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Review article

A review of the populations of tilapiine species in lakes Victoria and Naivasha, East Africa

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This paper discusses the catch trends, population attributes and biological characteristics of tilapiine species that are both native and that have been introduced into Lake Victoria and Lake Naivasha. Predation by *Lates niloticus*, species hybridisation, overfishing, pollution and eutrophication have negatively impacted endemic fish stocks in these lakes. Four tilapiine species, *Oreochromis niloticus, Oreochromis leucostictus, Coptodon zillii* and *Coptodon rendalli*, and three tilapiine species, *O. niloticus, C. zillii* and *O. esculentus*, were hence introduced into Lake Victoria and Lake Naivasha, respectively, to improve fish catches following collapse of native fish stocks. Establishment of these non-native species was associated with declines in populations of the native *Oreochromis esculentus* and *Oreochromis variabilis*, and *O. niloticus* now dominates commercial tilapiine fishery in Lake Victoria. The fishery catches in Lake Naivasha were dominated by the introduced *O. leucostictus* and *O. niloticus*, whereas *C. zillii* is rarely caught. The biological and population attributes of the tilapiines in both lakes have shown great variations over time. There is, therefore, a need for implementation of effective management measures, including control of fishing effort, pollution control and protection of surrounding wetlands, to promote recovery and long-term sustainability of the fishery resources of these lakes.

Keywords: overfishing, pollution, population biology, tilapiine catch trends, wetland degradation

Introduction

Tilapiines are native to Africa and the south-western Middle East, and have been introduced to other regions primarily for biological control of aquatic weeds and insects, as baitfish for capture fisheries, as a food fish in aquaculture systems, as aquarium species, and to boost capture fisheries (Canonico et al. 2005). Tilapiine fishes of the genera *Oreochromis, Sarotherodon, Coptodon, Heterotilapia* and *Pelmatolapia* are important in artisanal and commercial fisheries and aquaculture (Dunz and Schliewen 2013; Yongo et al. 2018a; Shechonge et al. 2019). Most of the tilapiine species have been heavily exploited in their native ranges, whereas some species have been introduced into new habitats (Njiru et al. 2005; Russell et al. 2012). Tilapiines are known to occupy both freshwater and estuarine environments within their native ranges, and some species have become invasive in both types of systems in other countries (Canonico et al. 2005).

The life history characteristics of tilapiines have been used to explain their invasive capabilities and successful exploitation or colonisation of a wide range of freshwater habitats (Russell et al. 2012). Previous studies suggest that the reason why tilapias have been able to colonise a range of habitat types is because of phenotypic plasticity that allows them to shift some of their life-history characteristics along a continuum between altricial and precocial styles (Arthington and Milton 1986). A precocial life-history style is characterised by prolonged somatic growth, deferred maturation, reduced fecundity, increased parental care and an extended life span; whereas, a altricial life-history pattern is characterised by short growth intervals, early maturation, higher fecundity, reduced parental care and a short life (Russell et al. 2012). Tilapiines offer high protection for their young, for example nest-building *Tilapia* species guard fertilised eggs in the nest, whereas mouth-brooding species of *Sarotherodon* and *Oreochromis* fertilise eggs in brooding bowers, and then incubate them in the mouth for several days after hatching (Canonico et al. 2005). Guarding the young considerably increases survival and reproductive success, whereas mouthbrooding protects their eggs from environmental conditions. Mouthbrooders do not have strict habitat requirements for reproduction, so they

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can occupy all available habitats within their spawning sites and even colonise a new environment by carrying eggs/young ones in their mouth, thereby increasing their invasive capability (Njiru et al. 2006).

Most tilapiine species have a prolonged spawning season that assists them to maximise the reproductive potential and, in turn, the ability to colonise new habitats. They are euryphagous as their diet comprises a wide range of food items, including plankton, some aquatic macrophytes, planktonic and benthic aquatic invertebrates, larval fish, detritus and decomposing organic matter (Njiru et al. 2004; Canonico et al. 2005). This great food plasticity and diversified feeding mode in tilapiines promotes their successful invasion in new habitats (Martin et al. 2010; Zengeya and Marshall 2008; Zengeya et al. 2011). The invasion of tilapiines can cause ecological problems in several ways, including potential to outcompete native species for food and habitats, localised extirpation of native fish species through preying on eggs and fry, increased eutrophication, because of bio-turbidity usually resulting from the feeding and excretion habits of tilapiines (Canonico et al. 2005; Russell et al. 2012; Chifamba and Videler 2014). In summary, invasion by tilapiine species can potentially stimulate growth of phytoplankton by increasing water turbidity and releasing of nutrients into the water column through resuspension of bottom sediments. Invaded systems are therefore usually associated with increased turbidity of the water, deteriorating water quality and eutrophication. Rapid population growth of invasive tilapiines in recipient systems can also cause decline in the biomass of native fish species through competition, and thus affects the sustainability of fishery resources.

Certain tilapiine species, such as *Oreochromis niloticus* and *Oreochromis mossambicus*, are well-suited for aquaculture production, because they are fast-growing and tolerant of a range of environmental conditions (Yongo et al. 2018a). These species adapt readily to changes in salinity levels and oxygen availability, can feed at different trophic levels, and, under certain circumstances, can tolerate overcrowding (Coward and Little 2001; Martin et al. 2010). Other tilapiine species used in aquaculture include blue tilapia (*Oreochromis aureus*), mango tilapia (*Sarotherodon galilaeus*), longfin tilapia (*Oreochromis macrochir*), redbreast tilapia (*Coptodon rendalli*), and the Mozambique × Wami hybrid (*O. mossambicus* × *Oreochromis urolepis hornorum*). The red hybrid tilapia (*O. mossambicus* × *O. niloticus*) is also being used for aquaculture (Hashim et al. 2002). *Oreochromis aureus*, *O. mossambicus*, *O. niloticus*, and the Mozambique × Wami hybrid are widely used in aquaculture in the Americas, and have also been reported to have established in the wild (Canonico et al. 2005). Populations of spotted tilapia (*Tilapia mariae*), blackchin tilapia (*Sarotherodon melanotheron*), *Oreochromis macrochir*, *C. rendalli*, and redbelly tilapia (*Coptodon zillii*) have also been established in US waters, whereas *O. mossambicus* has become established in northern Australia (Russell et al. 2012). *Oreochromis niloticus* is a favoured species for aquaculture expansion in Africa, because of its growth performance, tolerance of high stocking densities, marketability and stable market prices (Shechonge et al. 2019).

Oreochromis niloticus has been introduced into Lake Victoria to provide exploitable fisheries (Njiru et al. 2006; Yongo et al. 2018a). The earliest introductions of *O. niloticus* into Lake Victoria were done in the 1950s (Goudswaard 2002) and were sourced from elsewhere in the Nile catchment (Mwanja et al. 2008). The blue spotted tilapia, *Oreochromis leucostictus* was probably introduced into Lake Victoria alongside *O. niloticus*, *C. zillii* and *C. rendalli* during the 1950s (Goudswaard 2002). Various fish species, including tilapiines, have been introduced into Lake Naivasha over time (Hickley et al. 2015). *Coptodon zillii* and *O. leucostictus* were introduced from Lake Victoria into Lake Naivasha in 1956 to establish a population for commercial exploitation. *Oreochromis niloticus* was first introduced into Lake Naivasha in 1967 to diversify and boost the dwindling fishery of the lake (Kundu et al. 2010; Njiru et al. 2017). However, it disappeared from the lake in 1971 (Gozlan et al. 2010), but was later re-introduced in 2011 and 2014 (Waithaka et al. 2020).

This review focuses on the catch trends, population attributes and biological characteristics of both native and introduced tilapiine species in Lakes Victoria and Naivasha. The selection of these two lakes was informed by the availability of comprehensive data from previous studies. Among the aspects presented in this review are the chronology of historical introductions of tilapiines into the two lakes, trends in their catches, and changes in biological and population parameters largely attributed to fishing pressure and the alteration of the ecological conditions of the lakes. This information and the update on the current status of tilapiine fisheries in the two lakes is essential for informing sustainable management to secure the livelihoods and nutrition needs of fish-dependent communities in the region.

Lake Victoria fishery

Original stock composition and changes in catch levels

Lake Victoria is the second largest freshwater lake in the world and the largest in Africa. The lake is shared by Kenya (6%), Tanzania (51%), and Uganda (43%) (Johnson et al. 2000). The local communities in the catchment have relied on Lake Victoria for their livelihood for centuries. Before the introduction of exotic species, Lake Victoria had a multispecies fishery that comprised >500 endemic fish species, dominated primarily by the tilapiines *O. esculentus* and *Oreochromis variabilis* and, haplochromine cichlids (Ogutu-Ohwayo 1990). Other important species included *Rastrineobola argentea, Protopterus aethiopicus, Bagrus docmak, Clarias gariepinus, Schilbe intermedius* and species of the genera *Synodontis*, and of the family Mormyridae. Many of these native species suffered severe declines because of predation by *Lates niloticus*, hybridisation and competition with *O. niloticus*, as well as increased fishing pressure (Njiru et al. 2005; Yongo et al. 2018b). *Oreochromis* variabilis, for example, is classified as Critically Endangered on the IUCN Red List of threatened species, because it has suffered severe attrition in its native range, as a result of the introduction of *Lates niloticus*, *O. niloticus* and *O. leucostictus* from the 1950s onwards (Shechonge et al. 2019).

Lates niloticus was introduced from Lake Albert into the Ugandan and Kenyan parts of Lake Victoria between 1954 and 1963, with the aims of creating a recreational fishery and converting the large biomass of the indigenous small bony haplochromine cichlids into a less-productive but more valuable resource (Pringle 2005; Yongo et al. 2017a).Haplochromine cichlids were the dominant fish in Lake Victoria during the 1970s, forming the major prey item for the introduced *L. niloticus* (Figure 1). However, from 1970s to 1989 there was a boom in *L. niloticus* abundance that coincided with the decline of the endemic haplochromine cichlid species (Figure 2). The reduction in cichlid catches was attributed primarily to predation by *L. niloticus* and overfishing, hybridisation trigged by pollution, and eutrophication (Kolding et al. 2008; Njiru et al. 2008). After depletion of the haplochromine stocks in Lake Victoria at the end of the 1980s, *L. niloticus* shifted to feeding on shrimp, *Caridina nilotica*, juvenile *L. niloticus*, *O. niloticus* and *R. argentea* (Figure 1). The catches of other species, including *Clarias* and *Protopterus* declined, whereas *O. niloticus* instead increased and formed a peak during 2005, following the decline in *L. niloticus* catches (Figure 2). From 1989, *L. niloticus* catches began to decline, and some haplochromine cichlids reappeared in 2000 as shown in Figure 2, also reported by other authors (Balirwa et al. 2003). Accordingly, haplochromines again became the main prey items for *L. niloticus* in Lake Victoria (Figure 1).

According to Marshall (2018), the *L. niloticus* catch rate rose from 0.5 kg h^{-1} in the 1969–1971 trawls to 3.5 kg h^{-1} in 1981 in Ugandan waters (Table 1). This was followed by an increase from 3.5 to 234.7 kg h^{-1} between 1981 and 1985. The haplochromine biomass rose slightly between 1969 and 1971 and 1981, but fell from 391.7 kg h^{-1} in 1981 to 264.6 kg h^{-1} in 1983, followed by a collapse to zero in 1986 (Table 1). The biomass of other species declined from 1982 onwards, with the most rapid collapse beginning in 1984 when the biomass of *L. niloticus* exceeded that of all other species. Direct predation of haplochromines by *L. niloticus* was used as evidence to explain the role of this introduced species in driving the extinction of several native fishes in the lake (Kishe-Machumu et al. 2012; Marshall 2018). However, the impact of introduced tilapiines on the native species remains largely unclear. The reason is partly because of the many other changes taking place in the system over the same timescale, and extensive fisheries operations (Verschuren et al. 2002; Hecky et al. 2010).

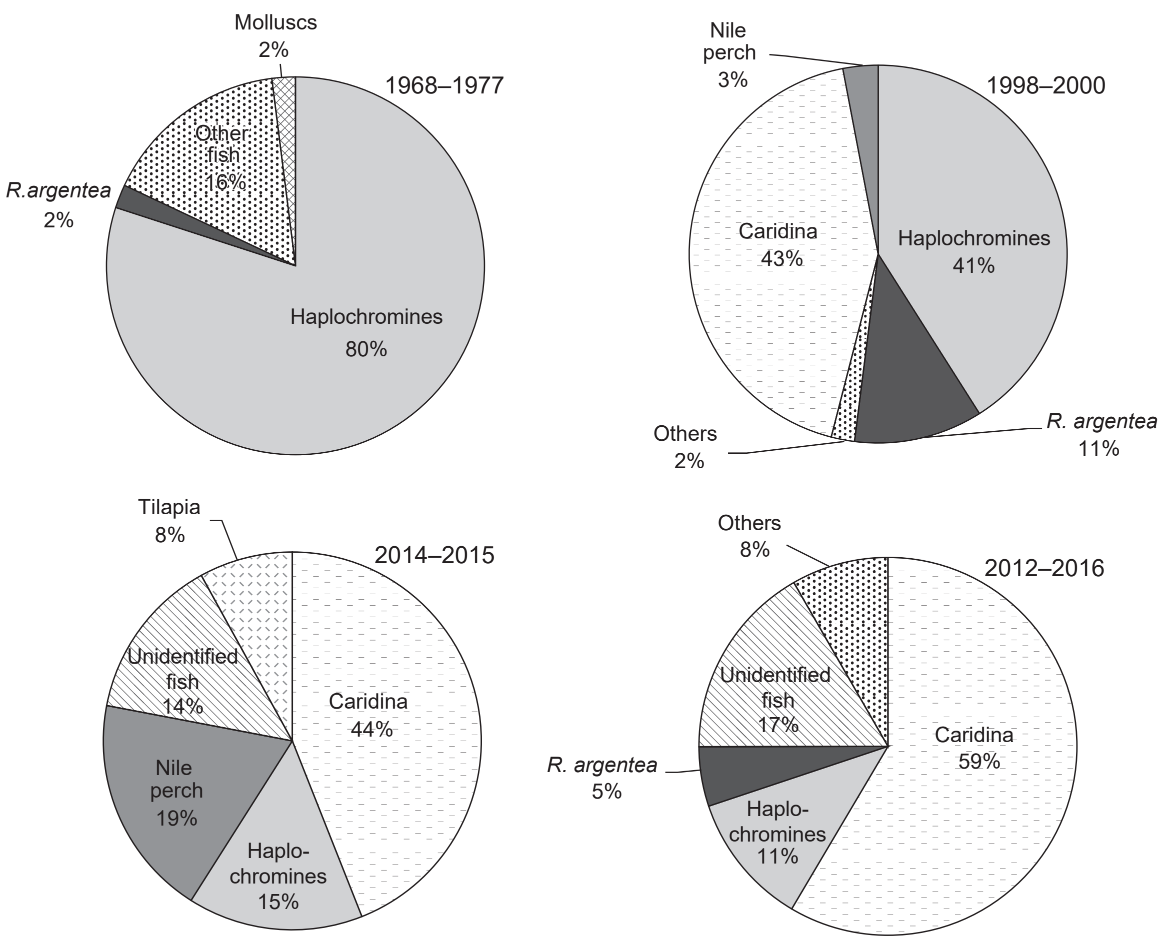

Figure 1: Diet of *Lates niloticus* in Lake Victoria showing *Oreochromis niloticus* not contributing main diet (data adapted from Njiru et al. 2005; Outa et al. 2017; Agembe et al. 2018)

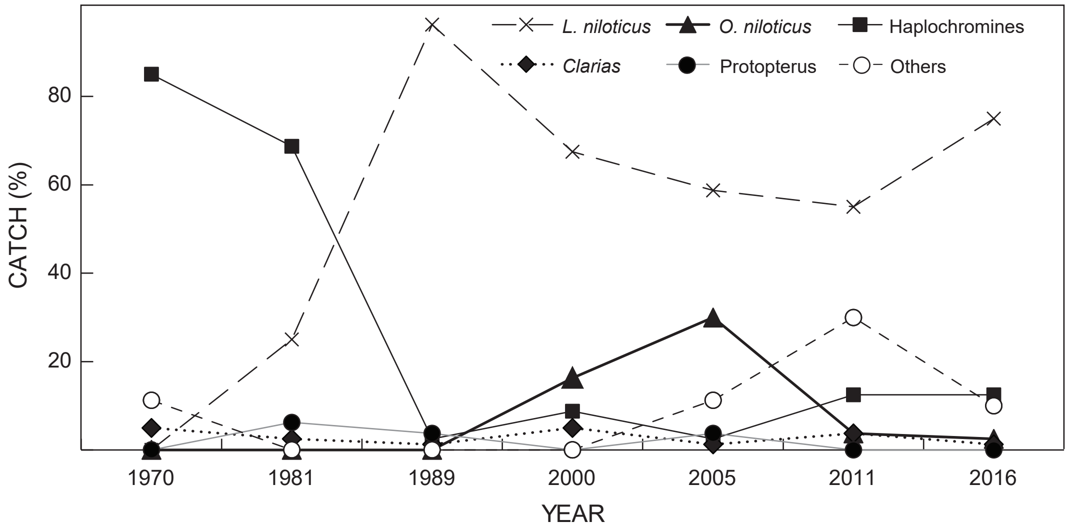

Figure 2: Trends in catches of some major commercial fish species in Lake Victoria from 1970 to 2016 (data adapted from Njiru et al. 2018)

Table 1: The relative abundance (kg h^{-1}) of demersal fish species caught in bottom trawls in the Ugandan waters of Lake Victoria (Adapted from Marshall 2018)

Fish species	1969–1971	1981	1982	1983	1984	1985	1986
Haplochromines spp.	327.4	391.7	295.7	264.6	113.9	17.8	–
Lates niloticus	0.5	3.5	45.3	54.3	140.2	234.7	80.1
Oreochromis niloticus	0.9	12.2	7.3	5.2	1.8	5.0	7.1
Oreochromis esculentus	2.6	0.5	0.1	–	–	–	–
Oreochromis variabilis	0.6	5.6	2.5	0.9	–	–	–
Bagrus docmak	23.5	9.0	9.3	11.3	4.3	1.5	0.3
Clarias gariepinus	17.3	14.4	8.0	4.4	1.8	0.1	–
Protopterus aethiopicus	5.8	4.9	0.1	0.8	0.6	0.1	–
Synodontis spp.	15.4	2.9	0.5	4	0.2	0.1	–
Other species	0.9	0.2	1.6	4.7	0.3	0.3	–
Total	394.9	444.9	370.4	346.6	264.3	259.6	87.5

Debate on the contribution of *L. niloticus* to the demise of Lake Victoria's 500 endemic haplochromine cichlids centres around the 'top-down' and 'bottom-up' hypotheses (Marshall 2018). The former suggests *L. niloticus* destroyed the haplochromines, causing the disruption of food chains and nutrient cycling and so initiating the accelerated eutrophication of the lake. The latter proposes that haplochromines suppressed *L. niloticus* by preying on its eggs and fry or competing with juveniles for food. A recent paper by Marshall (2018) argued that accelerated eutrophication caused by a climatic event led to their collapse, allowing *L. niloticus* to explode. A review of the impacts of eutrophication on Lake Victoria fishes concluded that the haplochromine decline was caused by *L. niloticus* (Witte et al. 2005), but it was later suggested that it was not possible to separate the effects of *L. niloticus* and eutrophication, because both occurred in the same time period (Witte et al. 2013). Other authors have argued that 'bottom up' influences are a more valid explanation for the changes in Lake Victoria, with *L. niloticus* being just one of a multiplicity of stressors (Kolding et al. 2008; Hecky et al. 2010).

Dominance of exotic Nile tilapia over native tilapiine species in Lake Victoria

The introduced tilapiine species quickly established themselves in the lake, particularly *O. niloticus*, which began to appear in commercial catches from the 1960s onwards (Njiru et al. 2005). The catches of *O. niloticus* in Lake Victoria increased progressively in the 1970s, whereas catches of the native species *O. esculentus* drastically declined during the same period (Figure 3). The increased dominance and establishment of *O. niloticus* over other tilapiines in Lake Victoria has been attributed to a number of factors:

(1) *Oreochromis niloticus* co-occurs with *L. niloticus* in their native range in Lake Albert, suggesting that it may have evolved diverse means to minimise predation by the Nile perch (Yongo et al. 2018a).

(2) The faster growth rate of *O. niloticus* is an important factor in enhancing the probability of survival of this species in the presence of a superior predator, compared with the other tilapiines (Njiru et al. 2006).

(3) Stomach content analyses have revealed that *O. niloticus* constituted the least proportion of the prey

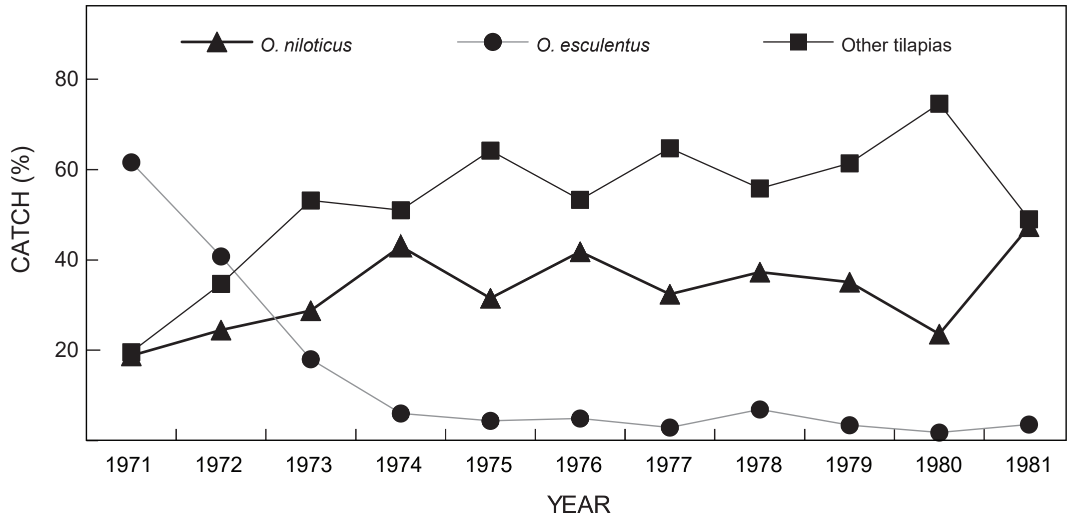

Figure 3: Trends in catches of the tilapiine species in Lake Victoria from 1971 to 1981 (data adapted from Wasonga et al. 2017)

items in the diet of *L. niloticus* (Figure 1; Agembe et al. 2018; Njiru et al. 2006; Outa et al. 2017).

The diversified feeding mode of *O. niloticus* also probably gave the species higher survival rate in the changing Lake Victoria ecosystem. It is an opportunistic omnivore with very diverse diet that includes insects, algae, fish, molluscs and detritus (Njiru et al. 2004). This feeding mode could have conferred competitive advantage against the other tilapiine species, as reported from other studies elsewhere (Zengeya and Marshall 2007). The endemic *O. esculentus* feeds almost entirely on diatoms (Coward and Little 2001); *O. variabilis* feeds mainly on phytoplankton, whereas *C. zillii* feeds mostly on macrophytes (Njiru et al. 2005; Canonico et al. 2005). Studies have reported complex interactions between native and exotic tilapiines in Lake Victoria, including considerable overlap in the diets of adult *O. leucostictus* and *O. variabilis*, as well as the diets of juvenile *O. esculentus* and the three exotic tilapiines (Coward and Little 2001). There was also overlap in habitat and preference for nursery area between *O. variabilis* and *O. leucostictus, C. rendalli* and *C. zillii* (Ogutu-Ohwayo 1990). Competitive interaction between introduced tilapiines and native species was inferred as the most plausible explanation for the decline of the native species (Coward and Little 2001). The introductions resulted in hybridization between *O. variabilis* and *O. niloticus* that could have contributed the decline in *O. variabilis* in some parts of the lake (Wasonga et al. 2017).

Oreochromis niloticus in Lake Victoria have a higher fecundity, which has probably contributed to its success in the lake. Lowe-McConnell (1955) reports that *O. variabilis* produces 324–1 627 eggs, *O. leucostictus* 99–950 eggs, *O. niloticus* 340–3 706 eggs and *C. zillii* 1 000–7 061 eggs in Lake Victoria. The previous studies showed that the fecundity of *O. niloticus* has increased to 905–7 619 eggs for fish of 28–51 cm TL (Njiru et al. 2006). Water hyacinth (*Eichhornia crassipes*) infestation in Lake Victoria provided feeding and breeding grounds for *O. niloticus* (Balirwa 1998; Njiru et al. 2004). Infestation of the lake by the water hyacinth also led to a drastic reduction in beach seining, a common fishing method in shallow waters, allowing the fish time to reproduce and grow (Njiru et al. 2005). This was shown by the increased catches of *O. niloticus* observed during the periods when water hyacinth infested Lake Victoria (Figure 4). *Oreochromis niloticus* has been able to establish in Lake Victoria, currently forming the third commercially important species after the introduced *L. niloticus* and the native *R. argentea*, whereas other tilapias are extinct or are occasionally caught in the lake (Njiru et al. 2008; Agembe et al. 2018; Yongo et al. 2018c)

Factors driving changes in Lake Victoria fish stocks

Management of Lake Victoria fisheries has faced various challenges. *L. niloticus* has also experienced stock decline, because of overfishing. The lake's ecosystem has been severely affected by human activities and environmental changes, including the introduction of exotic species, invasion of water hyacinth, climate change, overexploitation, pollution and eutrophication (Kolding et al. 2008). Increased human population has led to the encroachment of swamps surrounding the lake, clearing land for settlements and agriculture. Clearance of swamps for agriculture contributed to the decline in wetland areas, which are important nursery grounds for *O. esculentus* and feeding grounds for the introduced *C. zillii* (Njiru et al. 2008). Poor agricultural practices and deforestation caused land degradation and soil erosion that have accelerated nutrient loading and agro-chemical input into the water systems (Petr 2000). Nutrient input into the lake also comes from domestic and industrial effluent. Increased pollution has caused the lake's phytoplankton community to be dominated by unpalatable and toxic cyanobacteria, *Microcystis* (Lung'ayia et al. 2000). The algal bloom and increase in cyanobacteria is, because of increased nutrient rich sewage effluent and agricultural runoff. Algal blooms can cause fish mortality, because of the anoxic conditions.

Several studies have shown that the rapid growth and establishment of water hyacinth, *Eichhornia crassipes*

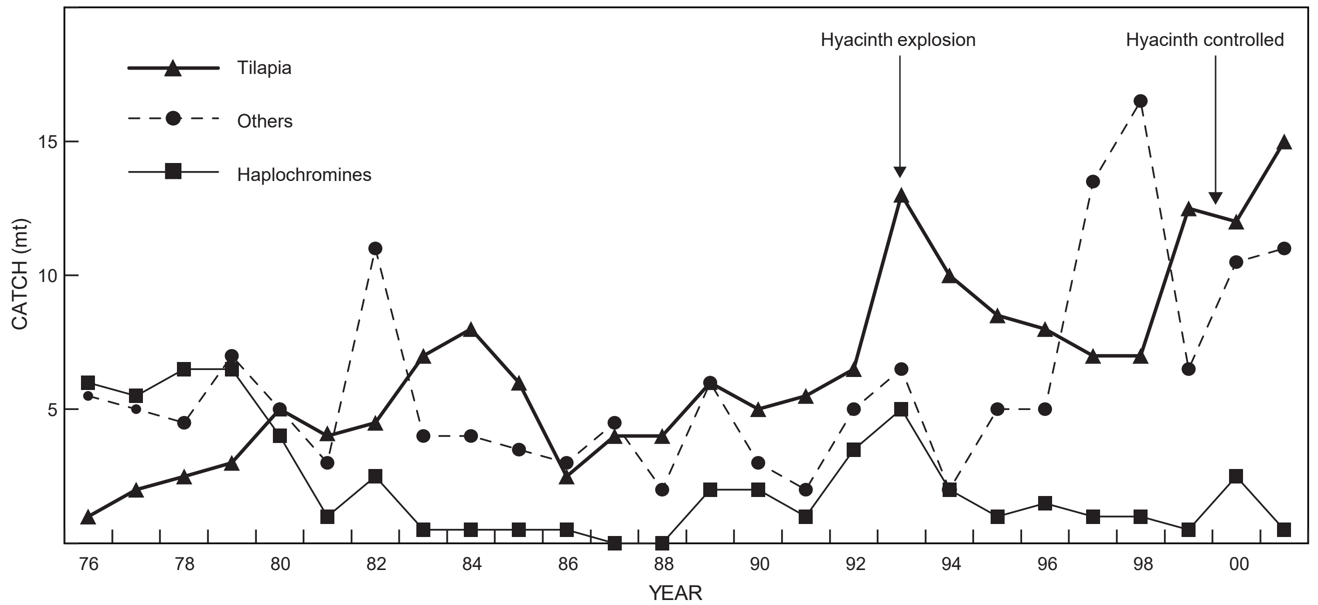

Figure 4: Catches of haplochromines, tilapias and other species (*Clarias, Protopterus*) in Lake Victoria during the hyacinth infestation from 1976 to 2001 (data adapted from Njiru et al. 2005)

in Lake Victoria was the result of increased nutrients levels (Petr 2000; Coward and Little 2001; Ogari and Van der Knaap 2002). Water hyacinth has caused negative environmental and socio-economic effects on the lake through interfering with lake transport, water quality and fisheries. Shading of the water by water hyacinth curtails phytoplankton photosynthesis, thus limits oxygen production. Microbial breakdown of the decaying hyacinth also uses the available oxygen. Water hyacinth mats decrease dissolved oxygen concentrations beneath by preventing the transfer of oxygen from air to water surface. The oxygen can be reduced to very low levels that could lead to massive fish mortalities (Yongo at al. 2017b). Water hyacinth, however, led to the recovery of those native fishes more tolerant to hypoxia conditions, such as catfishes, haplochromines and *P. aethiopicus* (Coward and Little 2001). This is because *P. aethiopicus* is an obligatory air breather, whereas *C. gariepinus* has an accessory organ that enables it to extract oxygen from the air in waters with low concentration.

Climate change and deforestation have likely contributed to a reduction in precipitation in the Lake Basin (Sutcliffe and Petersen 2007). These changes have an ecological impact on lake fisheries, including the reduction of fish habitats, because of declining lake water levels. Thermal stratification over the years regulates the balance between dissolved oxygen and nutrients from deeper water depths at the surface of the water layers, as well as the development of low oxygen concentrations, and the distribution of plankton and fish. Seasonal anoxic conditions and the accumulation of toxic compounds result in the movement of less-tolerant natives fish species into the oxygenated surface waters, where they are subsequently exposed to heavy predation by *Lates niloticus*, and possibly a higher fishing mortality (Witte et al. 1992; Getabu et al. 2003).

The decline in fish catches and changes in the fish populations in Lake Victoria have been attributed to increased fishing capacity, as a result of increased numbers of fishers, boats and illegal gears (Njiru et al. 2018). Fishers have resorted to the use of cast netting, smaller mesh size gillnets and beach seines. When used in shallow areas, seine netting results in capturing of immature fish, disrupt spawners and alters primary productivity through disturbance and destruction of bottom substrates (Njiru et al. 2018). Intensive fishing across the rivers and river mouths, the use of highly efficient fishing gears (e.g. monofilaments and small size gillnets) have prevented recovery of the once prominent potamodromous fishery of *Labeo, Labeobarbus*, *Synodontis* spp., as well as those in the family Mormyridae (Witte et al. 1992). Poverty has been reported as one of the stimulus to overfishing in Lake Victoria (Njiru et al. 2018).

Lake Naivasha fishery

Original stock composition and changes in catch levels

Lake Naivasha is a freshwater body in Kenya. The lake fishery provides a source of livelihood to approximately 650 000 people living around it and other cities in Kenya. The fishery of Lake Naivasha is based mainly on the introduced species namely Common carp, *Cyprinus carpio*, *O. niloticus*, *O. leucostictus*, *C. zillii*, largemouth bass, *Micropterus salmoides* and African sharptooth catfish, *Clarias gariepinus* (Njiru et al. 2017). Before the introductions, Lake Naivasha originally contained only the endemic black lampeye *Micropanchax antinorii* that was last recorded in 1962 and is thought to have gone extinct, because of predation pressure from the introduced *M. salmoides* (Petr 2000). Introduction of *C. carpio* into Lake Naivasha was accidental, with fish possibly having

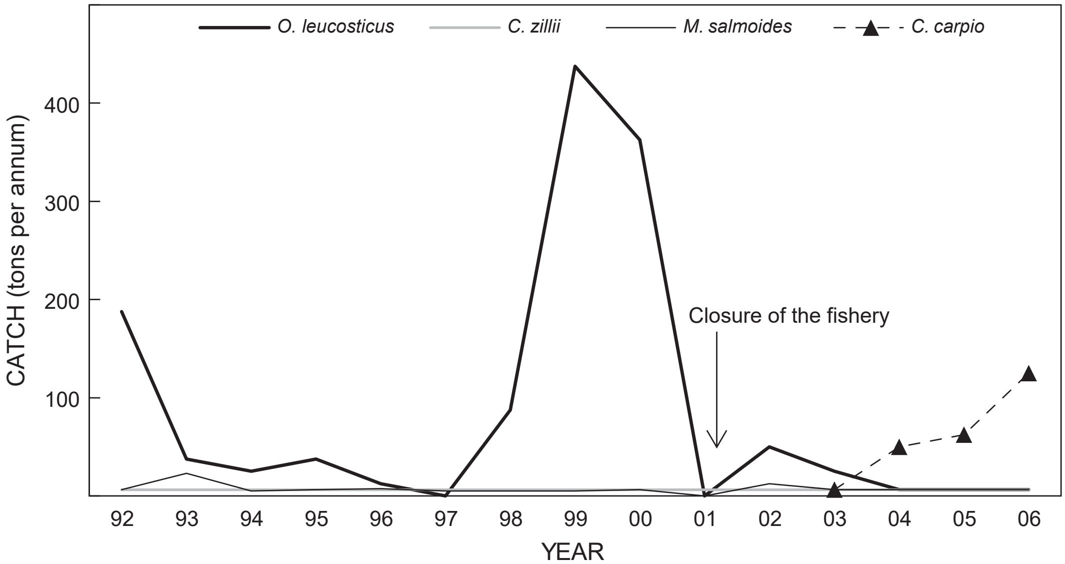

Figure 5: Trends in catches of the major commercial fish species in Lake Naivasha from 1992 to 2006 (data adapted from Ojuok et al. 2008)

escaped from fish farms adjacent to the Malewa River, the main inflow into the lake, and into which *C. carpio* fingerings had been stocked in 1999 (Ojuok et al. 2008).

From 1992 to 2000, Lake Naivasha was dominated by tilapiine fishery, mostly the exotic species, *O. leucostictus* with minor contribution from *C. zillii* (Figure 5). In 2001 the lake fishery was closed in a bid to increase catches especially of *M. salmoides* and *C. zillii*, which were dwindling. After reopening of the fishery in 2002, *C. carpio* began to appear in catches and since then it has increased and dominated the fishery of the lake (Hickley et al. 2015). This occurred shortly after its introduction into the lake in 1999. From 2011 to 2015 onwards, *C. carpio* has been the dominant species in the lake, whereas other species including *O. leucostictus, O. niloticus, C. zillii, M. salmoides* and *C. gariepinus* remained low (Figure 6). The establishment and sustainability of *C. carpio* in Lake Naivasha could be attributed to its life history traits of rapid growth and high fecundity as suggested by Ojuok at al. (2008) and Oyugi at al. (2011). The species is hardy, tolerant of degraded aquatic environment and thrives well in turbid waters (Ojuok et al. 2008; Hickley et al. 2015).

The increase in *C. carpio* could have several detrimental effects on other Lake Naivasha fishery species (Petr 2000). It feeds by uprooting aquatic plants, thus increasing water turbidity that in turn reduces light availability for the productivity of phytoplankton and submerged macrophytes (Ojuok et al. 2008). Reduction in algae and macrophytes threaten the food base for phytoplanktivorous *O. leucostictus* and herbivorous *C. zillii*. Disturbance of the bottom substrate in the lake by *C. carpio* could have major impact on *C. zillii* as this species lays adhesive eggs in bottom sections of the lake with pebbles or sand and abundant vegetation (Coward and Little 2001). Breeding of *M. salmoides* and *O. leucostictus*, which build their nests on muddy bottoms of shallow water, is also likely to be adversely affected by the feeding behaviour of *C. carpio.* The *C. carpio* and *C. zillii* both lay sticky eggs, therefore

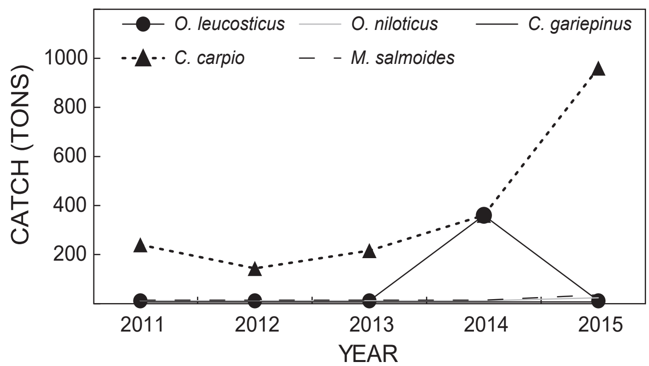

Figure 6: Trends in catches of the major commercial fish species in Lake Naivasha from 2011 to 2015 (data adapted from Njiru et al. 2017)

may likely compete for the substratum to attach their eggs (Petr 2000). The *C. carpio* also preys on juveniles and eggs of the other species in the lake (Oyugi et al. 2011).

Factors driving changes in Lake Naivasha fish stocks

The lake Naivasha ecosystem has been faced with several challenges that have negatively impacted the fish stocks. Some of these challenges include intense fishing, exotic species introductions, water abstraction, lake level fluctuations, wetland utilisation, eutrophication, and land degradation. There is rampant use of illegal gears, such as seine and monofilament nets. There is also use of gillnets of 90 mm and smaller to target the smaller sized *O. niloticus, O. leucostictus* and *C. zillii* (Njiru et al. 2017). The fishers regularly used illegal gears to fish in shallow areas that act as breeding and nursery grounds for most fishes in the lake. The growth in human population has increased domestic effluent discharge into the lake causing pollution. High volumes of fertilisers, pesticides and effluent produced by the Naivasha floricultural industry are the other diffuse and point sources of pollution into the lake. The population growth has caused increased degradation of the lake catchment with the cutting down of trees for firewood, charcoal and timber for construction (Mireri 2005). Reduction of the wetland swamp is attributed to direct human clearance, and lowering of the lake waters, through abstraction for agriculture (Harper and Mavuti 2004).

Degradation of wetlands has been identified as a potential cause for the decline of species such as *O. niloticus, O. leucostictus* and *C. zillii* that use these habitats for breeding and feeding (Njiru et al. 2017). The reduction in water levels in the lake is mostly associated with the use of water to irrigate horticultural farms, though it may also be related to deforestation in the catchment area, which has led to lower amount of rainfall. There has been an adverse impact on the interactions between the multiple exotic species in the lake. The dominance of *C. carpio* and the reduction of the other species in the lake may be attributed to changes in water quality and the ecosystem. Carp feeding mode uproots aquatic plants, stirs the sediments at the bottom, increases water suspended solids and affects water turbidity (Parkos et al. 2003). Increased turbidity decreases light penetration that is important for photosynthesis of submergent plants and phytoplankton. Decreased phytoplankton and aquatic plants reduces food-base for phytoplanktivorous fishes, such as *O. leucostictus* and the herbivorous *C. zillii* (Njiru et al. 2017).

Changes in biological and population attributes of tilapiines in lakes Victoria and Naivasha

Data on sex ratio, condition factor and size at first maturity of *O. niloticus* and *O. leucostictus* in lakes Victoria and Naivasha are available from 1998 to 2017 (Table 2). The sex ratio showed that males are predominant over females in both lakes. Njiru at al. (2006) suggested that male tilapias usually tend to grow faster and attain bigger sizes than their female counterparts, thus increasing their probability of capture. The size at first maturity of the female *O. niloticus* in Lake Victoria has declined from 31.0 cm TL (1998) to 26.0 cm TL (2015). Similarly, female *O. leucostictus* in Lake Naivasha tend to mature at smaller size (21.0 cm TL) as reported by Laurent at al. (2020). The reduction in size at maturity could be a strategy to maximise reproductive success in response to overexploitation of fish stocks (Njiru et al. 2006; Yongo et al. 2018a). The *O. niloticus* exhibited isometric growth (b = 3) in Lake Victoria (Yongo et al. 2018a), whereas it had negative allometric growth pattern (b < 3) in Lake Naivasha (Waithaka et al. 2020). Fish can attain either isometric growth, negative allometric growth or positive allometric growth. Isometric growth is associated with no change of body shape as an organism grows. Negative allometric growth implies the fish becomes more slender as it increase in weight, whereas positive allometric growth implies the fish becomes relatively stouter or deeper-bodied as it increases in length (Riedel et al. 2007). The growth and condition factor of fish can be affected by a number of factors, such as stress, sex, season, food availability, and other water quality parameters (Mutethya et al. 2020). Knowledge of length-weight relationship is important in studying fish biology.

The different variables of changes in population parameters of *O. niloticus* and *O. leucostictus* in Lake Victoria and Naivasha between 1985 and 2017 are shown in Table 3. Analysis of population parameters shows that growth coefficient (K), total mortality (Z), fishing mortality (F), natural mortality (M) and exploitation rate (E) have increased, whereas asymptotic length (L_∞) has decreased. Lake Victoria fishery is open access, and an increase in fishing boats, fishers, gears and the use of illegal gears have led to overexploitation (Cowx et al. 2003; Njiru et al. 2008). These changes in biological and population characteristics of *O. niloticus* could be tactics to maximise survival and reproductive success in response to intense fishing and changing ecological conditions (Njiru et al. 2006; Yongo et al. 2018a). Fishing mortality (F) is primarily induced by the fishing effects on the stocks. However, natural fish mortality (M) is caused by factors not associated with fishing, for example predation, competition, cannibalism, diseases, spawning stress, starvation and pollution stress (Yongo and Outa 2016)

Management strategies for lakes Victoria and Naivasha fisheries

Management of fisheries in Kenya has been a top-down approach led by the central government with little involvement of stakeholders (Kundu et al. 2010; Nunan 2010). It was recognised that for better management of the fisheries, a participatory management approach that is coupled with law enforcement was necessary (Kundu et al. 2010). It is in this context that the Kenyan government adopted bottom-up co-management framework and brought in stakeholders through community involvement by forming the Beach Management Units (BMUs). To protect the fisheries and biodiversity in these lakes, there is a need to limit access of the lake to fishing, and to eliminate illegal fishing gears.

Table 2: Sex ratio, slope of the length-weight relationship (b), condition factor (K) and maturity of *Oreochromis niloticus* and *Oreochromis leucostictus* in lakes Victoria and Naivasha from 1998 to 2017 (Lm_{50} = length at first maturity)

Lake period	Species	Sex ratio (M:F)	b	K	Lm_{50} males	Lm_{50} females	Source
Victoria–1998/1999	*O. niloticus*	1.49:1.0	3.14	0.71	34.0	31.0	Ojuok et al. (2000)
Victoria–1998/2000	*O. niloticus*	1.42:1.0	3.1–3.3	0.92–1.7	35.0	31.0	Njiru et al. (2006)
Naivasha–2013/2014	*O. niloticus*	2.24:1.0	2.3	2.46	17.7	18.0	Outa et al. (2014)
Victoria–2014/2015	*O. niloticus*	1.20:1.0	3.0	1.2–1.4	31.0	26.0	Yongo et al. (2018a)
Naivasha–2017	*O. niloticus*	2.21:1.0	2.86	1.1	28.0	28.0	Waithaka et al. (2020)
Naivasha–2017	*O. leucostictus*	2.19:1.0	2.33	1.4	26.0	21.0	Laurent et al. (2020)

Table 3: Population attributes of *Oreochromis niloticus* and *Oreochromis leucostictus* in Lakes Victoria and Naivasha from 1985 to 2017

Lake and period	Species	$L\infty$ cm TL	K y^{-1}	Ø¬	Z y^{-1}	M y^{-1}	F y^{-1}	E	Source
Victoria–1985/1986	*O. niloticus*	64.60	0.25	3.30	0.82	0.54	0.28	0.34	Getabu (1992)
Victoria–1995	*O. leucostictus*	38.00	0.48	2.80	3.50	0.19	2.60	0.74	Njiru and Ojuok (1997)
Victoria–1998/2000	*O. niloticus*	59.50	0.66		2.42	1.70	1.34	0.55	Njiru (2003)
Victoria–1998/2000	*O. niloticus*	58.80	0.56	3.14	1.92	1.00	1.32	0.55	Njiru et al. (2007)
Victoria–2007	*O. niloticus*	53.90	0.50		2.83		1.92	0.68	Njiru et al. (2008)
Victoria–2014/2015	*O. niloticus*	46.24	0.69	3.14	2.18	1.14	1.50	0.46	Yongo and Outa (2016)
Naivasha–2017	*O. niloticus*	42.00	0.21	2.57	0.80	0.55	0.26	0.32	Waithaka et al. (2020)

Complete eradication of illegal gears and limited access can be achieved by enforcement, surveillance and licensing/ permits of boats, fishers and gears through the BMUs.

Considering the Lake Victoria fishery, the three riparian countries (Kenya, Uganda and Tanzania), under the auspices of the East African Community, formed the Lake Victoria Fisheries Organization (LVFO) in 1994, in order to coordinate the management and conservation of the Lake and its basin. The three countries have subsequently established the Lake Victoria Basin Commission to coordinate environmental issues in the lake basin (Njiru et al. 2008). Lake Victoria Basin Commission (LVBC) coordinates several projects focusing on the health of the Lake Victoria ecosystem. The Lake Victoria Environmental Management Project (LVEMP), for example, is one of the major projects utilizing a holistic approach to manage the lake and its basin with stakeholders involvement (Njiru et al. 2008). Several closed areas have been established in Lake Victoria to protect the fishery during their spawning periods (Njiru et al. 2005). The closed areas need to be extended to river mouths, riverine environments and adjoining flood plains to also protect potamodromous fishes. The Kenyan government has indeed promoted aquaculture to increase food production in order to minimise fishing pressure. Laws regarding the treatment of effluents in the three countries should be harmonised and enforced to protect the lake and its resources.

The riparian land around Lake Naivasha is under the custodianship of a Non-Governmental Organisation (NGO), the Lake Naivasha Riparian Association (LNRA) that works through a committee representing stakeholders with an interest in the lake (Ballot et al. 2009). The goal of the committee is to achieve sustainable utilisation of the lake resources, including the fisheries. Imarisha program is a public-private partnership (PPP) initiative to mitigate destruction occurring around Lake Naivasha Basin, promote sustainability development, secure investments and improve community livelihoods (Njiru et al. 2017). The anticipated outcomes of these initiatives include: 'wise use' of Lake Naivasha resources and its riparian zone. Imarisha Naivasha has initiated several projects in collaboration with their partners towards realising its mandate. These include improvement of fisheries infrastructure, such as landing sites. Imarisha Naivasha Water stewardship Project`s (INWaSP) objective is to rehabilitate the lake basin through dedicated programs aimed at reducing erosion and nutrient input into the lake so as to improve water quality and habitat integrity in the lake.

Conclusion

To conclude, here we report that the tilapiine species in lakes Victoria and Naivasha ecosystems have shown declining trends in catches over time since their introduction. Similarly, the biological and population parameters of the tilapiines have changed greatly over time. These observations are attributed to the effects of the increasing fishing pressure, deteriorating environmental conditions and the introduction of non-native species. This therefore, calls for a need to improve on the management measures applicable in the two lake ecosystems, such as fishing effort control, pollution control and protecting the surrounding wetland from degradation. Additional work is required to carry out a stock assessment of the lakes to inform sustainable fisheries management decisions.

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