Impacts of Nile Perch, *Lates niloticus*, introduction on the ecology, economy and conservation of Lake Victoria, East Africa

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Abstract

Nile perch were secretly introduced into Lake Victoria in the 1950s, and officially in the 1960s, amid unresolved controversy. Proponents were of the view that the introduction would improve fisheries production and sport fishing. Although the former objective was achieved, the side effects were dire, including extinction of many native species, especially the ecologically important haplochromines, because of predation. The introduction also changed the habitat, trophic dynamics and water clarity. The change in water clarity is thought to be responsible for hybridization of haplochromines, further contributing to the loss of species diversity among cichlids. The establishment and expansion of the Nile perch also altered the fishery and socio-economic settings characterizing the lake. A local economy which, until the early 1980s, was based on native fish species has been replaced by an export-oriented exotic fish processing industry that destroyed the once-cherished traditional resource. Other socio-economic issues associated with Nile perch include the high HIV/AIDS prevalence among fishers, and border conflicts attributable to the migratory and transboundary nature of the fishery resource. Conservation measures for the fishery should include establishment of co-management units that have so far registered both successes and challenges. Other efforts include establishment of the Nile perch Fisheries Management Plans that focus on curbing overfishing and eradicating illegal fishing.

Key words

diversity, ecosystem, invasive, management, native.

INTRODUCTION

Nile perch, *Lates niloticus* (Linnaeus, 1758), is a predatory fish of high commercial and recreational value. Being indigenous to the Ethiopian eco-region of Africa, it can grow to a length of 2 m, weigh up to 200 kg and live up to 16 years. It occurs in the Congo, Niger, Volta and Senegal Rivers, and in Lakes Chad and Turkana. It also occurs throughout the Nile system as far as Lake Albert, although it was prevented from reaching Lake Victoria by Murchison Falls (Froese & Pauly 2016). The voracious predator was introduced into lakes Kyoga, Nabugabo and Victoria in Uganda from Lake Albert during the 1950s and early 1960s (Hamblyn 1961). Nile perch was introduced secretively in 1954 in the Ugandan side of Lake Victoria. Official introductions, however, were done about a decade later, in 1963, by authorities in Uganda and Kenya. It took >20 years for the species to establish and expand, replacing most indigenous species in fish catches (Downing *et al.* 2013).

Introduction of the species sparked considerable controversy (Fryer 1960; Anderson 1961; Lowe-McConnell 1994). Proponents argued that, by consuming the abundant and less-exploited haplochromine cichlids, Nile perch would be providing Lake Victoria with an important new fishery. The huge size of the perch made it a sport-fishing target that could attract tourists to the lake region. Archaeological evidence near Lake Victoria suggested an ancestor of the Nile perch was native to the Miocene predecessor of Lake Victoria (i.e. Lake Karunga), and it was argued that the perch could become a native fish once again (Lowe-McConnell 1994).

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Opponents found little ecological sense with this argument, claiming that a top predator such as Nile perch would do little to improve the overall ecological efficiency and the preferred introduction of an herbivore or detritivore (Fryer 1960). Further, the antagonists contended that it was wishful thinking that introduced Nile perch would feed exclusively on haplochromines, it being impossible to predict what might happen in a complex tropical ecosystem like Lake Victoria.

After its introduction in Ugandan waters, the perch steadily dispersed in a generally 'clockwise' (east–south–west–north) movement around the lakeshore. By the early 1970s (i.e. within just one decade), Nile perch was observed to have colonized the Nyanza Gulf in Kenya, establishing itself as a major fishery. Further to the south in Tanzanian waters, a few Nile perch were caught as early as 1964 (Gee 1965), although the catches remained incidental to the main fish species around Musoma and Mwanza through the 1970s. By the early 1980s, however, Nile perch was a commonly occurring fish in fish catches along the southern lakeshore (Acere 1985; HEST 1986).

Nile perch generally occupy almost all realms of the lake (Ochumba 1987), with exception of a few rocky littoral habitats (Witte *et al.*, 1992a). Studies indicated highest abundances occurred between 16 and 50 m in Tanzania waters (Goudswaard & Witte 1985), and at depths between 4 and 20 m in Kenyan waters, but declined in numbers at depths below 50 m. The decline in numbers with depth is in contrast to earlier observations (1969/70) (Kudhogania & Cordone 1974), when the decline in abundance was below 70 m deep, a phenomenon attributed to environmental changes over the last two decades and the presence of a hypoxic layer below 50 m (Hecky *et al.* 1994; Ochumba, 1995). Other than abiotic factors, there are several other factors that determine the distribution of Nile perch, including food availability, the presence of predators and the habitat of the parental fish (Wootton 1998).

The aforementioned factors are also essential determinants of reproductive strategies and the reproductive biology of Nile perch. The latter is particularly key to understanding the ecology, life history and population dynamics of the species. Several studies on the reproductive biology of *L. niloticus* have been conducted (Asila & Ogari 1987; Ligtvoet & Mkumbo 1990; Ogari & Asila 1992; Mkumbo 2002; Njiru *et al.* 2008). The size at 50% maturity has been decreasing over time (Table 1), a situation that generally attributed to increased fishing pressures, changes in food availability and the lake environment.

Table 1. Total length (TL) of Nile perch in Lake Victoria at 50% maturity

Date	Male (cm TL)	Female (cm TL)	Region/lake	Source
1979–1983	74	100	Winam Gulf	Asila & Ogari (1987)
1988–1989	60	110	Mwanza Gulf	Ligtvoet & Mkumbo (1990)
1985–1989	55	85	Lake Victoria, Kenya	Ogari & Asila (1992)
1998–2001	54	76	Mwanza Gulf	Mkumbo (2002)
2004–2005	54	62	Lake Victoria, Kenya	Njiru *et al.* (2008)

According to the IUCN's Invasive Species Specialist Group, the Nile perch is considered one of the world's 100 worst invasive species (Lowe *et al.* 2000). However, the introduction of Nile perch has had significant beneficial effects on the fisheries of Lake Victoria, on the other hand, a catastrophic effect on the ecosystem (Aloo 2009). Nonetheless, controversy over the role of *Lates* in the lake has continued. Lines of argument are usually divided between those who regard the Nile perch introduction as a great calamity, and those who assert that the fish is a blessing to the fishery. To this end, this study highlights the ecology, economy and conservation of Nile perch in Lake Victoria since its introduction.

ECOLOGICAL IMPACTS OF NILE PERCH

Loss of Species

Lake Victoria was once considered a habitat of a distinctive multispecies fishery dominated by the tilapiines (*Oreochromis esculentus* and *O. variabilis)*, and more than 500 species of haplochromine cichlids (Ogutu-Ohwayo 1990; Witte *et al.* 1999). An important subsidiary fishery existed, based on >20 genera of non-cichlids fishes, including *Protopterus aethiopicus*, *Bagrus docmak*, *Clarias gariepinus*, *Schilbe intermedius, Labeo victorianus, Alestes* spp, *Mormyrus kannume*, *Barbus altianalis*, *Synodontis victoriae* and *S. afrofischeri* (Kudhogania & Cordone 1974; Ogutu-Ohwayo 1990). Catch assessments and exploratory bottom trawl surveys conducted between 1968 and 1970 indicated that, although the lake was dominated by the haplochromines (Fig. 1), the most important commercial species were *B. docmak*, *O. esculentus*, *C. gariepinus* and *P. aethiopicus*. Haplochromine species are relatively small and bony, and not generally favoured in catches. By the late 1980s and early 1990s, Nile perch dominated the catches, with the native species hardly being caught in trawl surveys. Predation by the introduced Nile perch has been associated with the extinction of at least 200 haplochromine species, and virtual elimination of several endemic fish species (*O. esculentus; O. variabilis; B. docmak; Alestes* spp; *Barbus* spp; mormyrids; Witte *et al.* 1992a,b). The decline in the fish species in Lake Victoria is the largest documented loss of biodiversity in an ecosystem caused by humans (Witte *et al.* 1999). The decline of the haplochromines and other species after the early 1980s is attributed to predation by the booming Nile perch, habitat degradation, pollution, competition by the Nile tilapia and overfishing. The perch biomass in the lake started to decline by 1990, due largely to the exhaustion of its prey, and intense fishing pressure driven by an emergent lucrative export market (Nyamweya *et al.* 2016). There has been a resurgence of the native species in the recent past, being attributed among other factors to the decline in the predatory Nile perch (Fig. 1). One noteworthy item is that the resurgent fish are smaller in both maximum size and size at first maturity than those caught in the period before establishment of Nile perch, being an adaptation to survive in a changed environment (Witte *et al.* 2013).

Trophic dynamics

In the pre-Nile perch invasion period, Lake Victoria exhibited a diverse food web, with *Clarias* spp., *B. docmak* and *P. aethiopicus* as the top predators (Witte & Van Densen 1995; Njiru *et al.* 2005). At least five trophic groups were common in the lake in the 1970s to mid-1980s, including piscivores, zooplantivores, molluscivores and detritivores/phytoplanktivores (Fig. 2; Witte *et al.* 1999, 2013; Njiru *et al.* 2005). During the peak of Nile perch in the late 1980s and early 1990s, the trophic groups were dominated by zooplantivores and detritivores/phytoplanktivores. With the decline of Nile perch in the mid-1990s and late 1990s, the trophic groups became more diverse. The decline of haplochromines and their subsequent resurgence mirrors the diet of Nile perch (Fig. 3). Studies on the lake between the late 1960s and late 1970s indicated the diet of Nile perch consisted mainly of haplochromines, being the most preferred prey. Due to the decline in the haplochromine stocks, the perch diet of the 1980s was mostly perch juveniles and *R. argentea.* The late 1990s and 2000s saw the dominance of *Caridina nilotica* and haplochromines in the diet, the reason being that Nile perch predation on *R. argentea* was reduced when their preferred prey (haplochromines) are plentiful (Nyamweya *et al.* 2017). Increased haplochromines in perch diet are attributed to a resurgence of the species after the decline of Nile perch, although the dominance of *C. nilotica* in their diet could be attributed to increased hypoxia in the lake. *C. nilotica* have been observed to thrive in hypoxic conditions (Mugidde *et al.* 2005).

By the end of the 1980s, detritivores and phytoplanktivores, which previously comprised more than 50% of the bottom-dwelling ichthyofauna, had drastically declined, being replaced by *C. nilotica*. Nile perch predation was attributed to extinction of about 60% of the haplochromine species, especially the algae-feeding haplochromines (Witte *et al.* 1992a,b). In Tanzania, for example, a drastic reduction in some groups of haplochromines was observed soon after the Nile perch peak in 1986–1987 (Witte *et al.* 1992b). In shallow areas, however, which had relatively low Nile perch densities and contained structured bottoms (e.g. rocky shores), haplochromines were less affected (Witte *et al.* 1992b; Seehausen *et al.* 1997). Studies by Witte *et al.* (1999) also reported the pelagic-

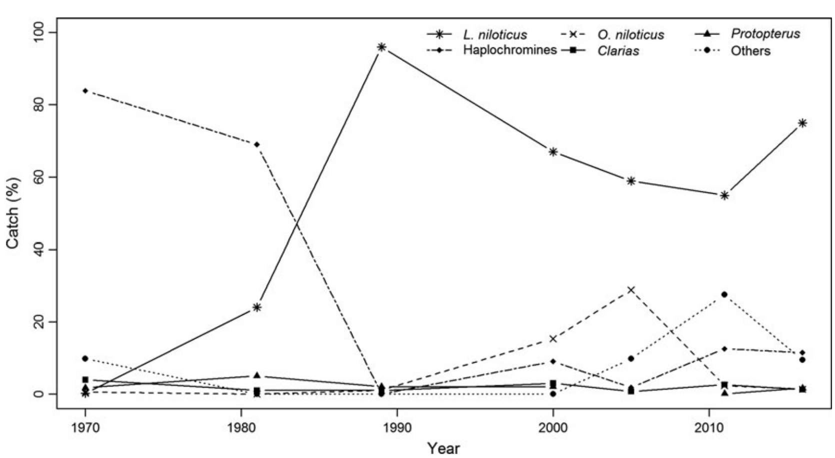

Fig. 1. Catch composition of bottom trawl surveys conducted in Lake Victoria, 1970–2016. (the 'others' category includes *B. docmak, O. esculentus, C. gariepinus* and *P. aethiopicus*; data sources: Njiru *et al.* 2005, Kenya Marine and Fisheries Research Institute, KMFRI).

dwelling cyprinid, *R. argentea,* which feed on zooplankton and insect larvae, replaced the surface-living *zooplanktivorous*/insectivorous haplochromines. Further, after Nile perch became established, with a subsequent reduction of the haplochromines in the lake, *R. argentea* exhibited a 50% decline in generation time to exploit the new niche (Wanink 1998). Studies by Sharpe *et al.* (2012) indicated fisheries-induced phenotypic changes in *R. argentea,* including decreased body size, maturation at smaller sizes and increased reproductive effort.

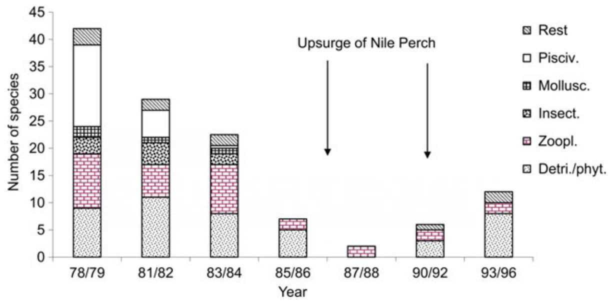

Fig. 2. Total number of species per trophic group in bottom trawl catches in Mwanza Gulf, Tanzania (Mollusc, molluscivores; Pisciv, piscivores; Rest, unknown and other groups; adapted from Witte *et al.* 1999; Njiru *et al.* 2005).

Altered habitats

Biodiversity loss caused an imbalance in the lake's ecosystem, including alterations in floral and faunal composition leading to water quality changes. Frequent algal blooms observed in the lake are partly attributed to a top-down effect caused by a decline in cichlid herbivores and detritus feeders by Nile perch predation (Hecky & Bugenyi 1992; Kaufman 1992). It was further suggested that reduced grazing pressures were responsible for the

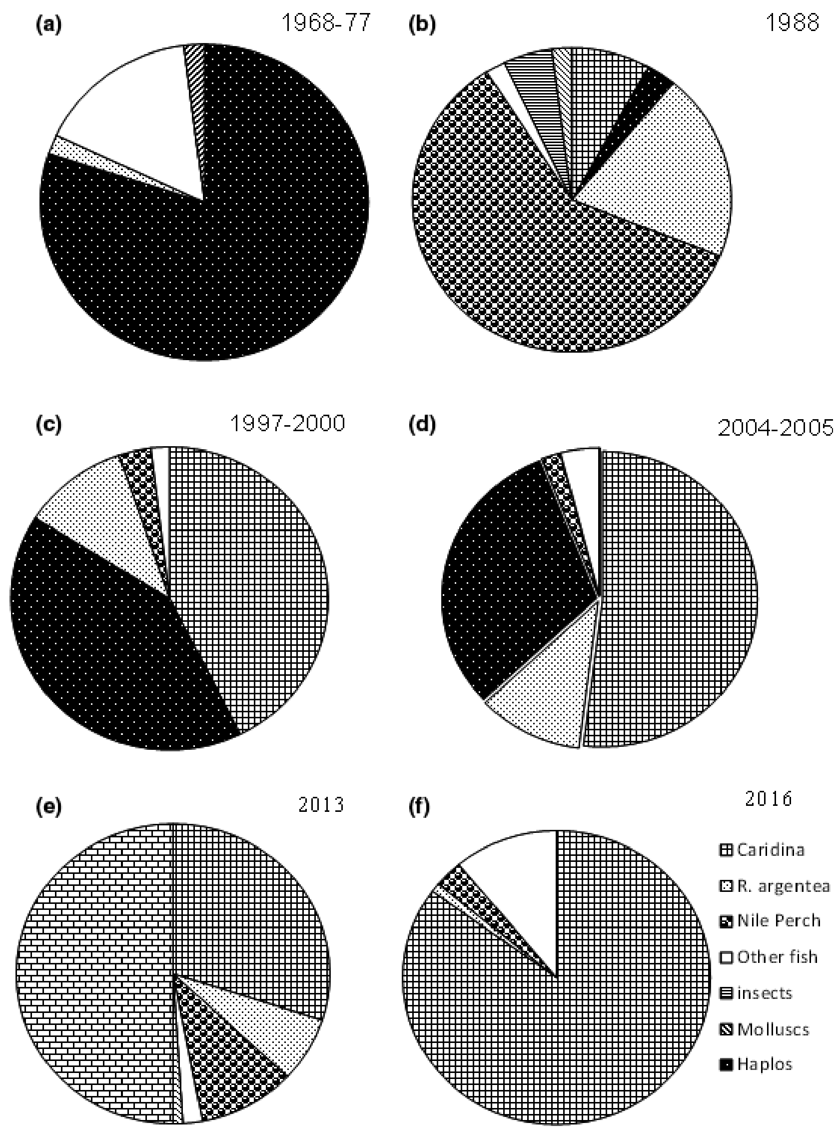

Fig. 3. Diet of *L. niloticus* in Lake Victoria ((a) 1968–1977; (b) 1988; (c) 1998–2000; (d) 2004–2005; (e) 2013–2016; (f) 2016; data sources: 1968–2004 adapted from Njiru *et al.*; 2005, and 2013–2016 are Njiru personal data; 'Other fish' included *Synodontis, Tilapias and Clarias;* Haplo, *Haplochromines).*

increased phytobiomass, with the subsequent microbial breakdown reducing the dissolved oxygen levels in the lake (Fig. 4). Further, increased hypoxia conditions rendered a large volume of the lake unusable by aerobic organisms, including fish (Mugidde *et al.* 2005). Trawl catches reveal a relationship between dissolved oxygen concentrations and fish catches (Fig. 5). Nile perch, which require a minimum dissolved oxygen (DO) concentration of 3 mg L^{-1} to survive, had its distribution limited by hypoxic waters (Kaufman 1992). In water with low dissolved oxygen concentrations, perch are forced to move upward in the water column above the oxycline, or to migrate to more oxygenated shallow waters (Taabu-Munyaho *et al.* 2013; Cornelissen *et al.* 2015). This movement to upper waters makes the perch more vulnerable to fishing. Other fish species are also more exposed to Nile predation because of this close association.

Incidental massive fish kills, especially large-sized Nile perch, in Nyanza Gulf and in the Mwanza Gulf in the 1980s was attributed to upwelling of anoxic water and increased noxious algal blooms (Ochumba 1990; Kaufman 1992; Wanink *et al.* 2001). Large-sized Nile perch are generally affected more by low oxygen concentrations than small-sized Nile perch because of their smaller gill surface area to biomass ratio (Njiru *et al.* 2012). Additionally, hypoxia also affects the size class distribution of fish, because it can limit physical growth and reproduction, resulting in a reduction in maximum fish size and length at maturity (Pauly 1984). The death of larger fish, limited growth and reproduction, coupled with overfishing, could jeopardize recruitment of the fish in a lake that already has very few large perch individuals. Recent estimates of Nile perch population structure from measurement of specimens retained by net hauls indicate the population was skewed to the juveniles. More than 97% of Nile perch caught are juveniles, while 3% lies are within the recommended slot size (50–85 cm TL), with a negligible number above slot size (Fig. 6). Very few fish are more than 50 cm TL (minimum legal size). The figure reveals a population dominated by juvenile fish (17–24 cm, TL; Taabu 2004). Such a situation could imply an adequate recruitment, despite intense fishing pressure.

Other environmental issues associated with Nile perch introduction include firewood demands for processing the fish (Njiru *et al.* 2005). The abundant haplochromines were mainly grass smoked. With the increase in the Nile perch, the need to deep fry or smoke them required firewood (Riedmiller 1994). At Wichlum Beach (Kenya), for example, the number of smoking kilns increased from 10 to over 50 between 1984 and 1991 (Riedmiller 1994). Fish trade was also associated with extensive harvesting of forestry resources for boat building, house construction, brick making and charcoal production (Yongo *et al.* 2005). An estimated 68 000 m^3 of wood was used annually to process fish, with wood for building boats increasing from 15 236 m^3 in 1998 to 60 000 m^3 in 2002 (Jambiya & Sosovele 2002; Yongo *et al.* 2005). Accordingly, the boom in the Nile perch aggravated deforestation around the lake, contributing to increased soil erosion, siltation and lake eutrophication.

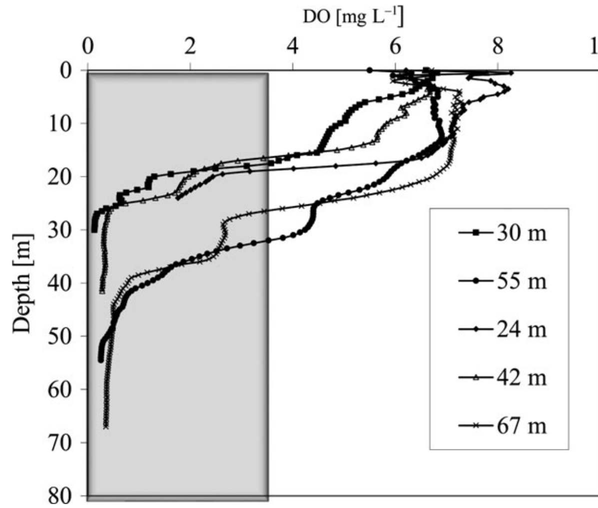

Fig. 4. Oxygen profiles in different locations in Lake Victoria taken during 2008 lake-wide acoustic survey (shaded region indicate oxygen concentrations below 3 mg L^{-1}, above which most fish in Lake Victoria fish populations survive best; data source: LVFO).

Hybridization of Haplochromines

Lake Victoria has been described as natural museum of cichlids because of a remarkable radiation of cichlid fishes that has given rise to several hundred endemic species within a very short evolutionary period. With over 500 species of haplochromines, Lake Victoria had one of the most diverse fish environments on earth at one time (Coulter *et al.* 1986). This speciation is threatened, however, by eutrophication and resultant water turbidity. Changes in water clarity in the lake are attributed to a number of factors, including predation of haplochromines by Nile perch, subsequent resultant increased algal productivity and changes in water transparency. Reduced water clarity has caused a loss of genetic and ecological differentiation among haplochromine species, contributing to the loss of species diversity among cichlids (Seehausen *et al.* 1997).

Cichlids are frequently found to mate by colour, both in nature (Elmer *et al.* 2009; Wagner *et al.* 2012) and in experimental settings (Pauers *et al.* 2012). Many other

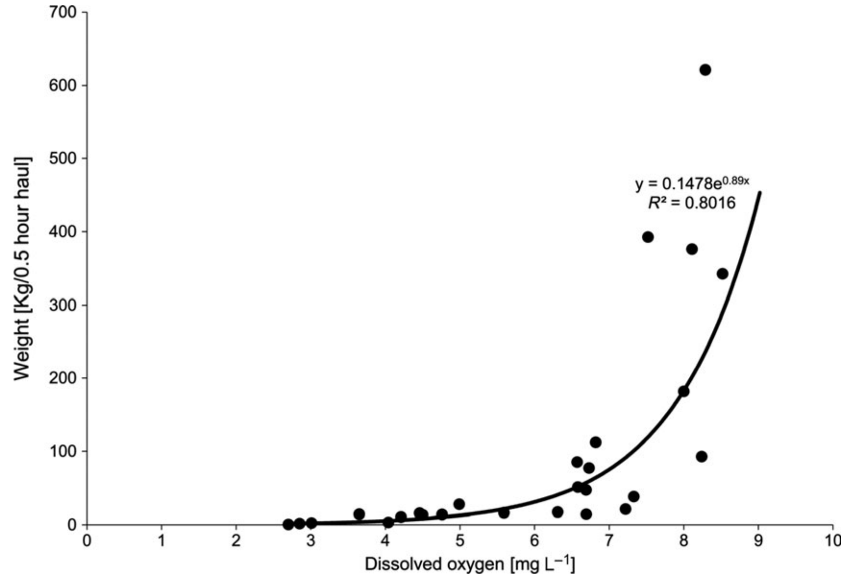

Fig. 5. Relationship between dissolved oxygen concentration and trawl catches in Lake Victoria, 2012 (KMFRI 2012).

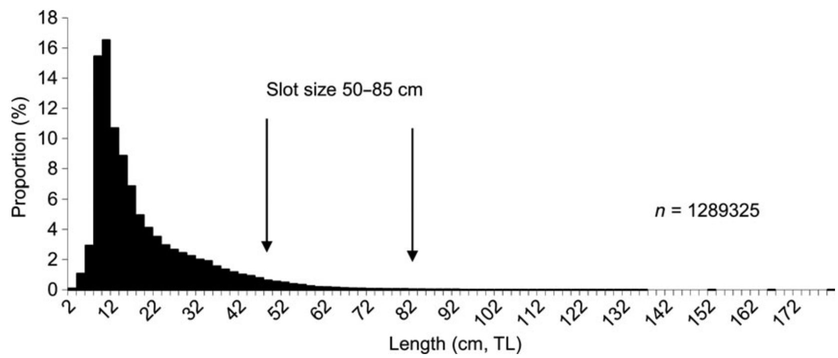

Fig. 6. Length frequency distribution of Nile perch in trawl catches in Lake Victoria, 2015 (arrows indicate recommended slot size (50–85 cm TL); KMFRI).

traits, however, may also influence mate choice, including acoustic cues, olfactory cues and male territory characteristics (Maan & Sefc 2013). Laboratory studies have demonstrated that females mate with other males when conspecific males are not available (Crapon de Caprona & Fritzsch 1984). As reduced water clarity is thought to make haplochromines unable to identify their conspecific mates, increased turbidity has reduced the effectiveness of colour signals between breeding mates, leading to a collapse of reproductive barriers and ensuing attrition of cichlid species diversity in the lake (Seehausen *et al.* 1997). The loss of these haplochromine fishes, often before their biology and systematics have been elucidated, is a major loss to scientists (Coulter *et al.* 1986).

Nevertheless, there is no clear-cut relationship between the Nile perch upsurge, impacts on haplochromine cichlids and lake eutrophication. Some studies suggest increased eutrophication of the lake began as early as in the 1920s, becoming more pronounced in the 1960s and early 1980s. Further evidence from the sediments and water column indicated widespread water quality deterioration related to intense anthropogenic activities and local or global climate change (Hecky & Bugenyi 1992; Hecky 1993). Witte (2009) argues this early eutrophication of the lake had a negative impact on haplochromines, thereby providing an opportunity for the establishment of Nile perch. As ecological, biological and systematic information on haplochromines was not collected until 1969/70 and 1978 (Kudhogania & Cordone 1974), it may not be possible to clearly establish the number of haplochromines that were lost or declined.

SOCIO-ECONOMIC IMPACTS OF NILE PERCH

Economic boom

Up to the 1970s, the Lake Victoria fishery was primarily driven by subsistence requirements and a limited regional market. With increasing catches of the Nile perch, this fishery was transformed into a multimillion-dollar commercial fishery, with Nile perch accounting for about 90% of the total fish export, in both volume and value (Odongkara *et al.* 2005; Yongo *et al.* 2005). The foreign exchange earnings from Kenya fish exports increased from US $0.4 million 1980 to US $66 million in 2003 (Yongo *et al.* 2005). Fish export earnings in Uganda increased from less than US $30 m in 1995 to about US $145 in 2011, with fish becoming the second most important foreign exchange source after coffee.

Nile perch export and value from the three riparian states have generally increased between 1992 and 2005, declining thereafter (Fig. 7). The exports rose more or less continuously from 1991, until reaching a peak of around 110 000 t (whole fish equivalent) in 2005. The value also rose to reach a maximum of US $321 million in 2008. Thereafter until 2013, both the export volume and value decreased, although not at corresponding rates because of recent price increases in the international market. The decline in exports correlates with the Nile perch biomass trends, which have also been on the decline since 2014 (LVFO, 2016). Despite a continued decrease in the exports, however, a major increase of about 220% of values was recorded from 2013 to 2014, mainly from Tanzania. The Lake Victoria Fishery Organization (LVFO) reported the lake produces US $650 million worth of fish annually. With the Nile perch boom, the harvesting, processing and marketing sectors also experienced transformations. The increased Nile perch catches spurred the establishment of fish processing plants along the shores of Lake Victoria, which produced chilled and frozen fishery products for international markets. The first fish processing plants were established in the early 1980s in Kenya, and in the early 1990s in Uganda and Tanzania. The number of factories increased to 30 during the peak Nile perch boom of the 1990s (Abila 2000; Ntiba *et al.* 2001).

The fishery boom included the creation of many new jobs, especially in the processing industries and trade sectors. There were 50 000 fishermen and 12 000 fishing boats on Lake Victoria in the 1970s. Since the Nile perch boom, the lake has exhibited an exponential increase in fishers and boats targeting the newly found 'jewel'. The lake had over 200 000 fishers in 2014, using over 70 000 craft (Fig 8a), with more than 2000 new vessels appearing every year (LVFO 2014). There was also a revolution in fishing in the lake, whereby outboard motors and trawlers entered the fishery. There were 90 boats using inboard in 2000, declining to 10 in 2014. The trawlers have since been banned. Boats using outboard engines increased from 4000 in 2000, to 22 000 in 2014. The long lines, which mainly target Nile perch, increased from 3.5 million in 2012 to 14 million in 2014. Despite the increasing effort, Nile perch catches have remained stable after the Nile perch boom, indicating fishing pressure may not be the only driver of the species' abundance in Lake Victoria (Nyamweya *et al.* 2017). The Food and Agricultural Organisation (FAO) of the United Nations calculated that the boom created 180,000 jobs in the fishing industry in the 1980s alone. By the early 1990s, the number of fishers and their dependents increased to about 480 000, and to almost 3 million in the late 1990s (SEDAWOG 1999;

Fig. 7. Temporal trends in exports tonnage and value from Lake Victoria (LVFO).

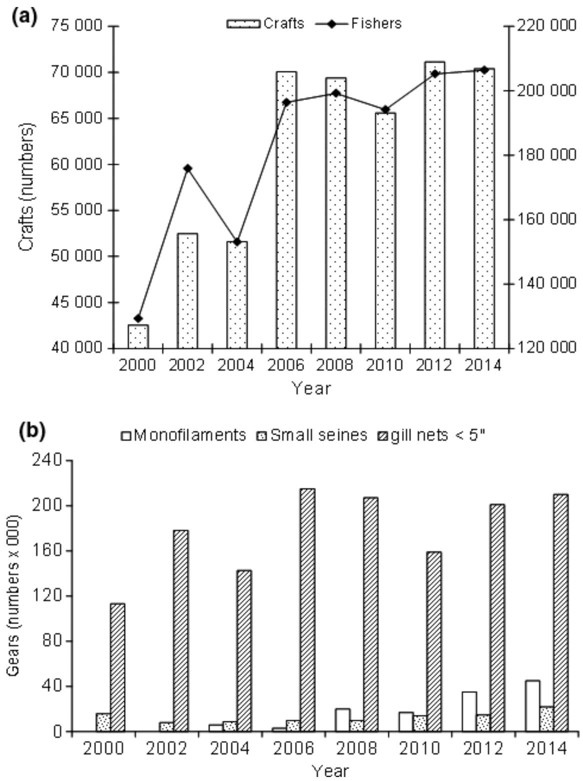

Fig. 8. Trends in Lake Victoria fishing capacity ((a) crafts and fishers; (b) illegal gears; LVFO Frame Survey 2014).

Yongo *et al.* 2005). It is estimated that 35 million people currently depend directly or indirectly on Lake Victoria fisheries for their livelihood (Weston 2015). Among others, the trade also stimulated the building sector, air industry, net manufacturing and packing industry. Apart from the fishers, there were fish driers, fish smokers, fish fryers, fish buyers and sellers, net menders, boat builders and boat repairers.

Edging out small-scale fish operators

Despite the economic expansion related to the Nile perch boom, the earnings from the Lake Victoria fishery involved only a small percentage of participants in the fish industry (Abila 2000; Yongo *et al.* 2005; Geheb *et al.* 2007). At the beginning of the century, about 1.2 million people were directly or indirectly dependent on the Lake Victoria fishery for their livelihoods. In the pre-Nile perch period, small-scale fish operators dominated the fish processing and trading subsectors (Yongo *et al.* 2005), mainly comprising women from communities surrounding the lake. They sold fresh fish and processed the surplus using simple technology (e.g. smoking, salting and sun drying) for later sale. There were hardly any wholesalers or large processors.

With the boom of Nile perch, employment chances in traditional fish trading and processing sectors for Nile perch and its products, previously the activity of women, were integrated into the marketing chain for fish processing and fish meal. This resulted in an equitable distribution of income from the fishery sector, with local communities being disadvantaged. Commercialization of the Nile perch fishery slowly edged local people out of fish production, pricing, marketing and processing activities, with fish factories and their agents taking up most of these activities (Abila 2000). Harvesting of Nile perch was left in the hands of a few rich fishers, most not being natives of the lake region (FAO 2003). Some factories entered into agreements with selected fishers, whereby they offered facilities such as boats and gears, on the condition they supply fish to them. The arrangement further alienated the poorer fishers, who found it more difficult to participate in this long-distance fishing than fishers with access to more resources and superior boats and gears. There were also reduced employment chances in the processing and trading of Nile perch skeletons, with the latter being sent to fishmeal factories (Abila 2000). It should be noted that the Nile perch skeletons rejected by the factories were processed mainly by women, forming a vibrant industry. Commercialization of the Nile perch led to a serious imbalance in the social sector, disadvantaging the small-scale fish operators, and indirectly affecting the sustainability of the fish resources. With the employment loss directly related to the Nile perch fishing industry, more pressure was directed to the other commercial species of *R. argentea* and *O. niloticus* (Geheb *et al.* 2007). This was accompanied by an increase in the use of small seines and illegal gear such as monofilaments nets and gillnets (<5 in. mesh size), which targeted juveniles and young fish (Fig. 8b). These types of illegal gears are efficient in capturing undersize fish, which could lead to both growth and recruitment overfishing. Native fish species, especially haplochromines, which had shown signs of recovery, were jeopardized by the increased fishing pressures (Mkumbo 2002; Njiru *et al.* 2002). It should be noted that Nile perch could grow up 200 kg, although this average weight decreased to 50 kg in the 1980s and is currently less than 10 kg, an indication of growth overfishing resulting in reduced yield per recruit.

HIV/AIDS

The Nile perch migrates seasonally across the lake, following a pattern that seems to be related to rainfall distribution (Harris *et al.* 1995). Fishers follow the fish on these movements, as much as their boats and gears can allow them. The increased mobility of fishers has vast implications not only on fisheries, but also on the human population. Fishers may undertake fishing expeditions across the lake for several weeks at a time and away from their spouses (Harris *et al.* 1995). The fishers tend to engage in high-risk sexual behaviour leading to contracting of HIV/AIDS. High prevalence of HIV/AIDS among the fishing communities is partially attributed to this mobility.

Further, with diminishing catches from the lake, women fishmongers formed sexual relationships with fishermen to secure their fish (Kwena *et al.* 2012*)*. The women wishing to sell fish in the market secured the rights to purchase the fish caught by the fishermen in return for sexual favours. These women engage in a network of these relationships, conducted in situations that compromise their ability to practise safe sex, thereby increasing the risk of contracting HIV. The overall HIV prevalence among fishing communities in Uganda, for example, increased 22% (Opio *et al.* 2013). The prevalence in Kenya increased to 28% among fishing communities, compared to the value of about 6% in the general population (Ondondo *et al.* 2014). Individual fishers and fish workers with AIDS-related illnesses have a declining ability to engage in physically demanding labour, such as fishing (Abila 2000). Fishing households in which one or more people are affected by AIDS have reduced incomes, spend their savings on medical care, sell their productive assets (e.g. fishing equipment) and withdraw their children from school. Thus, their poverty deepens, their food security decreases and their vulnerability increases. High levels of illness undermine commitment to such collective, long-term goals as community fishery management and conservation. Sick fishers are bound to fish near the inshore waters, using illegal gears. These are the lake waters that act as breeding and nursery grounds for most fish in the lake, thereby comprising fish recruitment (Njiru *et al.* 2005). In the Lake Victoria riparian countries, some action has being taken to address different aspects of the impacts of the AIDS epidemic. The interventions encompass (i) prevention by provision of toolkits for HIV prevention among fishermen to awareness campaigns to trigger behaviour change; (ii) care by providing nutritional and positive living support for orphans and people living with HIV/AIDS; and (iii) mitigation by establishing life schools for orphans and vulnerable children in fishing/farming communities. These initiatives are done mainly by united agencies such as FAO, fisheries and health line ministries, NGOs and BMUs (Opio *et al.* 2013).

Border conflicts

The Nile perch fishery has fundamentally transformed the social and economic aspects on cross-border fishing and fish trade since its emergence as a commercially exploited species in the 1980s (Harris *et al.* 1995). This situation has resulted in occasional cross-border conflicts attributed to the diminishing, but still lucrative, Nile perch fishery. In 2008–2009, for example, the Ugandan and Kenyan governments claimed a tiny (2000 m^2) island (Migingo Island) (https://en.wikipedia.org/wiki/Migingo_Island). A joint re-demarcation survey by the two governments (which diffused the tension) found the island was within Kenya, while much of the waters near it were Ugandan. This report, however, was not wholly accepted. To diffuse any further tensions, the two governments in early 2016 again established a committee to review the Migingo Island issue, with the report still being awaited.

The consequences of the conflict affect fisheries and beyond. On a fundamental level, 'infringing' fishermen suffer constant harassment and detention by police (Shaka 2013). The primary dispute is over fishing rights in Lake Victoria. If the situation escalates to a full-blown war, the economies of the two countries will be seriously damaged in regard to cross-border trade. The dreams of East African Integration the East African Community is working to realize might be thwarted by the Migingo conflict. Trivial as it may seem, the Migingo issue should not be underestimated, noting that people have gone to war for far less substantial reasons all over the world (Shaka 2013).

Food security

Traditionally, communities living around Lake Victoria consumed much of the fish landed (Abila 2000; Odongkara *et al.* 2005; Njiru *et al.* 2008). Commercialization of the fishery led to the development of a vibrant, export-oriented industry. The relatively higher prices offered by the processing factories made Nile perch unaffordable to the local consumer. Further, the export market took the big mature and good-quality Nile perch, although they could not satisfy the market demand. Only juvenile Nile perch, or those rejected by factories, plus the skeletons of Nile perch, remained for local consumption, leading to limited access to fish by the local communities. It also caused food insecurity and reduced available nutrition because of the export of substantial quantities of fish to global markets, which would otherwise be available to local consumers (Abila 2000; Odongkara *et al.* 2005).

Mushrooming of fishmeal industries also leads to more direct losses of protein to the locals, and a reduction in employment opportunities (50%–60%) and power of purchasing alternative food sources. About 60% of Nile perch frame from factories went to fishmeal factories, as did 70% of the harvested 'poor person food' (*R. argentea)* (Abila 2000). It is worth mentioning that all the Nile perch skeletons were used for human consumption up to the late 1980s. Further, all the *R. argentea* was consumed by humans in the early 1990s (Abila 2000). The protein produced using animal feeds (e.g. poultry, beef and pork) is not as readily accessible to poor people as fish because of their weakened purchasing power. To bridge the gap in income reduction from fishery, the communities embarked upon clearing wetlands in order to facilitate the growth of horticultural cash crops. Exploitation of wetlands degraded the surrounding environment, reduced the wetland ability to protect the lake from siltation and pollution, and interfered with aquatic life in the lake, thereby threatening the sustainability of the entire lake ecosystem (Njiru *et al.* 2007). The local communities around Lake Victoria can be characterized as being very insecure with regard to food, because of the above dynamics (Abila 2000; Odongkara *et al.* 2005; Geheb *et al.* 2007). Malnutrition among the lake communities is high, with one study estimating that 40.2% of the children in fishing communities are stunted because of the lack of a balanced diet (Geheb *et al.* 2007). Further, about 5.7% of mothers were found to be chronically malnourished at fish landing sites (Geheb *et al.* 2007).

CONSERVATION EFFORTS

Co-management

The riparian governments have, for a long time, made decisions on the management of fisheries resources in Lake Victoria with little or no input from the resource users and stakeholders (Ogwang *et al.* 2009; Nunan 2010). Fisheries co-management approaches have been widely adopted internationally in response to the ineffectiveness of government to prevent the devastation of fish stocks occurring in many places around the world (Nunan 2010). It is in this regard that the three riparian governments around Lake Victoria came to realize that improved effectiveness and efficiency of fisheries management required the involvement of stakeholders through co-management of the resource.

Formation of co-management in Lake Victoria through Beach Management Units (BMUs) was facilitated through the Lake Victoria Fisheries Organization (LVFO), being initially financed by the EU-funded Implementation of a Fisheries Management Plan (IFMP) project, 2003–2010. About 1069 BMUS located across 1400 landing sites were formed around Lake Victoria, consisting of members of the fishing community, including boat owners, boat crew, managers, fish processors, fishmongers, local gear makers and dealers in fishing equipment. The functions of the BMUs encompassed both fisheries management and beach development tasks, including keeping registers of fishers, boats, gears, raising awareness about fisheries regulations, and working with government and police to increase compliance.

Co-management initially improved the effectiveness and efficiency of Lake Victoria fisheries management. Studies indicated the formation of BMUs improved relationships between fishing communities and fisheries staff, although the experiences varied around the lake (Luomba and Mhagana 2007; Odongkara *et al.* 2007). Some empowerment and power sharing begun around the lake through the BMUs (Nunan 2010). In 2007 and 2008 lake-wide surveys, many boat crew and women, previously more marginalized in fisheries management, responded that they believed they had more voice in decision-making since the formation of the BMUs. The communities took an active role in eliminating illegal fishing activities, being more involved in revenue collection on behalf of the governments, and in decision-making processes on fisheries-related issues.

While successes were recorded in all three riparian countries, there were also new challenges to be addressed as the new institutions grow. Many of the challenges related mostly to management and governance issues, and an inability to enforce the BMU bylaws (due in part to an ineffectual scheme of penalties). Such shortfalls resulted in ongoing illegal fishing activities, non-payment of catch levies or permits, and conflicts between outsiders and resident fishermen. These challenges can be addressed by enhancing the ability of the BMUs to implement and enforce their bylaws. Other recommendations include developing business plans to increase revenue generation, improving the role of the BMUs in data collection and monitoring, and offering opportunities to increase offshore fishing. They must also collaborate with other BMUs, as well as with government agencies and other stakeholder groups, a goal that can be achieved through the formation of effective BMU networks. Concerns have been raised on the limited involvement of community members in monitoring, control and surveillance activities of government, and the lack of opportunities for fishing communities to participate in government planning, leading to old vices such as illegal fishing and use of banned gears finding their way back to the lake site.

Nunan (2010) argued that the co-management structures and systems in place on Lake Victoria have the capacity to be more responsive and flexible, but also require more technical and financial support, as well as adoption of adaptive governance. She further contends that co-management is a process, rather than a static arrangement designed to yield immediate results. Thus, the co-management process is dynamic and can only evolve in practice over time with the support of stakeholders and the government. Going forward to solve the problem of 'unlimited access to the fishery', the stakeholders must define property ownership rights with alternatives offered to BMUs or fishers that may be 'denied' access, even if they previously depended on the fishery for their livelihoods.

Fishery management plan for Nile perch

The LVFO has thus far developed two management plans for Nile perch in Lake Victoria. The first Nile perch Fishery Management Plan for Nile Perch (NPFMP1) covered the period 2009–2014. The top priority of this plan was to reverse overfishing, using a group of measure, including reduced fishing efforts via such approaches as closed seasons and closed areas. The plan also emphasized the need to eradicate the illegal trade in undersized, immature fish and the most harmful illegal fishing practices, including beach seining and the use of undersize gillnets. The NPFMP1 was adopted by the LVFO Council of Ministers (LVFO-CoM) in June 2009. The main aim of the plan was to optimize sustainable fish production; maximize contributions to macro-economic growth through foreign exchange generated by exports of fish products; and maximize net income of participating artisanal fishers.

The NPFMP1 was revised through the EU-financed ACP Fish II project, giving rise to NPFMP2. The NPFMP2 furthered the previous objective of reducing the overall fishing effort through closed seasons. NPFMP2 also emphasized on the need for stronger enforcement of existing regulations to combat illegal unregulated and unreported (IUU) fishing.

CONCLUSIONS AND RECOMMENDATIONS

The controversial introduction of Nile perch in Lake Victoria upsets the existing ecological balance, setting the stage for the extirpation of many haplochromine cichlids. The reduced abundance and diversity of the haplochromines had 'knock-on effects' on other ecosystem components. The haplochromine destruction, for example, disrupted the complex food webs existing prior to the Nile perch introduction. This altered floral and faunal composition leads to changes in water quality. The prevalent algal blooms observed in the lake are attributable partly to the decline of herbivorous cichlids and detritus feeders, attributed to Nile perch predation. The change in water clarity is thought to be responsible for hybridization of haplochromines, further contributing to the reduced species diversity among cichlids.

The establishment and eventual expansion of Nile perch changed the socio-economic setting for Lake Victoria. About 35 million people currently depend directly or indirectly on its fisheries for a living. The commercialization of the fishery, however, concentrated the export earnings to a small percentage of participants. Other socio-economic issues associated with Nile perch include the high HIV/AIDS prevalence among fishers, and border conflicts attributable to the migratory and trans-boundary nature of the fishery resource.

With support from its development partners, the LVFO established co-management units (BMUs) for Lake Victoria. Although successes were recorded, there were also challenges that suggested the institutions must be strengthened or restructured to be effective and efficient. Other conservation efforts include establishment of the Nile perch Fisheries Management Plans focusing on curbing overfishing and eradicating illegal fishing activities in the lake. In view of the complex nature of the Lake Victoria ecosystem, however, a whole ecosystem approach to management that takes care of the biophysical resource and the socio-economic aspects into account is advocated.

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REFERENCES

Abila R. O. (2000) The development of the Lake Victoria fishery: A boom or bane for food security. IUCN Report No. 8 Nairobi, Kenya.

Acere T. O. (1985) Observations on the biology of the Nile perch (*L. niloticus*) and growth of its fishery in the northern waters of Lake Victoria. *FAO Fish. Rep.* **335**, 42–61.

Aloo P. A. (2009) The Fisheries Industry in Kenya: A window of opportunity for development. In: Kenya's Economic History: Land, Water, Railways, Education, and Entrepreneurship (ed Amutabi M.) pp. 394–411. Amazon.com, The Edwin Mellen Press, New York.

Anderson A. M. (1961) Further observation concerning the proposed introduction of Nile perch into Lake Victoria. *E. Afri. Agri. For. J.* **26**, 701–33.

Asila A. A. & Ogari J. (1987) Growth parameters and mortality rates of Nile perch (*Lates niloticus*) estimated from length-frequency data in the Nyanza Gulf (Lake Victoria). In: Contributions to Tropical Fisheries Biology (eds S. Venema, J. Moller-Christensen and D. Pauly) pp. 272–87. Papers by the participants of FAO/DANIDA Follow-up Training Courses. FAO Fisheries Report 389.

Cornelissen I. J. M., van Zwieten P. A. M., Peter H. K. & Nagelkerke L. A. J. (2015) Nile perch distribution in south-east Lake Victoria is more strongly driven by abiotic factors, than by prey densities. *Hydrobiologia* **755**, 239–55.

Coulter G. W., Allanson B. R., Bruton M. N. *et al.* (1986) Unique qualities and special problems of the African Great Lakes. *Environ. Biol. Fishes* **17**, 161–83.

Crapon de Caprona M. D. & Fritzsch B. (1984) Interspecific fertile hybrids of haplochromine Cichlidae (Teleostei) and their possible importance for speciation. *Nether. J. Zool.* **4**, 503–38.

Downing A. S., Galic N., Goudswaard P. C. *et al.* (2013) Was Lates late? A null model for the Nile perch boom in Lake Victoria. *PLoS ONE* **8**, e76847.

Elmer K. R., Lehtonen T. K. & Meyer A. (2009) Color assortative mating contributes to sympatric divergence of neotropical cichlid fish. *Evolution* **63**, 2750–7.

FAO (2003) Report on Expert Consultation on International Fish Trade and Food Security. Casablanca, Morocco. FAO Fisheries Report 708. FAO, Rome, Italy, 213 p.

Froese, R., Pauly, D. (Editors) (2016) FishBase. World Wide Web electronic publication. www.fishbase.org version.

Fryer G. (1960) Concerning the proposed introduction of Nile Perch into Lake Victoria. *East Afr. Agric. J.* **25**, 267–70.

Gee J. M. (1965) The spread of Nile perch, *Lates niloticus*, in East Africa, with comparative biological notes. *J. Appl. Ecol.* **2**, 407–8.

Geheb K., Kalloch S., Medard M., Nyapendi A. T., Lwenya C. & Kyangwa M. (2007) Nile Perch and the hungry Lake Victoria: Gender, status and food in East Africa fishery. *Food Policy* **33**, 85–98.

Goudswaard P. & Witte F. (1985) Observations on Nile perch *Lates niloticus* (L.) 1758, in the Tanzanian waters of Lake Victoria. *FAO Fish. Rep.* **335**, 62–5.

Hamblyn E. L. (1961) Nile perch Project. EAFFRO Annual Report.26-32, Jinja, Uganda.

Harris C. K., Wiley D. S. & Wilson D. C. (1995) Socioeconomic impacts of introduced species in Lake Victoria fisheries. In: Impact of Species Changes in African Lakes (eds Pitcher T. J. & Hart P. J. B.). Chapman and Hall, London.

Hecky R. E. (1993) The eutrophication of Lake Victoria. Kilham Memorial Lecture. 25th Congress of SIL. *Verh. Internat. Verein. Limnol.* **25**, 39–48.

Hecky R. E. & Bugenyi F. W. B. (1992) Hydrology and Chemistry of the African Great Lakes and water quality issues: problems and solutions. *Mitt. Internat. Verein. Limnol.* **23**, 45–5.

Hecky R. E., Bugenyi F. W. B., Ochumba P. *et al.* (1994) Deoxygenation of the deep waters of Lake Victoria. *Limnol. Oceanogr.* **39**, 1476–80.

HEST (1986). Report of the meetings on the Nile perch effect on Lake Victoria fisheries. Rep. Haplochromis Ecol. Surv.Team (HEST) Univ. Leiden, (34).

Jambiya G. & Sosovele H. (2002) Impact of Fisheries on the Resource Along the Shores of Lake Victoria. Lake Victoria Environmental Management Project Secretariat, Dar es salaam, Tanzania.

Kaufman L. (1992) Catastrophic change in species-rich fresh-water ecosystems. *Bioscience* **42**, 846–58.

Kudhogania A. W. & Cordone A. J. (1974) Batho-spatial distribution pattern and biomass estimation of the major demersal fishes in Lake Victoria. *Afr. J. Hydrobiol. Fish* **3**, 15–31.

Kwena Z. A., Bukusi E., Omondi E., Ng'ayo, M., Holmes, K. K. (2012) Transactional sex in the fishing communities along Lake Victoria, Kenya: a catalyst for the spread of HIV. *Afr. J. AIDS Res.* **11**, 9–15.

Ligtvoet, W., & Mkumbo, O. C. (1990). Stock assessment of the Nile perch in Lake Victoria. p. 35–74. In: CIFA, Report of the 5th Session of the Sub-committee for the Development of the Fisheries in Lake Victoria, Mwanza, Tanzania, 1989 September 12–14. FAO Fish Rep. 430, FAO, Rome.

Lowe S. J., Browne M., Boudjelas S. & De Poorter M. (2000) 100 of the World's Worst Invasive Alien Species p. 12. Published by the IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland, New Zealand.

Lowe-McConnell R. H. (1994) The changing ecosystem of Lake Victoria, East Africa. *Freshwat. Forum* **4**, 76–89.

Luomba, J. & Mhagana, F. (2007) Report on Governance in Co-management Survey in Lake Victoria, Tanzania. Mwanza, Tanzania: Implementation of a Fisheries Management Plan, Tanzania Fisheries Research Institute.

LVFO (2014) Regional Status Report on Lake Victoria Biennial Frame Surveys between 2000 and 2014. Lake Victoria Fisheries Organisation, Jinja, Uganda.

LVFO (2016) Report of the Lake-Wide Acoustic Survey. Technical ReportLake Victoria Fisheries Organization, Jinja, Uganda.

Maan M. E. & Sefc K. M. (2013) Colour variation in cichlid fish: Developmental mechanisms, selective pressures and evolutionary consequences. *Semin. Cell Develop. Biol.* **24**, 516–28.

Mkumbo O. C. (2002) Assessment and Management of Nile Perch (*Lates niloticus* L.) stocks in the Tanzanian waters of Lake Victoria. PhD Thesis, University of Hull, Hull, UK.

Mugidde R., Gichuki J., Rutagemwa D., Ndawula L. & Matovu X. (2005) Status of water quality and its implication on the fishery production. In: The State of the Fisheries Resources of Lake Victoria and Their Management. Proceedings of the Regional Stakeholders' Conference, pp. 106–12. Lake Victoria Fisheries Organization Secretariat, Jinja, Uganda.

Njiru M. A. N., Othina A., Getabu D., Tweddle D. & Cowx I. G. (2002) Is the invasion of water hyacinth, *Eichhornia crassipes* Solms (Mart.), a blessing to Lake Victoria fisheries? In: Management and Ecology of Lake and Reservoir Fisheries (ed Cowx I. G.) pp. 255–63. Fishing News Books, Blackwell Science, Oxford, UK.

Njiru M., Waithaka E., Muchiri M., van Knaap M. & Cowx I. G. (2005) Exotic introductions to the fishery of Lake Victoria: What are the management options? *Lakes Reserv. Res. Manage.* **10**, 147155. ISSN 1320-5331.

Njiru M., Getabu A., Othina A. & Wakwabi E. (2007) Are the management measures successful in Lake Victoria, Kenya ? The case of Nile perch and Nile tilapia Fishery. *Afr. J. Ecol.* **45**, 315–23.

Njiru M., Kazungu J., Ngugi C. C., Gichuki J. & Muhoozi L. (2008) An overview of the current status of Lake Victoria fisheries: Opportunities, Challenges and Management Strategies. *Lakes Reserv. Res. Manage.* **13**, 1–12.

Njiru M., Sitoki L., Nyamweya C. *et al.* (2012) Habitat degradation: Could it be the key to Lake Victoria fisheries changes? In: Advances in Environmental Research. Vol. **27** (ed Daniels J. A.) pp. 1–27. NOVA Science Publishers Inc, New York. ISBN: 978-1-62257-425-4.

Ntiba M. J., Kudoja W. M. & Mukasa C. T. (2001) Management issues in the Lake Victoria watershed. *Lakes Reserv. Res. Manage.* **6**, 211–6.

Nunan F. (2010) Governance and fisheries co-management on Lake Victoria: Challenges to the adaptive governance approach. *Mast* **9**, 103–25.

Nyamweya C., Sturludottir E., Tomasson T. *et al.* (2016) Exploring Lake Victoria ecosystem functioning using the Atlantis modeling framework. *Environ. Model. Softw.* **86**, 158–67. https://doi.org/10.1016/j.envsoft.2016.09.019.

Nyamweya C., Sturludottir E., Tomasson E. A., Taabu-Munyaho A., Njiru M. & Stefansson G. (2017) Prediction of Lake Victoria's response to varied fishing regimes using the Atlantis ecosystem model. *Fish Res.* **194**, 76–83. https://doi.org/10.1016/j.fishres.2017.05.014.

Ochumba P. B. O. (1995) Limnological changes in Lake Victoria since the Nile perch introduction. In: T. J. Pitcher & P. J. B. Hart (eds.) The impact of species changes in African Lakes. Chapman & Hall Fish & Fisheries Series 18, London

Ochumba P. B. O. (1987) Periodic massive fish kills in the Kenyan part of Lake Victoria. *Water Qual. Bull.* **12**, 119–122, 130.

Ochumba P. B. O. (1990) Massive fish kills within the Nyanza Gulf of Lake Victoria, Kenya. *Hydrobiologia* **208**, 93–9.

Odongkara K., Ntambi B. & Mbilingi B. (2007) Governance in Co-management on the Lake Victoria Fisheries, Uganda. IFMP Socio-Economic Series 8. Jinja: National Fisheries Resources Research Institute.

Odongkara K., Abila R., & Onyango P. O. (2005) Distribution of economic benefits from the fisheries. In: The State of the Fisheries Resources of Lake Victoria and Their Management. Proceedings of the Regional Stakeholders' Conference, pp. 124–31. Lake Victoria Fisheries Organization Secretariat, Jinja, Uganda.

Ogari J. & Asila A. A. (1992). Status of fisheries of Lake Victoria Kenya sector. p. 15–23. In CIFA. Report of the sixth session of the sub-committee for the development and management of the fisheries in Lake Victoria, 10–13 February 1992, Jinja, Uganda. FAO Fish. Rep. 475. FAO, Rome.

Ogutu-Ohwayo R. (1990) The decline of the native species fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus,* and the Nile tilapia, *Oreochromis niloticus*. *Env. Biol. Fish.* **27**, 81–96.

Ogwang V. O., Nyeko J. I. & Mbilinyi R. (2009) Implementing co-management of Lake Victoria's fisheries: Achievements and challenges. *Afr. J. Trop. Hydrobiol. Fish.* **12**, 52–8.

Ondondo R. O., Nganga Z. W., Mpoke S., Kiptoo M. & Bukusi E. A. (2014) Prevalence and Incidence of HIV Infection among Fishermen along Lake Victoria Beaches in Kisumu County, Kenya. *World J. AIDS* **4**, 219–31.

Opio A., Muyonga M. & Mulumba N. (2013) HIV infection in fishing communities of Lake Victoria Basin of Uganda – A cross-sectional sero-behavioral survey. *PLoS ONE* **8**, e70770. https://doi.org/10.1371/journal.pone.0070770.

Pauers M. J., Kapfer J. M., Doehler K., Lee J. T. & Berg C. S. (2012) Gross colour pattern is used to distinguish between opponents during aggressive encounters in a Lake Malawi cichlid. *Ecol. Freshwat. Fish* **21**, 34–41.

Pauly D. (1984) A mechanism for the juvenile-to adult transition in fishes. *J. Cons. Int. Explor. Mer.* **41**, 280–4.

Riedmiller S. (1994) Lake Victoria fisheries. The Kenyan reality and environmental implications. *Environ. Biol. Fish.* **39**, 329–38.

Seehausen O., van Alphen J. J. M. & Witte F. (1997) Cichlids diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–11.

Shaka J. (2013) Migingo Island: Kenyan or Uganda Territory? *J. Conflictol.* **4**, 34–7.

Sharpe D. M. T., Wandera S. B. & Chapman L. J. (2012) Life history change in response to fishing and an introduced predator in the East African cyprinid *Rastrineobola argentea*. *Evol. Appl.* **5**, 677–93. https://doi.org/10.1111/j.1752-4571.2012.00245.x.

Socio-Economic Data Working Group (1999) The survey of Lake Victoria's fishers. LVFRP, Jinja, Uganda. No. LVFRP/TECH/99/05.

Taabu A. (2004). Assessment of the Status of the Stock and Fishery of Nile Perch in Lake Victoria, Uganda. Project Report. Reykjavik: United Nations University - Fisheries Training Program.

Taabu-Munyaho A., Kayanda R. J., Everson I., Grabowski T. B. & Marteindottir G. (2013) Distribution and exploitation of Nile perch *Lates niloticus* in relation to stratification in Lake Victoria, East Africa. *J. Great Lakes Res.* **39**, 466–75.

Wagner C. E., McCune A. R. & Lovette I. J. (2012) Recent speciation between sympatric Tanganyikan

Wanink J. H. (1998) The pelagic *Rastrineobola argentea* as a crucial link in the disrupted ecosystem of Lake Victoria: Dwarfs and Giants – African adventures. PhD thesis. Rijksuniversitent, Leiden, the Netherlands. ISBN 90-5651-042-8, 288p

Wanink J. H., Kashindye J., Goudswaard, P. C. & Witte, F. (2001) Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*? *Freshwat. Biol.* **46**, 75–85.

Weston M. (2015) Troubled Waters. Why Africa's largest lake is in grave danger. http://www.slate.com/articles/news_and_politics/roads/2015/03/lake_victoria_is_in_grave_danger_africas_ largest_ lake _is_ threatened_by.html [uploaded 7/05/2016).

Witte F. (2009) *Lates niloticus*. Invasive Species Compendium (CABI). Available: http://www.cabi.org/isc/?compid=5&dsid=77994&loadmodule=datasheet&page=481&site=144. (June 2016).

Witte F. & Van Densen W. L. T. (1995) Fish Stocks and Fisheries of Lake Victoria. A Handbook for Field Observations. Samara Publishing, Cardigan, UK.

Witte F., Goldschmidt T., Goudswaard P. C., Ligtvoet W., Oijen M. J. P. & van Wanink J. H. (1992a) Species extinction and concomitant ecological changes in Lake Victoria. *Neth. J. Zool.* **42**, 214–32.

Witte F., Goldschmidt T., Wanink J. H. *et al.* (1992b) The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Env. Biol. Fish* **34**, 1–28.

Witte F., Goudswaard T., Katunzi E. F. B., Mkumbo O. C., Seehausen O. & Wanink J. H. (1999) Lake Victoria's ecological changes and their relationships with the riparian societies. In: Ancient Lakes: Their Cultural and Biological Diversity (eds Kawanabe H., Coulter G. W. & Roosevelt A. C.) pp. 189–202. Kenobi Productions, Belgium.

Witte F., Kishe-Machumu M.A., Mkumbo O.C. *et al.* (2013) The fish fauna of Lake Victoria during a century of human induced perturbations. In: Proceedings of the Fourth International Conference on African Fish and Fisheries (eds Snoeks J. & Getahun A.), pp 49-66. Addis Adaba, Ethiopia, 22-26 September 2008. Tervuren: Royal Museum for Central Africa, 'Zoological Documentation Online Series'. https://doi.org/https://doi.org/10.13140/2.1.3731.8087

Wootton R. J. (1998) Ecology of Teleost Fishes p. 386. Kluwer Academic Publisher, Dordrecht.

Yongo E., Keizire B. B. & Mbilinyi H. G. (2005) Socioeconomic impacts of trade. In: The State of the Fisheries Resources of Lake Victoria and Their Management. Proceedings of the Regional Stakeholders' Conference, pp. 124–31. Lake Victoria Fisheries Organization Secretariat, Jinja, Uganda.