).

Dispersal and increase of introduced organisms

The impact of introducing non-native species is one of the most damaging anthropogenic impacts on biodiversity (Mills et al. 1993; Kolar and Lodge 2002). The great lakes of the world are particularly vulnerable because of their high degree of endemism and their relatively stable physical and chemical characteristics. The adverse impacts of the introduction of non-native fishes are exemplified in the Great Lakes of North America. Native fish communities in this region have been irreparably harmed by the introductions, both accidental and intentional, of exotic species (Jude et al. 1995). Piscine invaders such as Sea Lampreys (*Petromyzon marinus* Linnaeus), Alewives (*Alosa pseudoharengus* (Wilson)), and Rainbow

Smelt (*Osmerus mordax* (Mitchill)) have had cascading detrimental effects on the native biota of the Great Lakes region in North America (Fuller et al. 1999; Jude et al. 1995). Invasive species have been linked to habitat alteration including: (1) Vegetation removal, (2) Changes in water quality (Mitchell 1986), (3) Introduction of parasites and diseases (Moyle et al. 1986), (4) Trophic alterations, competition for food, predation (Meffe 1985; Hindar et al. 1988; Townsend and Crowl 1991; Moyle et al. 2003), (5) Hybridization (Hocutt and Hambrick 1973; Raesly et al. 1990; Leary 1995; Stauffer et al. 1996), (6) Spatial alterations and competition for space (Moore et al. 1983; Gatz et al. 1987, Peterson and Fausch 2003, Van Snik Gray et al. 2005), and (7) Extirpation of native species (Schoenherr 1981; Taylor et al. 1984; Lemly 1985; Stauffer et al. 2016). Ross (1991) found that the majority of studies (77%) examining effects of non-native species documented a decline of native fishes following the introductions. In the few cases in which a fish introduction was thought to have no effect, small, localized populations or habitats heavily influenced by stochastic events were involved (Moyle et al. 1986; Courtenay and Moyle 1996; Brown and Moyle 1997).

Although the above studies have shown that invasive species can decrease native biodiversity, the biotic resistance hypothesis suggests that a highly diverse native system limits the ability of invasive species to successfully colonize (Freestone et al. 2013; Bufford et al. 2016). If true, then the loss of biodiversity caused by invasive species, habitat degradation, etc. can result in a positive feedback system which would increase the success of future invaders. Beaury et al. (2020) states that although experimental studies suggest that high native diversity retards invasive species, there is inconsistent support for the effectiveness of biotic resistance in plant communities; however, Beaury et al. (2020) did show that the richness of plant species reduced the presence of non-native plants in areas surveyed by the National Park Service of the U.S.

At one time, it was assumed that the predominant factor that controlled the organization of natural communities was interspecific competition (Dunham et al. 1979). This assumption was inferred from niche shifts and morphological changes in the form of character displacement, which are correlated with geographic variation (Dunham et al. 1979). Simberloff and Wilson (1969), however, indicated that competition may not be as important as previously thought, at least for insular areas. Pianka (1981), based on work by several authors, stated that the outcome of interspecific competition depends upon (1) Initial population densities (Neyman et al. 1956), (2) Environmental conditions (Park et al. 1964), and (3) The genetic constitution of competing populations (Park et al. 1964). Nevertheless, initial numbers may not be important in terms of which species "wins" (DeBach 1966). The above discussion assumes that competition is influenced by the improvement of a species' own intrinsic capabilities through either an r or K strategy. A species, however, can also successfully compete by developing means to impair its competitors (i.e., α-selection; Gill 1974). Irrespective of the above theoretical discussion, the outcome of two ecological homologues was probably best described by DeBach (1966:189) when he stated: "If two ecological homologues simultaneously happen to invade a new area by chance – an unlikely possibility – or by purposeful manipulation by man – which is more probable – then the winner will be the species which produces the more female progeny which survive to reproduce per parental female per unit time." DeBach (1966) further states that two species do not have to be homologues for one to displace the other. This phenomenon can occur if the broad niche of one species completely overlaps the narrow niche of the other.

Oreochromis niloticus – a threat to the fisheries of Lake Malawi?

Oreochromis niloticus is a freshwater cichlid species indigenous to the tropical and subtropical parts of the eastern and western Africa such as the Nile, Benue, Niger, Senegal and Volta river basins, and lakes Albert, Edward, Kivu and Chad, and many small-size drainages, and the Middle East, especially the Yarkon river in the south-western Middle East (CABI 2015; Nico et al. 2015). In addition, evidence strongly suggests Nile Tilapia is indigenous to Lake Tanganyika too (Trewavas 1983). The Nile Tilapia is cultured more than any other tilapiine species throughout the world (Watanabe et al. 2002; Green and Duke 2006). Its tolerance to a wide range of environmental conditions has made it a preferred species for aquaculture;

additionally, this tolerance has contributed to its ability to successfully establish viable populations where it has been introduced (Grammer et al. 2012). Its preferred temperature ranges between 14 and 33 °C but can tolerate a temperature range of 11–42 °C (FAO 2016). The species occurs in a wide range of freshwater habitats such as lakes, rivers, irrigation and sometimes even sewage canals, and estuarine habitats (Froese and Pauly 2015). Although it has been reported from estuarine systems, it is less salt tolerant than some other *Oreochromis* spp. (Watanabe et al. 1985a, 1985b; Avella et al. 1993). In lakes, the fish is benthopelagic (Riede 2004), being usually found in shallow, still waters of depth range 0–6 m (Wudneh 1998), sometimes venturing into 20 m deep water (Van Oijen 1995). It also prefers large river systems with adequate vegetation cover (Picker and Griffiths 2011).

This tilapiine species has a flexible and opportunistic feeding habit, with an omnivorous diet ranging from phytoplankton, zooplankton, periphyton, aquatic plants, detritus, benthos, small fish, and fish eggs (FAO 2016). Nile Tilapia can filter water by entrapping suspended particles, including phytoplankton and bacteria, on mucus in the buccal cavity, although its main source of nutrition is obtained by surface grazing on periphyton mats. The species is also known to exhibit opportunistic feeding strategies and Nile Tilapia have been shown to feed at any trophic level, including small insect stages, microcrustaceans, and fish (McKaye et al. 1995; Njiru et al. 2004; Zengeya et al. 2011). Nile Tilapia shows considerable trophic plasticity depending on the environment and the presence of food competitors (Bwanika et al. 2007). Dissolved oxygen is often not a big problem as the fish can survive in as low dissolved oxygen as 3–4 mg L^{-1} although it prefers at least 5 mg L^{-1} (Boyd 2004). Depending on temperature and environment, the fish reaches sexual maturity in 3–6 months (FAO 2016). Maturity size range is 6–28 cm, but the maximum SL for males is 60.0 cm (Eccles 1992). It can attain a maximum weight of up to 10 kg (IGFA 2014) and can have a lifespan of up to 10 years (Noakes and Balon 1982) The fish is a maternal mouthbrooder and hatched larvae and fry remain brooded in the mouth until the yolk sac is completely absorbed after two weeks (Froese and Pauly 2015).

The Nile Tilapia is widely introduced for augmentation of capture fisheries, aquaculture, and recreational fishing (Trewavas 1983; Welcomme 1988). *Oreochromis niloticus* is used especially where native fisheries for tilapias are inadequate or overfished (Ogutu-Ohwayo and Hecky 1991). The species is also used as a biocontrol agent because it feeds on aquatic weeds such as *Chara* spp., *Najas marina* Linnaeus, duckweed (*Lemna* spp.), and benthic filamentous algae (Kour et al 2014). The aquaculture of the Nile Tilapia is widely seen as a means of food security, economic development, as well as the reduction of poverty in most countries in Africa (NEPAD 2005). Tilapias are among the most widely cultured fish species in the world and are the third most cultured species after carps and salmonids (FAO 2010). Of the tilapias, *O. niloticus* is the most preferred because of its fast growth and reduced tendency to stunt, its hardy nature, broad ecological and feeding adaptations, and flexible life history traits that enable it to inhabit diverse ecosystems (Pillay and Kutty 2005; Trewavas 1983). It is a fast-growing fish, achieving a market size of 700 g in 6 months (Watanabe et al. 2002). Presently, *O. niloticus* dominates production from aquaculture (FAO 2010). Its popularity as an aquaculture species has resulted in it being referred to as “aquatic chicken” by the World Fish Center, an organization that promotes the farming of tilapias globally (Tweddle and Wise 2007). The species has also been dubbed a "poor man’s" fish for its suitability in ending poverty through aquaculture (Mair 2003). Consequently, *O. niloticus* is one of the top ten most introduced species globally (Picker and Griffiths 2011), has been introduced into 102 countries worldwide including all countries in the tropics, and is the primary species for tropical aquaculture (CABI 2015).

Although *O. niloticus* has invaded the Lake Malawi catchment, it was not yet in the lake itself in 2013 (Genner et al. 2013; Kanyerere et al. 2019). Historically, however, the Nile Tilapia has been successful in dispersing once it has been introduced in the catchment area. After *O. niloticus* was introduced for aquaculture in the catchment of the Kafue River in Zambia in 1982, it was then found in the Kafue River by the mid-1990s after escaping from a nearby fish-farm (Schwank 1995). The Nile Tilapia also escaped from a fish-farm in the upper Revue River near Chimoio town in Mozambique and was found in Lake Chicamba a few years later (Weyl 2008). After the Nile Tilapia was introduced into Lake Kariba, it later dispersed to most parts of the middle Zambezi and other drainages (Van der Waal and Bills 2000; Tweddle and Wise 2007; Weyl 2008). In all the areas surveyed through literature, the Nile Tilapia was able not only to establish itself where it was introduced but was also able to spread to the water bodies in the catchments. Several authors (e.g. McIntyre 2009; Weyl et al. 2010) have discussed the vulnerability of Lake Malawi to invasion by the Nile Tilapia because of the widespread use of the species for aquaculture in the countries bordering the lake. Kanyerere et al. (2019) warns that if Nile Tilapia escapes from the aquaculture farms in Tanzania and enters Lake Malawi, the effects will be disastrous especially on the indigenous *Oreochromis* species.

Invasion risks

The probability of the Nile Tilapia successfully colonizing Lake Malawi is enhanced by many of its life history attributes. The Nile Tilapia is larger (i.e., 63 cm; 10 kg) than the native tilapiine fishes (31–39 cm TL and 0.5–1.1 kg; Trewavas 1983). The Nile Tilapia has a diverse repertoire of feeding options and consumes benthic algae, phytoplankton, macro-invertebrates, and fishes (Njiru et al. 2004; Bwanika et al. 2007; Zengeya et al. 2011). Although there is only one substrate brooding cichlid in Lake Malawi, *C. rendalli*, the Nile Tilapia is known to prey on the eggs or young of other species (Zambrano et al. 2006). Males of Nile Tilapia are particularly aggressive and readily attract and spawn with other tilapiine species, thus opening the avenue for introgression and dilution of gene pools of native species (Fessehaye et al. 2006; Kour et al. 2014). The introduction of diseases and parasites (e.g., whirling disease, spring viraemia carp disease) to native fishes has been associated with the introduction of the Nile Tilapia (Soliman et al. 2008; Montana Water Center 2011). Finally, the decrease in underwater native plant diversity and its associated fauna that follows the introduction of the Nile Tilapia has resulted in habitat loss (Kour et al. 2014), bioturbation, and nutrient recycling (Starling et al. 2002; Figueredo and Giani 2005) all of which enhances eutrophication. Thus, the fish easily invades new environments and has become one of the top ten most widely distributed invasive alien species, successfully establishing feral populations in most parts of the tropical and subtropical world (Gu et al. 2015). Specific examples of the impacts rendered by the introduction of the Nile Tilapia are listed in Table 1.

Impacts

The great success of Nile Tilapia as an invasive species has been attributed to aggressive spawning behavior, high levels of parental care, the ability to spawn multiple broods throughout the year, and its broad diet (Canonico et al. 2005). In areas where this species has become established, ecological effects include decreased abundance and extinction of native species resulting from habitat and trophic overlaps and competition for spawning sites (See reviews by Canonico et al. 2005; Tweddle and Wise 2007), habitat destruction and water quality changes (Figueredo and Giani 2005), and hybridization with other *Oreochromis* species (Firmat et al. 2013). Shechonge et al. (2019) summarizes the literature of hybrids noted between the Nile Tilapia and other *Oreochromis* spp. throughout Africa.

Where introduced, Nile Tilapia has had devastating impacts through competition or hybridization with native congenerics (Canonico et al. 2005; Tweddle and Wise 2007). In Nicaragua, the escape of Nile Tilapia from aquaculture and its subsequent establishment resulted in a decline in native cichlid catches of more than 50% (McKaye et al. 1995). In Lake Alaotra, Madagascar, the progressive introductions of different species including Nile Tilapia induced a drastic decline of native fish (Lévêque 1997) and in changes in phytoplankton communities in Brazil (Figuerdo and Giani 2005). The most devastating impact of introductions of the Nile Tilapia in Africa is via hybridization. Nile Tilapia are able to hybridize with several other *Oreochromis* species. In the Lake Victoria basin, hybridization has been reported between *O. niloticus* and the endemic *Oreochromis variabilis* (Boulenger) (Welcomme 1967) and *Oreochromis esculentus* (Graham) (Mwanja et al. 2012). In southern Africa, Nile Tilapia introductions have resulted in extensive hybridization and introgression with native *Oreochromis mossambicus* (Peters) in the Limpopo River system (D'Amato et al. 2007; Firmat et al. 2013), with *Oreochromis andersonii* (Castelnau) and *Oreochromis*

Table 1 A summary of the impacts of *Oreochromis niloticus* on aquatic ecosystems

Impact	Country	References
Oreochromis esculentus & *Oreochromis variabilis* (native tilapias) became extinct after 30 years of its introduction in Lake Victoria; Other east African lakes also experienced declines of native tilapias	Tanzania, Kenya, Uganda	Tweddle and Wise (2007), Ogutu-Ohwayo (1990)
Increased total fish catch by between 2 and 12% in Lake Victoria	Kenya	Tweddle and Wise (2007)
Decline of endangered Moapa dace (*Moapa coriacea*) and Moapa White River Springfish (*Crenichthys baileyi moapae*)	Nevada & Arizona, USA	Scoppettone et al. (1992)
Implicated in an outbreak of trematodes in Lake Nicaragua	Nicaragua	McCrary et al. (2007)
Improved fish production in fisheries and aquaculture, but depressed local fish diversity	Bangladesh	Welcomme (1988), Jalal and Rouf (1997)
Replaced native species and became pests in open waters after excessive reproduction success	Thailand	De Iongh and Van Zon (1993)
Played a part in the extinction of cyprinids in Lake Lanao, Mindanao, and have contributed to driving the endemic "sinarapan" of Lake Buhi to the edge of extinction	Philippines	Bleher (1994), Juliano et al. (1989)
Caused the displacement of endemic species, and resulted in their own over-population and stunting; 31% of native fishes are considered at risk or already extinct	Mexico	FAO (2010)
Replaced native cichlid fish in Lake Nicaragua's fishery, and led to 80% decline in native cichlids	Nicaragua	McKaye et al. (1995), Coleman (2001)
In Lake Itasy, Nile Tilapia hybridised with the formerly introduced *O. macrochir*, which led to the disappearance of the latter	Madagascar	Welcomme (1984)
Competition between Nile Tilapia and indigenous species for food and breeding territories with the subsequent danger for native fish populations in the Darling River system	Australia	Arthington and Blühdorn (1996)

macrochir (Boulenger) in the Kafue River in Zambia (Deines et al. 2014) and they have almost replaced the native *Oreochromis mortimeri* (Trewavas) in Lake Kariba, Zimbabwe (Tweddle 2010). In South Africa, the impact of *O. niloticus* introductions including hybridization and introgression with native *O. mossambicus* has been well studied (Moralee et al. 2000; D'Amato et al. 2007; Firmat et al. 2013). Hybridization is recognized as a primary threat to *O. mossambicus* and the latter is consequently IUCN redlisted as 'Vulnerable' (Kazembe 2010). Finally, the Nile Tilapia has hybridized with *Oreochromis placidus rovumae* (Trewavas) (Blackwell et al 2020), which is closely related to *Oreochromis shiranus* (Trewavas) (Ford et al. 2019), which is endemic to Lake Malawi.

Thresher et al. (2020) includes both overfishing and introduced fishes as reasons for the decline in native fishes in a lake in Papua New Guinea but suggested that the rapid increase in numbers of the Nile Tilapia may relieve the pressure of fishing on native fishes and thus have a positive impact. Although overfishing is a detriment to native fishes in Lake Malawi, there is already a fishery for tilapia, and we reject any suggestions that the introduction of the Nile Tilapia would have a positive impact on this diverse system. We postulate that should a reproducing population become established, it would be virtually impossible to eradicate them. Historically, control methods for an established alien fish, including chemicals, physical barriers, and biological agents would be ineffective in Lake Malawi (Stauffer et al. 1988).

Conclusions

Trendall (1988) discussed the intra-lake translocations of rock-dwelling cichlids at Thumbi West Island. He concluded that the introduced species did not cause extirpation of the native fishes, but that any potential impact needed further study. This is true in this case because all studies were performed after the introductions and there is no baseline study available for Thumb West Island before 1970. There are some species or geographical variants of species endemic to the island and one or more may have already been extirpated before the latter studies were conducted. One species, *Aulonocara* sp. 'yellow collar', occurs all around the Nankumba Peninsula and its islands but is absent from Thumbi West Island. It is conceivable that it was present around the island before another species of *Aulonocara*, *Aulonocara stuartgranti* Meyer and Riehl, was introduced there in the early 1970s. Stauffer et al. (1996) reported on hybridization between the native *M. zebra* and the introduced *C. zebroides*. We hypothesize that the most vulnerable species to the introduction of the Nile Tilapia are the native "Chambo" (*Oreochromis* spp.). These prized food fishes are currently severely overfished, and many populations have collapsed. *Oreochromis karongae* and *Oreochromis squamipinnis* (Günther) are now listed as Critically Endangered on the IUCN Red Data List (Kanyerere et al. 2019; Phiri and Kanyerere 2018) and *Oreochromis lidole* (Trewavas) is listed as Critically Endangered and Possibly Extinct (Konings 2018). Thus, they are particularly vulnerable to the invasion of a congeneric species. Popovic and Bernatchez (2020) discussed the threats of introgressive hybridization to Tanzania's endemic biodiversity. *Oreochromis korogwe* (Lowe) from southern Tanzania was threatened by the invasion of the Nile Tilapia (Blackwell et al. 2020). With Lake Malawi harboring more species of fishes than any other freshwater lake in the world, a loss of species diversity due to the introduction of Nile Tilapia would be catastrophic for this unique system.

Aquaculture of the Nile Tilapia is prohibited in Malawi within the catchment area of the lake. If Mozambique and Tanzania adopted a similar restriction and populations within aquaculture facilities were prohibited it may be possible to prevent the invasion of Nile Tilapia into Lake Malawi. If breeding populations are established within the lake, its dispersal cannot be halted. Certainly, its establishment and spread in the lake will negatively impact the native fishes. Even if the high diversity of fishes inhabiting Lake Malawi created an effective biotic resistance to the spread of Nile Tilapia, the fact that it will undoubtably hybridize with endemic *Oreochromis* spp. will result in a negative impact as noted by Blackwell et al. (2020) who reported the genetic impact of Nile Tilapia introductions on native *Oreochromis placidus* (Trewavas).

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Data availability The data that support the findings of this study are in the literature cited or catalogued into the Penn State University Fish Museum.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Consent to publication All authors have consented to publish this version of the manuscript.

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