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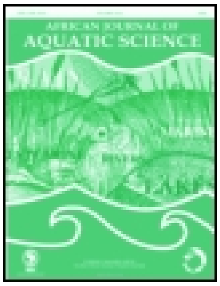

African Journal of Aquatic Science
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/taas20

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Published online: 27 Aug 2013.

To cite this article: African Journal of Aquatic Science (2013): Variations and changes in habitat, productivity, composition of aquatic biota and fisheries of the Kyoga lake system: lessons for management, African Journal of Aquatic Science, DOI: 10.2989/16085914.2013.795886

To link to this article: http://dx.doi.org/10.2989/16085914.2013.795886

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African Journal of Aquatic Science 2013: 1–14
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This is the final version of the article that is published
ahead of the print and online issue

AFRICAN JOURNAL OF
AQUATIC SCIENCE
ISSN 1608-5914 EISSN 1727-9364
http://dx.doi.org/10.2989/16085914.2013.795886

Review Paper

Variations and changes in habitat, productivity, composition of aquatic biota and fisheries of the Kyoga lake system: lessons for management

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The Kyoga lake system, which is c. 4 m deep, originally had a diverse fish fauna, extensive macrophytes and wetlands. Most (82%) of its water comes from Lake Victoria, is controlled through three dams and has a short residence time of c. 3 months. Physical and chemical factors, plankton productivity and composition vary across the lake from east to west. The macrophyte cover decreased after the heavy El Niño rains of 1961, and the area of wetlands decreased by 48.5% between 1994 and 2008 mainly because of their conversion to agriculture. The main lake was infested with water hyacinth in the 1990s but subsequently this was brought under control. The native fishes were overexploited and non-native fishes, including a top piscivore, Nile perch *Lates niloticus* L., were introduced and boosted fish production, but they also were overexploited. Nile perch also preyed upon and decimated native species, which survived only in satellite lakes. Populations of some of these species recently have started to recover in the main lake. Efforts should be made to control habitat loss and water-level fluctuations, wetland loss, overexploitation of the fishes, conserve the surviving fish species and address the emerging challenge of climate change.

Keywords: climate change, fisheries, fishes, hydrology, macrophytes, management, morphometry, overexploitation, productivity, species introductions, wetlands

Introduction

The Kyoga lake system in central Uganda, which is located between longitudes 32°05′ and 33°35′ E and latitudes 1°05′ and 1°55′ N at 1 034 m above sea level (Figure 1), consists of two main arms, Kyoga and Kwania, and over 30 smaller lakes that are separated from the main lake by swamps (Vanden Bossche and Bernacsek 1990). The Nile River flows through the lake at its western edge. The Kyoga catchment below Lake Victoria extends over 60 000 km^2 and covers about 25% of Uganda's surface area of 240 000 km^2. It spreads from the wetter south, with bimodal average annual rainfall of up to 2 100 mm, to the predominantly arid north with unimodal average annual rainfall of about 500 mm, with an area of higher rainfall of about 1 500 mm around Mount Elgon to the east (LCCS 1999, Mubiru et al. 2009). The area of open water in the lakes varies around 2 600 km^2 and the lakes have a mean depth of 2–4 m, except for a 7–9 m deep channel marking the course of the Nile River. Virtually all the people living in the Kyoga lake basin depend on agriculture and natural resources, with fish being particularly important to them.

Hydrology and water balance

The hydrology of the Kyoga lakes is largely determined by the Nile River, draining out of Lake Victoria, which contributes c. 82% of the inflow, the balance coming from the catchment (9%) and direct rainfall (9%). The Nile water does not remain long in the lake and the outflow into the lower Victoria Nile accounts for 83.7% of the losses, with evapotranspiration accounting for 16.3% (Table 1). The total outflow of about 33.7 km^3 per annum is 4.5 times greater than the lake's volume of c. 8 km^3, giving it a hydraulic retention time of c. 3 months (ILM 2004). Since 1954 the flow of the Nile has been regulated by the Owen Falls (Nalubaale) Dam, as well as by the Kiira (2002) and Bujagali (2012) dams, and the control of water passing through these dams affects the water level of the Kyoga lakes. For instance, when the level of Lake Victoria decreased by 1.64 m between 1998 and 2004, that of the Kyoga lakes fell by 1.5 m (EAC 2006). The fall in the level of Lake Victoria was attributed partly to reduced rainfall and to the excessive release of water from Owen Falls Dam. Swenson and Wahr (2009) showed that there was no similar decrease in the level of Lake Edward, which is not influenced by the Nile, during this time. This supports the hypothesis that excessive discharges from the dams contributed to the drop in water level in Lake Victoria and the two downstream lakes, Kyoga and Albert.

Physical and chemical conditions, plankton and invertebrates

Physical and chemical conditions, and plankton productivity and composition, vary along an east–west gradient

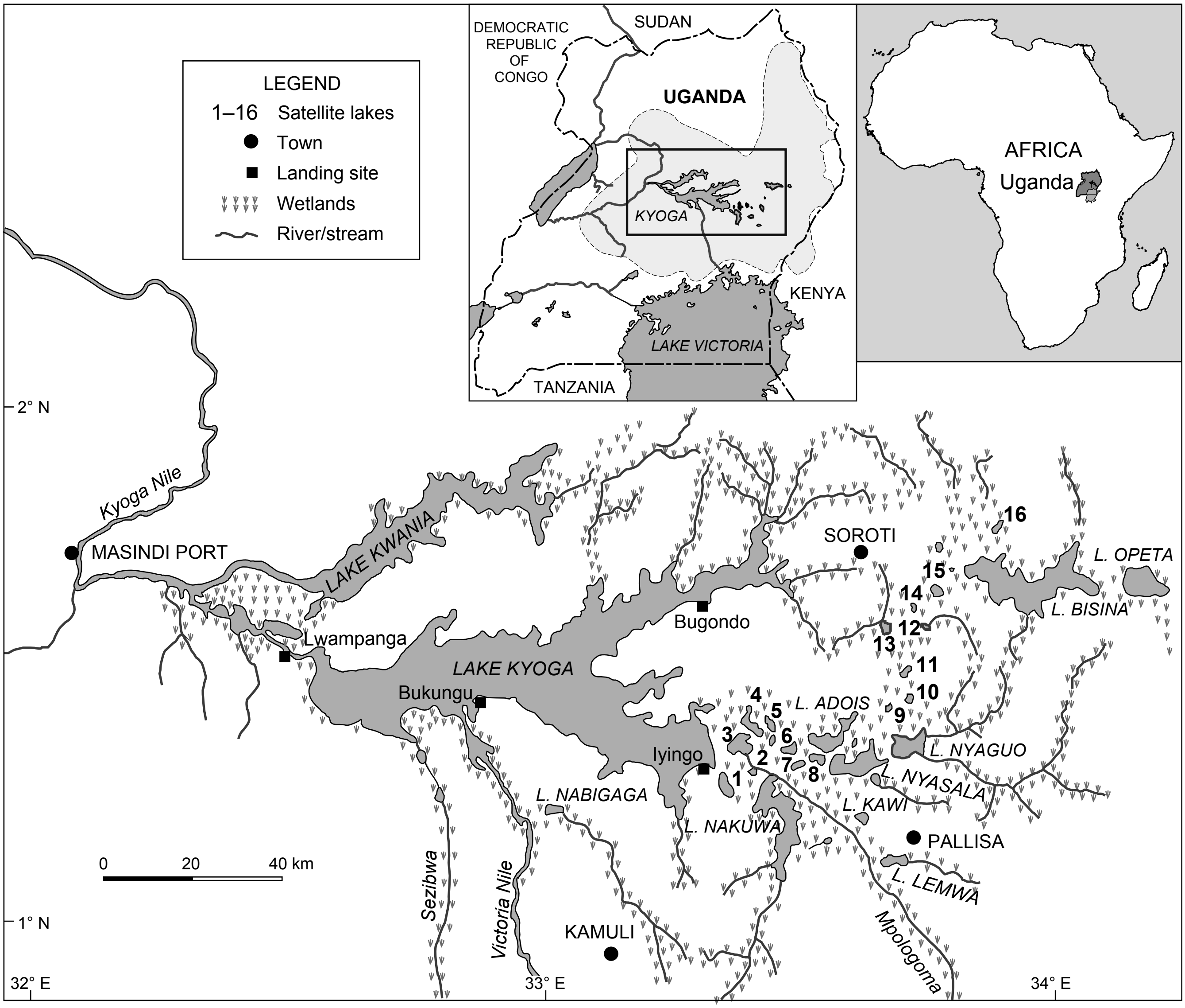

Figure 1: Map of the Kyoga Basin lakes. Satellite lakes: 1 = Nawampasa, 2 = Murlu, 3 = Namasajeri, 4 = Kiondo, 5 = Naragaga, 6 = Pachoto, 7 = Kadiko, 8 = Gigati, 9 = Kodiki, 10 = Gawe, 11 = Agu, 12 = Kasago, 13 = Opare, 14 = Ajama, 15 = Semere, 16 = Owapet

Table 1: Water budget of the Kyoga lakes, adapted from Talling and Lemoalle (1998), and average flows based on data from MWE (2007)

Parameter	Water budget (km^3 y^{-1})	Average water flow (m^3 s^{-1})
Lake volume	7.6	
Inflow from Victoria Nile	28.4	1 074.2
Inflow from local catchment		118.0
Precipitation	5.5	121.5
Total gains	33.9	1 313.7
Lake evaporation	6.9	213.2
River outflow	26.8	1 097.6
Total losses	33.7	1 310.8
Storage	0.2	2.9

(Table 2). The decrease in conductivity from >168 µS cm^{-1} in the eastern part of the system to <100 µS cm^{-1} in the centre of the lake has been attributed to water flowing into the eastern part of the lake from Mount Elgon, a nephelinitic Miocene volcano (Kilham and Hecky 1972). This water is diluted in the central part of the lake by water from the Nile River, which has a conductivity of 99 µS cm^{-1}. Cyanobacteria are the dominant algae in the east, where conductivity is higher, whereas the diatom *Aulachoseira* sp. dominates the western region where conductivity is lower (Green 2009). Human activities in the mountain areas and in the catchment seem to contribute to the increase in soluble reactive silica concentration in the eastern part of the lake. Although the total phosphorus (TP) concentration ranged from 48 to 62 µg l^{-1} in the entire lake during the 1990s to 2000, the overall concentration in the 1960s was higher (174 µg l^{-1}) (Evans 1962). The decrease in

Table 2: Limnological characteristics (mean ± SD) of the general, western, central and eastern sections of Lake Kyoga from the 1960s to 2000s. Data for the eastern section were collected from Iyingo, for the central section from Bukungu and for the western section from Lwampanga regions of the main lake. TP = Total phosphorus, SRSi = soluble reactive silicon, Chl *a* = chlorophyll *a*

Characteristic	1960s[a]	1980s[b]		1990s[c]			2000s[d]	
	General	Central	East	West	Central	East	Central	East
Secchi depth (m)		1.7 ± 0.3	0.8 ± 0.2	0.9 ± 0.0	1.2 ± 0.0	1.1 ± 0.0	1.2 ± 0.0	1.0 ± 0.0
Conductivity (µS cm^{-1})	100	98	168 ± 21	102 ± 0.2	96.5 ± 0.0	218.3 ± 0.0	99.4 ± 0.0	245.4 ± 0.0
pH		7.2 ± 0.2	7.4 ± 0.2	8.4 ± 0.0	7.1 ± 0.0	7.0 ± 0.0	7.6 ± 0.0	7.6 ± 0.0
Temperature (°C)				25.9 ± 0.1	26.0 ± 0.0	26.3 ± 0.0	26.3 ± 0.0	26.9 ± 0.0
TP (µg l^{-1})	174			80.0 ± 2.5	48.8 ± 0.1	62.0 ± 0.2	49.9 ± 0.1	49.7 ± 0.1
SRSi (µg l^{-1})	1 400			550.0 ± 30.5	232.2 ± 0.5	1 592.2 ± 0.8	231.3 ± 0.2	7 576.9 ± 0.7
Chl *a* (µg l^{-1})				70.0 ± 2.5	37.6 ± 0.1		22.0 ± 0.0	18.5 ± 0.0

Data sources: [a] Evans (1962), [b] Mungoma (1988), [c] Mugidde (1992), [d] NaFIRRI (unpublished data)

Table 3: Number and densities of zooplankton species in different regions of the main Lake Kyoga, the Victoria Nile and selected minor lakes of the Kyoga system. Data for 1962 are from Green (2009), those for the Nile from Mwebaza-Ndawula et al. (2005), and those for the remaining sites were collected by NaFIRRI between 2001 and 2009

Zooplankton groups	1962	2001–2009					
		Nile	West	Central	East	Bisina	Lemwa
		Number of species					
Overall	–	27	28	30	29	18	8
Copepods	–	6	3	3	4	2	2
Rotifers	21	16	8	10	8	17	6
Cladocera	11	2	2	1	2	4	–
		Density of species (ind. m^{-2})					
Overall	–	–	2 195 980	2 689 066	6 078 429	95 343	301 333
Copepods	74 000	84 455	441 769	445 310	294 237	41 245	92
Rotifers	7 732	1 462	76 853	74 331	51 619	24 079	77
Cladocera	3 487	875	9 427	2 569	4 042	1 038	19

phosphorus concentration could have arisen from the 1997/98 El Niño rains that dislodged papyrus *Cyperus papyrus* L. and water hyacinth *Eichhornia crassipes* (Mart.) Solms, the combined effects of which can strip nutrients from water (Okurut et al. 1999, Kansiime et al. 2003). Inflows from the extreme north-eastern catchment along the Lake Bisina arm, which are deficient in total phosphorus (≤40 µg l^{-1}), could also have contributed to the dilution. However, the higher TP of 80 µg l^{-1} in the western portion of the lake, associated with a higher phytoplankton biomass of 70 µg l^{-1}, is likely to derive from the inflow from an area of intense agricultural activity via the Sezibwa River and from the flushing effect of the Nile. These variations have implications for aquatic productivity processes, in which the carbon source supplying complex aquatic food webs depends on phytoplankton primary production. Primary productivity of 3 800 mg C m^{-2} d^{-1} recorded in the main lake during the 1990s (Mugidde 1992) was lower than that of 5 213 mg C m^{-2} d^{-1} in Lake Victoria (Mugidde 1993) and much lower than that of 11 670 mg C m^{-2} d^{-1} in Lake George (Ganf and Horne 1975, Okello et al. 2010).

Lake Bisina is the only Kyoga lake without papyrus and in addition is transparent. This may be a consequence of its high fluoride concentration (6.65 mg l^{-1}) compared to that of the main Lake Kyoga (0.47 mg l^{-1}) or the Victoria Nile (0.38 mg l^{-1}), which Kilham and Hecky (1972) attributed to a selection factor affecting the distribution of higher plants, phytoplankton and zooplankton. Other minor lakes in the Bisina wetlands, such as Gawe and Adois, are also transparent and have low algal productivity (National Fisheries Resources Research Institute [NaFIRRI] unpublished data), which supports this hypothesis.

About 30 species of zooplankton, comprising copepods, rotifers and cladocerans, were identified in the Kyoga system, with rotifers comprising the highest number of species (Table 3). The overall zooplankton density decreased from 6.1 × 10^6 ind. m^{-2} in the east to 2.7 × 10^6 ind. m^{-2} in the central region, and to 2.2 × 10^6 ind. m^{-2} in the western region of the main Lake Kyoga, which is similar to the pattern observed for physico-chemical conditions. Copepods were numerically dominant, followed by rotifers and cladocerans. The trends in distribution and density were similar to those recorded in 1962 (Green 2009). The zooplankton density was much lower along the Nile and in the minor lakes.

Wetlands and macrophytes

The Kyoga Basin has the largest expanse of wetlands in Uganda, and the entire Kyoga lake system is a wetland, based on the Ramsar Convention definition of wetlands as transitional ecosystems between dry land and aquatic ecosystems where land is covered by water less than 6 m deep (UNESCO 1994). Wetlands have important hydrological and ecological functions as they retain water and release it slowly, trap silt, provide refugia, and serve as nursery and feeding grounds for fish and other organisms (Chapman et al. 2001).

When Worthington (1929) surveyed Lake Kyoga in 1928 it had only a narrow portion of open water, and most of the water ≤3 m deep was covered by sudd and marsh. The shoreline was fringed by papyrus, and swamp vegetation and floating sudd mats were common. At that time the smaller lakes appear to have been completely covered by swamp vegetation. Following a rise in water level during the exceptionally heavy El Niño rains of 1961 (Figure 2), open-water macrophytes and marginal swamps were submerged and the open-water portions of the lakes expanded. Similarly, the El Niño rains of 1997/98 dislodged macrophytes, primarily water hyacinth and papyrus, which floated downstream and blocked the outlet of Lake Kyoga, raising its water level by about 1.5 m and increasing its volume from an average of 7.7 km^3 in 1997 to 13.6 km^3 in 2003. This flooded an additional 580 km^2 of land, displaced human populations and destroyed infrastructure (ILM 2004). The blockage was opened in 2000 and by 2003 the lake level had fallen by 0.8 m. Historically, macrophytes have played a part in the hydrology of Kyoga lakes and therefore measures to improve the outflow by clearing them should take this into account.

Between 1994 and 2008 the area of wetlands in the Kyoga lake basin declined by 48.5% from 2 615 to 1 346 km^2, which was much higher than the national decrease of 4.7% from 37 600 to 26 308 km^2 (Table 4). Much of this loss was accounted for by large commercial rice schemes and numerous small-scale rice farms, some of which extend to the edges of lakes, destroying their vegetation and exposing them to siltation. Between 1994 and 2008 the shift from wetland to woodland in the Kyoga region also increased by about 7% and Mubiru et al. (2009) attributed the changes in spatial patterns and acreage of land-cover types in the Kyoga region to fluctuations in water levels related to climatic factors, especially rainfall. Whereas the wetlands around lakes Bisina, Opeta and Nakuwa are nominally protected under the Ramsar Convention, and Ugandan law prohibits cultivation and development within 100–200 m of lake shores and river banks, these regulations are not effectively enforced.

Water hyacinth invaded the Kyoga lakes in 1989 and covered 60% of the shoreline (Twongo 1996), interfering with fishing, fish breeding and nursery areas, and impacting on biodiversity. The water below water hyacinth mats was low in oxygen and became dominated by air-breathing fishes, especially *Protopterus aethiopicus* Heckel and *Clarias gariepinus* (Burchell), which have the capacity to survive under these conditions (Wanda et al. 2001, Njiru et al. 2005). Water hyacinth was brought under control using an integrated approach involving mechanical removal and biological control, and hippo grass *Vossia cuspidata* (Roxb.) Griff. established itself on hyacinth mats and reduced the expansion of the weed. In 1997 the association between water hyacinth, *V. cuspidata* and other aquatic macrophytes created large masses of buoyant vegetation that became dislodged and were pushed by wind to block the outlet of the Nile from Lake Kyoga (ILM 2004). Water hyacinth is, however, now a permanent component of the Lake Kyoga system and its monitoring and control should be sustained.

Native fishes and fisheries

Lake Kyoga once had a diverse fish fauna of at least 45 species in 12 families (Worthington 1929). Most species <30 cm in length, with the exception of *Rastrineobola argentea* (Pellegrin), were confined to the macrophyte

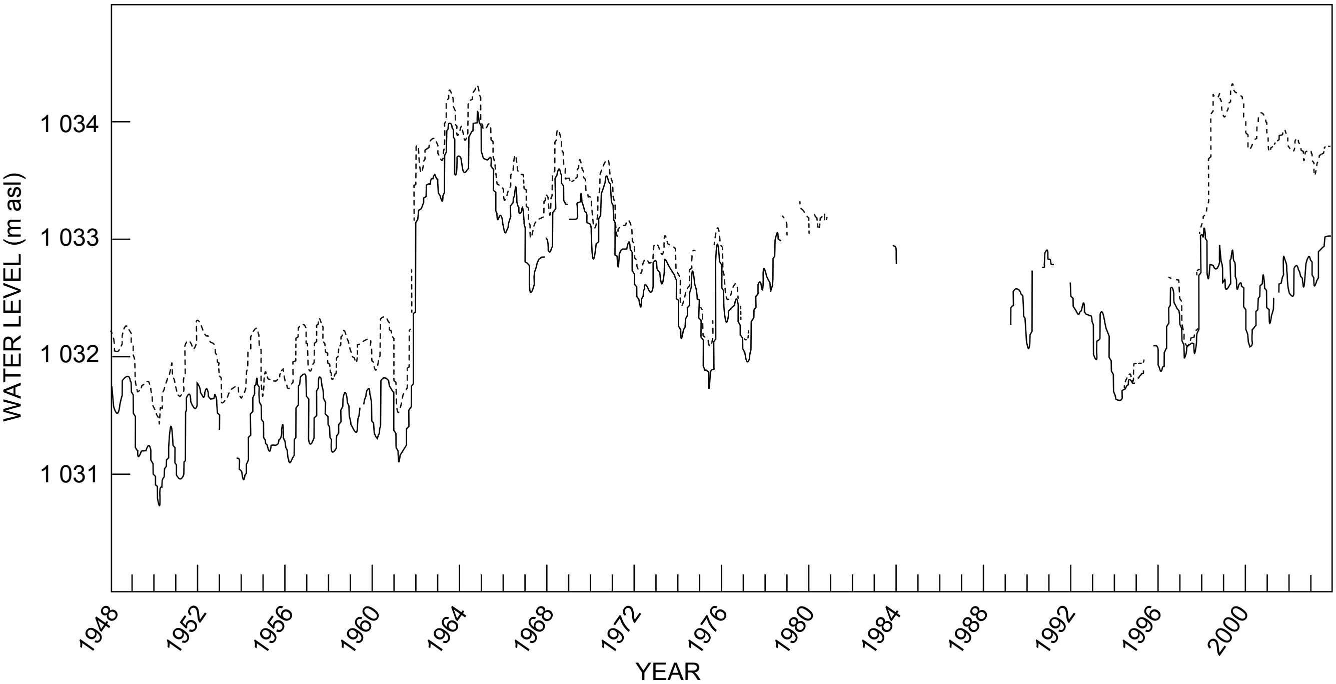

Figure 2: Average water levels of Lake Kyoga at Bugondo (broken line) and Masindi Port, on the Nile downstream (solid line), from 1948 to 2003. Data were obtained from Directorate of Water Resources Management (unpublished)

zone, whereas the larger species occurred in open waters. The fish fauna included two tilapia species endemic to the Lake Victoria/Kyoga region, namely *Oreochromis variabilis* (Boulenger), which inhabited the macrophyte zone, and *O. esculentus* (Graham), which was found in open water.

The fishery of the Kyoga lakes was originally dominated by native tilapias, which contributed over 90% of the catch between 1937 and the early 1950s (Figure 3), after which their contribution declined. The decline was attributed to the introduction of gillnets, which were more efficient than the indigenous fishing methods that consisted of locally made basket traps, seine nets made of papyrus, and hook and line fishing. Native fishermen had initially fished mainly during the dry season and reverted to farming during the rains. The fishing effort was therefore low and had little impact on the fish stocks. This changed from about 1940, when the demand for fish rose, almost doubling by 1945 because of increased access to distant markets, following improved communication owing to the advent of railways. Fishing effort fell by almost 50% in 1946, when fishermen switched to hunting crocodiles because of the high price offered for their skins and the targeting of crocodiles to reduce the destruction of nets and threats to human life (UGFD 1948). Nevertheless, the stocks of the native tilapias continued to

Table 4: Changes in wetland area coverage by wetland land-cover class for the Lake Kyoga catchment between 1994 and 2008. Source: MWE (2010)

Coverage/wetland land-cover class	1994		2008		Change	
	Area (km²)	% coverage	Area (km²)	% coverage	Area (km²)	% coverage
National coverage	37 575	15.6	26 308	10.9	−11 268	−4.7
Kyoga coverage						
Papyrus and sedges	2 615	17	1 346	12.2	−1 269	−48.5
Farmland	2 198	15	1 514	13.7	−684	−31.1
Grassland	8 625	57	6 626	60.1	−1 999	−23.2
Bush and thicket	365	2.4	252	2.28	−113	−30.9
Woodland	1 206	8	1 290	11.7	+84	+7.0
Total	15 009		11 029		−3 980	

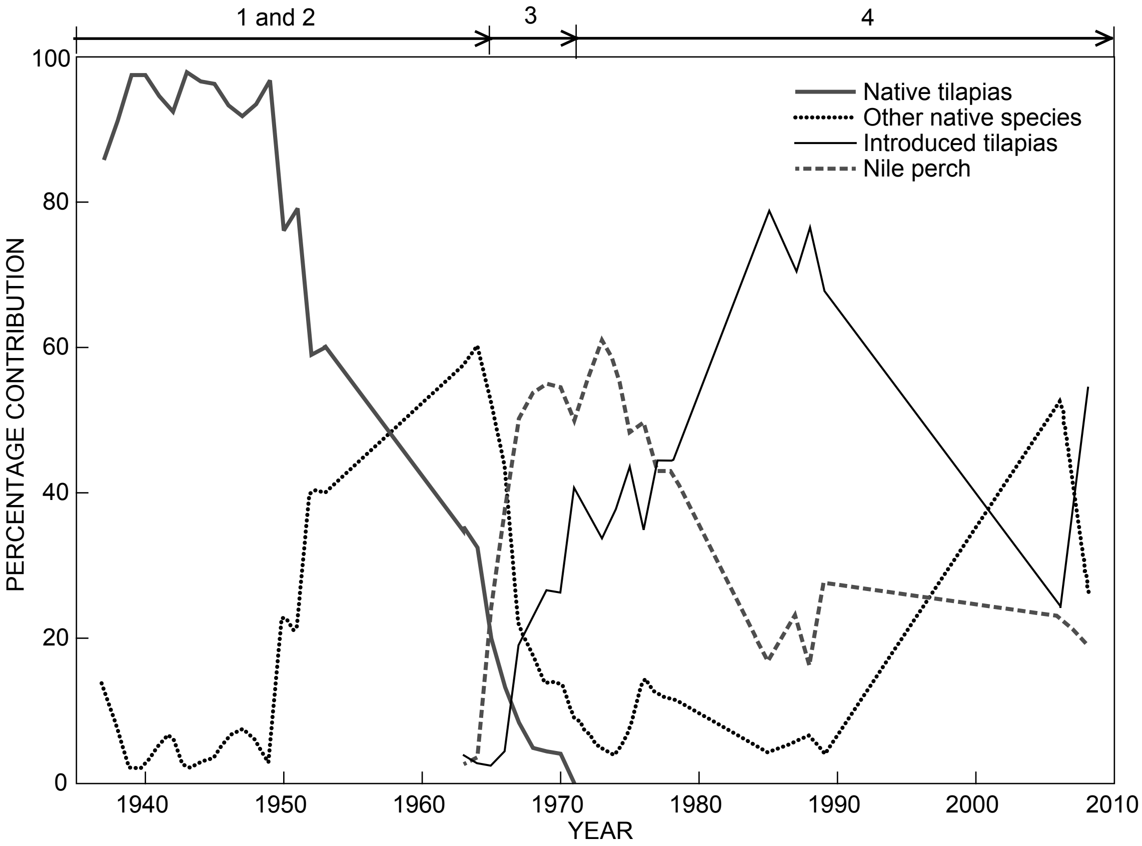

Figure 3: Relative importance of dominant fish groups in commercial catches in the Kyoga lakes, 1936–2010. Major factors thought to have influenced the catches: 1 and 2 = overexploitation and water-level fluctuations; 3 = introduction of non-native species; 4 = water hyacinth and climate change. Data from Worthington (1929), Gee (1969), Stoneman and Rogers (1970), and unpublished statistics from the Uganda Fisheries Department from 1937 to 1953

decline. Fishing pressure increased markedly in 1949, after arrival of fishermen from Kenya, who fished through most of the year (UGFD 1950). In 1951 and 1952 there was a shift to gillnets, a more efficient fishing gear, and this contributed further to the decline in catches of the native tilapias (UGFD 1952). In addition, there was no limit on the mesh sizes of gillnets used, with very small mesh-size gillnets of 64 mm to 102 mm being freely used. The 89–102 mm mesh-size nets were most suitable for native tilapias, whereas 64 mm nets, which were intended for *Schilbe intermedius* L. and *L. victorianus*, also caught juveniles of the larger species. The number of nets sold in the region increased 10-fold over nine years (UGFD 1956). This increased the fishing effort and contributed to the decline in native tilapias, the catch rates of which decreased from 30 fish net^{-1} night^{-1} in the 1940s to 7.7 fish net^{-1} by 1950 (UGFD 1948, 1951), after which the native tilapia fishery collapsed. Many fishermen then shifted to longlines, which increased the contribution of *P. aethiopicus*, *Bagrus docmak* (Forsskål), *C. gariepinus*, large *Barbus* spp. and *S. intermedius* to the catches. By 1957, 70% of the catch was from longlines, 20% from gillnets and 10% from basket traps (UGFD 1959).

The changes in the fishery of the Kyoga lakes up to about 1950 were therefore a result of overexploitation, but thereafter other factors such as habitat alteration as a result of water-level fluctuations, the loss of macrophytes and the introduced non-native fishes became increasingly important. Lake Victoria, which had fisheries similar to those of the Kyoga lakes, has also been subjected to multiple stresses including population growth, destructive land use, intensive exploitation, non-native species introductions, pollution and climate warming (Hecky et al. 2010). There is increasing debate as to which of these stressors is the most important and should be targeted in the development and management of fisheries and fish habitats (Kolding et al. 2008). There is, therefore, a need to examine the different stressors in aquatic systems to help predict the changes that may result from them, so as to guide management.

The post-introduction fisheries

Three non-native tilapias, Nile tilapia *Oreochromis niloticus* (L.), *O. leucostictus* (Trewavas), and *Tilapia zillii* Gervais, as well as a top predator, Nile perch *Lates niloticus* (L.), were introduced into the main Lake Kyoga and several of the satellite lakes, including Bisina and Nakuwa, in 1954/55 to boost the fishery (Stoneman and Rogers 1970, Pringle 2005). It took about 10 years for the introduced fish species to become well established and their stocks started increasing rapidly in the mid-1960s (Figure 4). The increases occurred after the reduction in macrophyte cover and expansion of open waters that followed a rise in lake level after the heavy El Niño rains of 1961. The reduction in macrophyte cover could have exposed many of the native species that had used them as a refuge from the predatory Nile perch, and the expansion of the open waters could have extended the breeding areas for tilapias, as was the case in Lake Victoria where increases in water level following the heavy rains of the early 1960s were associated with increases in stocks of introduced tilapias (Welcomme 1970). Submerged macrophytes could also have increased productivity by releasing nutrients as their organic matter decayed.

Following establishment of the introduced species, fish catches increased rapidly, rising from 18 000 t in 1964 to 165 200 t in 1978 (Figure 4). Nile perch were the first to increase, with their catch rising from 700 t in 1964 (0.3% of the catch) to 71 000 t (54%) in 1978, followed by the non-native tilapias (mainly Nile tilapia), whose catch rose from 600 t in 1964 (0.4%) to 81 000 t in 1985 (54%). Fishery data were collected only sporadically after 1978, but by 2008 the catch had fallen to 38 000 t and was dominated by Nile tilapia (61%), followed by Nile perch (15%) and *R. argentea* (17%), with the remainder being mostly *P. aethiopicus* and *C. gariepinus.* These changes were similar to those that occurred in Lake Victoria, except that Nile tilapia and *R. argentea* became the dominant species in Kyoga, whereas *R. argentea* and Nile perch dominated the fishery in Victoria (Table 5). The success of the two introduced species, Nile perch and Nile tilapia, and the persistence of the native cyprinid *R. argentea* can be attributed to the reduction in competition, especially following the depletion of the haplochromine stocks. Nile perch are able to feed on almost any species of fish, and haplochromines in Lake Kyoga had never been exposed to such a predator.

Stocks of Nile tilapia increased after that of the Nile perch. Overfishing of native tilapias and the depletion of haplochromines and other fishes, especially through predation by the Nile perch, seems to have allowed stocks of the Nile tilapia to increase after the depletion in stocks of their potential competitors. In addition, the life-history characteristics of Nile tilapia may have been advantageous because it grows faster than other tilapias and, although predominantly herbivorous, it can diversify its diet by ingesting invertebrates and fish, it is highly aggressive and outcompetes other species, and can tolerate low-oxygen conditions (Fryer and Iles 1972, Pauly et al. 1988, Martin et al. 2010, Attayde et al. 2011, Sanches et al. 2012). Some of these attributes have been reported in Nile tilapia introduced into Lake Victoria (Njiru et al. 2004, 2007, 2008). Nile tilapia, although predominantly a shallow-water species, can expand its ecological range. In the early 1970s it was restricted to waters less than 10 m deep in Lake Victoria (Kudhongania and Cordone 1974), but by 2006 it had extended to waters 20 m deep (Njiru et al. 2008). The parallel successes of Nile tilapia and Nile perch could have been because both species originate from the same habitats in the Nile system and West Africa, and over time have developed the capacity to coexist (Lowe-McConnell 1988).

The only native species that initially persisted in Lake Kyoga alongside Nile perch and Nile tilapia was *Rastrineobola argentea*, which increased in abundance after Nile perch had depleted the haplochromines. The situation in Kyoga was similar to that in Lake Victoria where initial depletion of haplochromines was followed by an increase in stocks of *R. argentea* (Wanink and Witte 2000). *Rastrineobola argentea* seems to have persisted amidst Nile perch predation and fishing pressure because of its life-history characteristics, which include year-round breeding and a high turnover (Wandera 1992, Wanink 1998, 1999), and while its body size decreased and its age at maturity fell, relative fecundity and overall reproductive

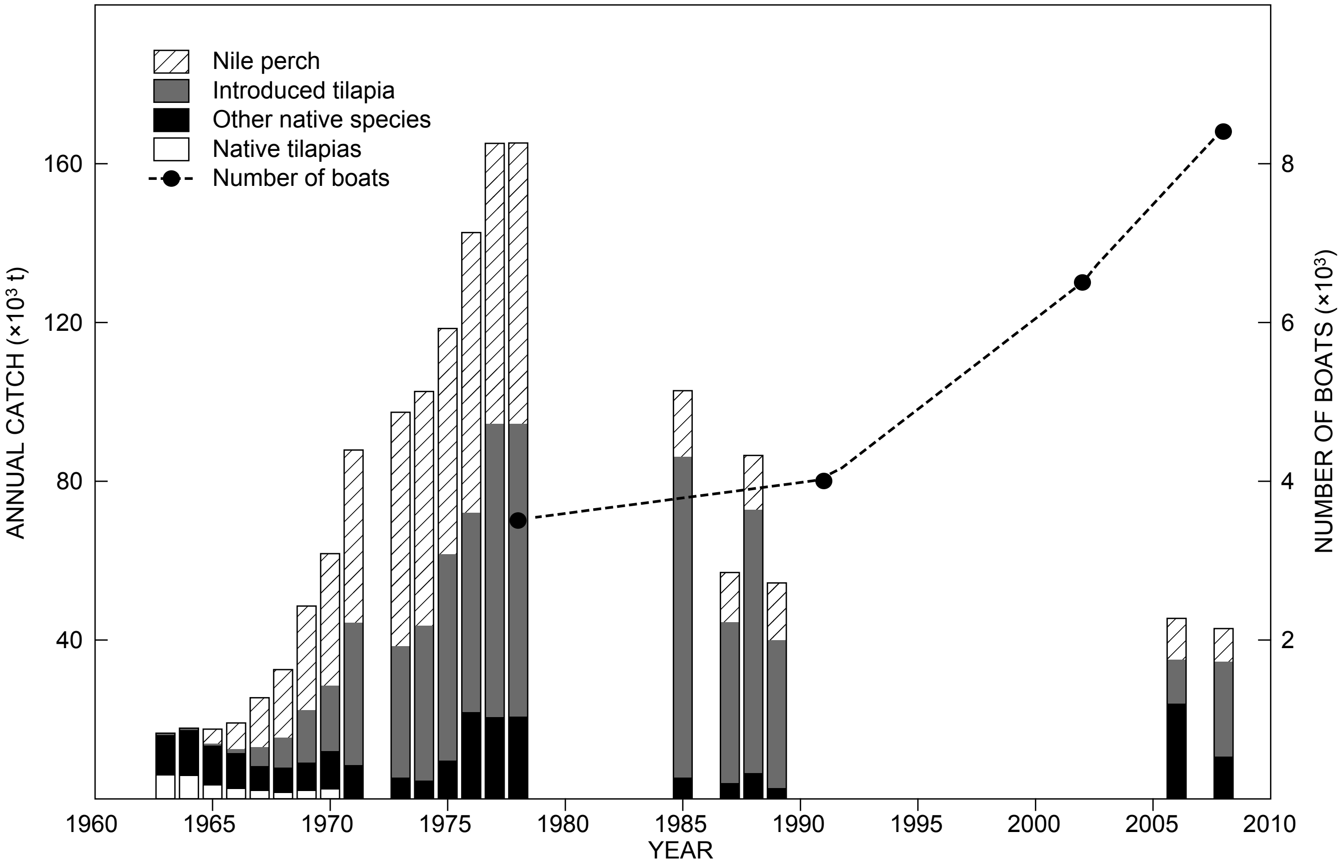

Figure 4: Total fish catches from the main Lake Kyoga system, 1963–2008. Points indicate numbers of boats on the lake, i.e. an approximate measure of fishing effort. Data were obtained from the Department of Fisheries Resources and NaFIRRI (unpublished)

effort was enhanced (Wanink 1998, Wanink and Witte 2000, Sharpe et al. 2012). It is also the only small-sized native species that was originally common in open waters in Lake Kyoga (Worthington 1929), suggesting that it has the capacity to evade predation.

From the beginning of the 1990s, stocks of some haplochromine taxa in Lake Kyoga began to increase following the decrease of Nile perch stocks through intensive fishing and the corresponding reduction in predation pressure. The catch rates of haplochromines in the 25.4 mm and 38.1 mm mesh-size gillnets increased from 2 to 22 and 40 fish net^{-1} night^{-1} in 1988, 1993 and 2010, respectively, with the dominant haplochromine taxa being insectivorous *Astatotilapia* species (Ogutu-Ohwayo 1995, NaFIRRI unpublished data). The resurgence of haplochromines in Lake Kyoga coincided with water hyacinth invasion. The mobile mats of this plant could have facilitated the redistribution and re-establishment of remnant populations of fish that have the capacity to survive under low-oxygen conditions and that had survived among marginal macrophytes. Similar haplochromine resurgences occurred in lakes Victoria and Nabugabo following depletion of Nile perch by intensive fishing, although there were differences in species composition (Witte at al. 2000, Chapman et al. 2003, Witte et al. 2007). In the deeper Lake Victoria, it comprised primarily zooplanktivorous and detritivorous species (Witte at al. 2000, 2007), whereas in the shallower lakes Nabugabo and Kyoga the resurgence of haplochromines originated from species that had survived among marginal macrophytes (Chapman et al. 2003). In Lake Victoria the resurging detritivores diversified their diet to include large proportions of invertebrates (Kishe-Machume et al. 2008). Before the

Table 5: Proportions (%) of the major commercial fish species in commercial catches from Lake Kyoga following the establishment of non-native species, compared to similar data from Lake Victoria. Lake Kyoga data were obtained from the Department of Fisheries Resources and NaFIRRI, and Lake Victoria data from statistics collected by fisheries departments in Kenya, Tanzania and Uganda. Successive dates represent (1) the start of the upsurge in numbers of introduced species, (2) peak numbers and (3) the most recent data available

Year	Proportional contribution to catch (%)				Total landing (t)
	Nile perch	Nile tilapia	Dagaa	Others	
		Lake Kyoga			
1963	0.4	0.3	0	99.3	17 000
1978	43	45	0	12	165 200
2008	15	61	17	7	38 000
		Lake Victoria			
1980	29	14	52	5	43 300
1990	56	12	32	–	724 100
2007	23	5	60	12	998 900

collapse of haplochrimine stocks in lakes Victoria, Kyoga and Nabugabo, Nile perch shifted to a fish diet at a smaller size of about 20 cm, but after their collapse the predator shifted to a fish diet at a larger size of 60 cm, and following the haplochromine resurgence Nile perch again shifted to a fish diet at a smaller size of about 20 cm (Ogutu-Ohwayo 1990b, 1995, Chapman et al. 2003, Kishe-Machumu et al. 2012), which supports the observation that haplochromines were the preferred prey of Nile perch. Although the recovery in haplochromines is expected to be followed by improvement in stocks of Nile perch, this is likely to be followed in future by oscillations in predator–prey cycles.

Although the introduced Nile perch and the tilapias increased the fishery yield in their new habitats, they affected native species. The Nile tilapia occupied habitats previously utilised by native tilapias, which could have contributed to the final displacement of native tilapias that had already been depleted by overexploitation (Ogutu-Ohwayo 1990a). In the Kyoga system, remnant populations of those fish species that virtually disappeared from the main lakes, such as haplochromines, *O. esculentus*, *P. aethiopicus* and *C. gariepinus*, still occur in the smaller lakes that were not stocked with Nile perch and to which they have not been able to gain access because they are unable to penetrate the swamps (Ogutu-Ohwayo 1995, Ogutu-Ohwayo et al. 1999, Mbabazi et al. 2004, 2010). There is pressure from some quarters to introduce non-native species into some of the lakes to increase fish productivity, but this should be avoided because they hold the last remaining populations of native fish species.

Historically, the fish fauna of the Kyoga lake system has been permanently separated from that of Lake Albert by Murchison Falls and, although it was previously loosely connected by Owen Falls to that of Lake Victoria with which it has a similar fish fauna, it has been permanently separated from that of Lake Victoria by three dams. The fish fauna of the Kyoga system, from below the dams to the Nile above Murchison Falls, can therefore be regarded as belonging to a closed system. Surveys of lakes Kyoga, Kwania, some of the satellite lakes and the Victoria Nile since 1998 suggest that the Kyoga lake system still has a rich fish fauna (Tables 6 and 7). Between 1998 and 2010, 17 out of the 27 non-cichlids, the two endemic tilapias and four of the 15 haplochromine cichlids recorded by Worthington were recorded in the main lake. The Kyoga lake system had over 50 haplochromine species, most of them surviving in the minor lakes and along the Nile system, and most of which have not yet been described. The Victoria Nile and the minor lakes had many haplochromine species that were not found in the main Lake Kyoga and Kwania. This emphasises the importance of minor lakes and the Nile in the conservation of fish species diversity in the region, as well as the need for a more comprehensive study of the fishes of the Kyoga lake system.

Management considerations

They key factors that affect the aquatic environment, productivity, fisheries and the livelihood of fishery-dependent communities are overexploitation, habitat alteration, invasive species, pollution and climate change (Loh 2008). The magnitude of these factors varies in time and space and some of them interact to affect aquatic organisms and resources. Management of the resources requires adequate understanding of the roles of these factors and the response of aquatic habitats and organisms to their impacts.

Overexploitation of the fish stocks through uncontrolled fishing and use of destructive fishing gears and methods contributed to the early decline of the native fishes of Lake Kyoga, especially the native tilapias, and to the decrease since the 1980s of the catches of introduced species. The legal minimum mesh size of gillnets is 127 mm and the use of beach seines is illegal, but these restrictions are not adhered to and gillnets as small as 51 mm mesh and beach seines of 25–51 mm mesh are widely used. Given that the lake is shallow, these nets sweep the entire water column capturing small species and the juveniles of large species. Although a legal limit of 10 mm has been imposed on seine nets used for catching *R. argentea* and fishing for the species is supposed to take place at least 2 km from the shore to minimise the capture of juveniles of large species, nets of 3–5 mm are widely operated in shallow inshore waters in tilapia breeding and nursery areas. A frame survey in 2008 revealed that 60% of the gillnets on the main lake were below the legal mesh size and that 12% of the boats were using illegal seines (NaFIRRI unpublished data).

Because the fisheries of Lake Kyoga have been unregulated, fishing effort has increased continuously, as shown by the number of boats, which more than doubled from 3 500 in 1978 to 8 400 by 2008 (Figure 4). By 1991 the fish catches were already declining, which suggests that the optimal number of boats should have been below 4 000, although boats alone do not accurately represent fishing effort because fishing takes place by both day and night and throughout the year, as compared to the time when the fishery was exploited by local communities who fished mainly during the dry season and reverted to growing crops during rainy seasons.

The rapid increase in fishing effort is partly a result of Uganda’s exceptionally high population, which grows at rate of 3.5% per annum, and the consequent increase in the demand for fish, which makes it difficult to regulate fishing effort. The fish stocks in the Kyoga lakes are already depleted and this trend is likely to continue as fishermen turn to more destructive methods in an attempt to sustain their livelihood, as has happened in some other African lakes such as Lake Malombe, Malawi, which is a similarly shallow lake in an impoverished region, where the stocks were destroyed by destructive fishing methods and the destruction of the habitat that had supported large macrophyte beds (Weyl et al. 2004). The situation in Kyoga will be aggravated by habitat changes such as variability in water levels, loss of wetlands and macrophytes, siltation and climatic factors. The population in the districts bordering the Kyoga lakes is amongst the poorest in Uganda (UBOS 2010), and a decrease in fisheries productivity will contribute to their further impoverishment.

Fisheries have been the main livelihood for fishing communities around Lake Kyoga and in 2008 contributed 67% of their incomes, but this contribution has been diminishing as the stocks decrease. Consequently, some fishermen supplement their livelihoods through subsistence

Table 6: Percentage numerical contribution of different fish species in the catches of 25 mm to 127 mm mesh-size gillnets in some lakes of the Kyoga system. All data collected between 1998 and 1999 (Ogutu-Ohwayo et al. 1999), except those for lakes Bisina (collected 2001–2010) and Kwania (collected 2006–2010). √ = Not caught in gillnets, but observed in most lakes

Species	Kyoga	Kwania	Nile River	Nakuwa	Nawampasa	Gigati	Kawi	Lemwa	Nyaguo	Agu	Bisina
Protopterus aethiopicus [a]	0.46	0.39	0.09	1.69	0.25				0.13		0.44
Mormyrus kannume [a]			17.52						0.13		
Mormyrus macrocephalus [a]		0.10	0.56						2.94	0.47	0.22
Petrocephalus catostoma	0.09	0.03							2.40	1.42	1.00
Pollimyrus nigricans [a]									0.53		
Hippopotamyrus grahami [a]		1.21	2.70						0.13	6.16	5.39
Gnathonemus longibarbis [a]	0.07	0.13	0.19						3.47	41.71	0.11
Marcusenius victoriae [a]	10.90	0.23	0.09	1.13	0.04				10.41	4.74	1.39
Brycinus jacksoni [a]											
Brycinus sadleri [a]	18.79	5.61	4.01		27.22	38.27			47.26	1.90	17.41
Labeo victorianus [a]	0.65	0.03	0.28								0.11
Barbus altianalis [a]	0.13	1.30	1.68	7.91							
Barbus paludinosus			0.09								
Barbus radiatus		0.81									
Barbus trispilopleura								0.15			
Barbus spp.					0.04			0.15	4.14	0.95	1.33
Bagrus docmak [a]		0.03	0.56								0.50
Schilbe intermedius [a]		1.27	0.84	11.86							0.72
Clarias gariepinus [a]	0.09	0.26	0.28	1.13	0.41	0.12	0.28	1.51	0.13		3.84
Clarias liocephalus [a]		0.03		2.82	0.12						
Synodontis afrofischeri	0.07	3.42	16.78	20.34	3.26		0.85	0.45	0.93	0.95	58.68
Synodontis victoriae [a]	1.33	0.16	2.33	10.73	1.28			0.30	4.14		2.45
Lates niloticus [b]	11.27	49.67	19.66	26.55							
Tilapia zillii [b]	1.22	0.46	0.84	0.56	0.62					0.47	3.11
Oreochromis esculentus [a]				0.56	1.03	0.03	0.57	0.90	0.80	0.95	0.11
Oreochromis leucostictus [b]	0.98		0.28	1.13		0.45	1.13	2.26	1.20		0.39
Oreochromis niloticus [b]	2.33	0.49	1.58	3.39	0.08	0.22		0.15	0.27		0.50
Oreochromis variabilis [a]			0.19		0.08						2.28
Haplochromines	51.63	34.26	29.36	10.17	65.57	60.91	97.03	93.67	20.83	40.28	
Ctenopoma muriei [a]	0.02						0.14	0.45			
Aethiomastacembelus frenatus [a]		0.10							0.13		
Rastrineobola argentea	√	√	√	√	√	√	√	√	√	√	√
Total number of fish taxa	18	12	12	12	10	6	7	11	10	12	12

[a] Species recorded by Worthington (1929)

[b] Introduced species

farming, with 88% of them growing crops on small agricultural plots, whereas 64% of them also keep livestock. Others are involved in trade, but very few have undergone training in fishing methods (23%), the adoption of new tools (16%) and alternative innovations (31%), with the fishing crew, many of whom do not own any land, being the least innovative and most vulnerable. If fishing pressure is to be reduced so that stocks can recover, these communities would need support in identifying and developing alternatives to fishing.

As regards African inland fisheries and aquatic ecosystems, an emerging challenge that has received little attention to date is the impact of climate variability and change. Natural variations in climate can affect fisheries productivity, as exemplified by the situation in lakes Kyoga and Victoria where the exceptional El Niño rains of 1961 caused water levels to rise and may have caused changes in fisheries (Welcomme 1970). Climate change became more intense during the last two decades of the twentieth century (IPCC 2007) and Africa became warmer by an average of 0.5 °C during that period (Hulme et al. 2001). The implications of a changing climate on inland fisheries are still unclear and have received little attention. Climate change is expected to modify energy balance, circulation dynamics and production processes, to increase stratification, and to reduce mixing and recycling of nutrients and oxygen (Lorke et al. 2004, Verburg and Hecky 2009, Vollmers et al. 2009, Sitoti et al. 2010, Tierney et al. 2010). At an organism level, climate change is expected to affect the physiology, composition abundance, population structure, distribution, phenology, regime shift and life history of fishes and other aquatic organisms (Barange and Perry 2009). Some efforts have been made to relate aquatic productivity processes and fisheries production to changes in climate parameters. In Lake Tanganyika a 20% decrease in algal productivity and 30% decline in fisheries yield have been attributed to climate warming (O'Reilly et al. 2003). Some correlation was established between fluctuations in water level and fishery yield in Lake Chilwa (Allison et al. 2007). In Lake Chad the number of fish species decreased from about 40 to 15 between 1971 and 1977 following a period of drought (Lévêque 1995).

Table 7: Percentage contributions of haplochromines in catches of 25–56 mm mesh-size gillnets in the Kyoga lake system. All data were collected between 1998 and 1999 (Ogutu-Ohwayo et al. 1999), except those for Lake Bisina, which were collected between 2001 and 2010. Undescribed species are designated by a 'cheironym'

Species	Kyoga	Kwania	Nile River	Nakuwa	Nawampasa	Gigati	Kawi	Lemwa	Nyaguo	Agu	Bisina
Astatoreochromis alluaudi	0.27		2.15		0.15	0.87	1.19	0.72	0.50	3.19	0.70
Astatotilapia brownae			3.49								
Astatotilapia 'Kyoga astato'	6.97	61.18	1.10	77.77	39.18	26.22	64.37	54.66	49.13	17.57	21.40
Astatotilapia latifasciata[a]					1.41	0.69				0.64	7.97
Astatotilapia 'macrops'					0.07	0.28	0.16		1.49		
Astatotilapia martini						0.04			0.74		0.28
Astatotilapia 'miniblack'	25.97	2.28	0.20	22.22	6.2	1.17	8.71	23.08	25.81	11.18	0.84
Astatotilapia 'orange anal'		0.10									
Astatotilapia 'pseudo martini'					0.22						
Astatotilapia 'red tail'		0.29			0.04						
Astatotilapia 'thick-lipped'		0.10			0.04	0.07					
Gaurochromis sp.	0.05				0.15						0.14
Haplochromis lividus	0.14	3.33	0.10		32.27	43.74	0.63	13.04	0.50	43.13	24.76
Haplochromis 'unicuspid'					0.07						
Harpagochromis argenteus[a]		1.52			4.79	0.60	2.38	0.62		5.11	5.31
Harpagochromis guiarti[a]	0.68		0.30								
Harpagochromis 'mental'		0.10									
Harpagochromis michaeli											1.96
Harpagochromis 'pedicel'		0.48									2.24
Harpagochromis 'red tail'		0.38									0.28
Harpagochromis 'shovel mouth'	19.27	1.52			2.90	1.60	8.31		13.90	2.24	10.63
Harpagochromis squamulatus									1.99		0.56
Lipochromis 'black cryptodon'	0.14	0.48			0.82	0.39	3.48	0.21	0.74	0.64	
Lipochromis cryptodon						0.05	0.40		0.50		0.98
Lipochromis maxillaris					0.52	0.05	0.32			0.64	2.52
Lipochromis microdon					0.41	0.44	0.24			0.64	0.28
Lipochromis obesus					0.67	0.97	2.69		0.50	4.79	1.12
Lipochromis parvidens	0.14	0.10			0.97	1.22	0.16			1.92	1.96
Lipochromis 'white'							0.16				
Lithochromis rubripinnis			8.08								
Lithochromis xanthopteryx			0.10								
Mbipia mbipi		0.57	22.26								
Mbipia 'red pelvics'			0.20								
Mbipia 'yellowfin'			0.20								
Neochromis gigas			3.14								
Neochromis greenwoodi			3.59								
Neochromis 'lemon britti'			0.20								
Neochromis omnicaeruleus			0.50								
Neochromis 'red simotes'			1.35								
Neochromis rufocaudalis			11.13								
Neochromis simotes			0.75								
Neochromis 'yellow rufocaudalis'			1.95								
Paralabidochromis 'black para'	40.73	11.80				0.02	1.43	6.83			
Paralabidochromis chromogynos		1.05									
Paralabidochromis cyaneus			0.05								
Paralabidochromis 'deep body'						0.04					
Paralabidochromis flavus			0.25								
Paralabidochromis 'redfin'					0.59	0.25	0.63	0.10			
Paralabidochromis 'rock kribensis'			0.55								
Paralabidochromis 'silver para'		0.57				0.07					
Paralabidochromis 'victoriae'							0.00		0.74	0.32	
Prognathochromis acutirostris		8.85			1.89		0.08			0.32	0.56
Prognathochromis 'black red tail piscivore'					0.07				0.74		1.96
Prognathochromis 'long lower jaw piscivore'						0.04			0.50		
Prognathochromis 'pedicel'											0.56
Prognathochromis pellegrini[a]		0.57			3.79					2.56	2.24
Prognathochromis 'silver arrow'			0.05								
Psammochromis 'blue'											0.14
Psammochromis 'riponianus'		0.10	4.49								0.14

Table 7: (cont.)

Species	Kyoga	Kwania	Nile River	Nakuwa	Nawampasa	Gigati	Kawi	Lemwa	Nyaguo	Agu	Bisina
Ptyochromis 'Gigati sheller'					0.04	0.04			0.25		
Ptyochromis sauvagei		0.29	0.20								
Ptyochromis xenognathus			0.05								
Pundamilia azurea			0.20								
Pundamilia igneopinnis			0.15								
Pundamilia macrocephala			0.35								
Pundamilia pundamilia			0.50								
Pundamilia 'yellow multispot'			0.05								
Pyxichromis orthostoma	0.27	0.95	0.05		0.41	0.34	4.35	0.41	1.99		5.17
Xystichromis bayoni			11.08								
Xystichromis 'earthquake'	2.32										0.14
Xystichromis 'flame back'	2.41										
Xystichromis nuchisquamulatus			20.61								
Xystichromis phytophagus	0.27		0.60		2.34	20.81	0.16			5.11	4.62
Yssichromis 'Lemwa zooplanktivore'	0.36						0.16	0.21			
Total number of fish taxa	15	23	36	2	25	24	21	11	16	16	27

[a] Species recorded by Worthington (1929)

FAO (2010) has predicted that climate change will shift fisheries to smaller, faster-growing, opportunistic species that can adapt rapidly to a changing environment and this appears to be happening in some fisheries. In West Africa the pelagic fisheries for *Sardinella aurita* Valenciennes 1847 increased following pronounced warming (Binet et al. 2001). In Lake Kariba it has been noted that the changing climate has had implications for the kapenta stocks (Ndebele-Murisa et al. 2011), although the magnitude of the role of climate compared to other stressors, especially exploitation, has been questioned (Marshall 2012). In Uganda, stocks of the pelagic *R. argentea* have increased in lakes Kyoga and Victoria and a related species, *Neobola bredoi* Poll, has increased to contribute 80% to fishery yield in Lake Albert (NaFIRRI unpublished data). Although the changes in *R. argentea* have been attributed to fishing and predation (Sharpe et al. 2012), the role of environmental factors, especially climatic factors, need closer scrutiny as the species has spread to waters where it was previously not recorded among the Victoria and Kyoga minor lakes, where predation and fishing are either minimal or do not exist. Other stressors, especially exploitation, are likely to remain key players in stock depletions, but it is important to start examining the contribution of climate change, especially as this has started and is expected to become more intense in future. Examination of a 50-year trend in Uganda has revealed an increase in temperature that has been linked to spatial changes in land cover in the Lake Kyoga region, with receding of water areas of up to 4.2% attributed to climatic factors (Mubiru et al. 2009). Such changes will affect this tilapia-dominated lake as shallower inshore breeding and nursery areas are reduced. Although Lake Kyoga receives most of its water from Lake Victoria, its location towards the more arid north and its very short water-residence time will require examination of the relationship between aquatic and fisheries productivity processes, because these vary across the lake and are influenced by environmental factors in the catchment.

Fisheries management institutions around the lakes also need to be reformed if the fisheries are to be saved. During the twentieth century, fisheries in Uganda were managed by government agencies through a centralised system, with very limited involvement of communities in decision-making. The management of fisheries has been decentralised to the districts and 192 community-based Beach Management Units (BMUs) were established on Lake Kyoga in 2002 to co-manage the fisheries alongside government agencies. A Lake Kyoga Integrated Management Organization (LAKIMO) was formed in 2004 to bring together the BMUs and representatives of central and local governments. It was expected that a Lake Kyoga management plan would be prepared and implemented, but this has not been accomplished as the organisation lacks the resources to do this. A sustainable system for funding co-management is urgently needed if the BMUs are to make a significant contribution to fisheries management. Finally, it should be noted that water, wetlands and fish, which are closely interlinked, are currently managed by different institutions, and that close cooperation between them must be developed and strengthened if these resources are to be managed successfully.

As in other lakes, such as Lake Victoria, the productivity and composition of the biotic communities of the Kyoga lakes have become increasingly affected by multiple stressors, some of which are little understood, appreciated or incorporated in management plans. There is a need to understand adequately the main drivers of the lake ecosystem to guide the management of its resources. Specific emphasis is required to understand and address the impacts of habitat loss, water-level fluctuations, loss of wetlands and macrophytes, overexploitation of the fishes and the emerging challenge of climate change.

Acknowledgements — This paper is part of a study of ecosystems in the African Great Lakes region, the emerging challenge of climate change and its interaction with other stressors, the demands of the increasing human population and the management needed to sustain ecosystem health. The project is supported by The Rockefeller Foundation. We are grateful to Professor Brian Marshall, New Zealand, and two anonymous referees for reviewing the manuscript, and to Mr Timothy Galandi, NaFIRRI, for preparing some of the figures.

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Received 18 April 2012, revised 21 March 2013, accepted 10 April 2013
Edited by OLF Weyl