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The responses of Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) in Lake Wamala (Uganda) to changing climatic conditions

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Abstract

Changes in the catches of Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), in Lake Wamala (Uganda) have been observed since its introduction. The factors contributing to these changes, however, are not well understood. This study examined changes in species composition, size structure, size at first maturity, length–weight relationship and condition factor of Nile tilapia in Lake Wamala, in relation to changes in temperature, rainfall and lake depth, to provide a better understanding of the possible role of changing climatic conditions. There was an increase in the minimum, maximum and average temperatures since 1980, but only the minimum (0.021 °C year^{-1}) and average temperatures (0.018 °C year^{-1}) exhibited a significant trend ($P < 0.05$). Rainfall increased by 8.25 mm year^{-1} since 1950 and accounted for 79.5% of the water input into the lake during the period 2011–2013, while evaporation accounted for 86.2% of the water loss from the lake. The lake depth was above 4 m during the years when the rainfall exceeded the average of 1180 mm, except after 2000. The contribution of Nile tilapia to total fish catch and catch per unit effort (CPUE) increased with rainfall and lake depth up to the year 2000, after which they decreased, despite an increased rainfall level. The lake depth was positively correlated with the average total length and length at 50% maturity ($r = 0.991$ and 0.726, respectively), while the slopes of the length–weight relationships differed significantly between high and low lake depths [$t_{(6)} = 3.225$, $P < 0.05$]. Nile tilapia shifted from an algal-dominated diet during the wet season to include more insects during the dry season. The results of this study indicate Nile tilapia in Lake Wamala displays a typical r-selected reproductive strategy, by growing to a small size, maturing faster and feeding on different food types, in order to survive high mortality rates under unfavourable conditions attributable to higher temperatures, low rainfall and low lake water levels.

Key words

catches, lake depth, Nile tilapia, rainfall, r-selection.

INTRODUCTION

Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is the third most important commercial fish species in capture fisheries in Uganda after the Nile perch, *Lates niloticus* (Linnaeus, 1758) and the cyprinid, *Rastrineobola argentae* (Pellegrin, 1904) (MAAIF 2012). Nile tilapia is also the second most important species in regard to aquaculture after the African catfish, *Clarias gariepinus* (Burchell, 1822), and is most preferred among the commercially important species for consumption by the lakeside communities (DFR 2011).

Nile tilapia was introduced into most aquatic systems in Uganda in the 1950s to boost the native tilapia fishery, which had declined due to overfishing (Welcomme 1970; Ogutu-Ohwayo 1990). Nile tilapia was introduced along with three other species, including *Tilapia zillii* (Gervais, 1848), *Oreochromis leucostictus* (Trewavas, 1933) and *Tilapia rendalli* (Boulenger, 1897) (Welcomme 1970). Of the four introduced tilapias, only Nile tilapia flourished and became abundant (Ogutu-Ohwayo 1990), with the establishment of Nile tilapia in different lakes being attributed to several factors. In Lake Victoria, for example, the suc-

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cess of Nile tilapia was attributed to increased lake levels in the early 1960s which expanded breeding and nursery areas (Welcomme 1970), as well as the overfishing of native tilapias which, in turn, reduced competition (Balirwa 1998). The establishment and dominance of Nile tilapia in Lake Kyoga, however, was attributed to the clearance of swamps and submersion of macrophytes following El Niño rains that raised lake water levels by 2.5 m (Ogutu-Ohwayo *et al.* 2013). Clearing the swamps and submersion of the macrophytes improved the nutrient input and food production, as well as opening up more areas for fish spawning (Ogutu-Ohwayo *et al.* 2013).

Nile tilapia is known to survive under a wide range of environmental conditions and feeds on a variety of food items (Njiru *et al.* 2002, 2004). Nile tilapia can grow to different sizes, mature at different rates and alter their fecundity and size of oocytes in response to factors such as overexploitation, habitat changes and predation (Bwanika *et al.* 2004; Njiru *et al.* 2008; Martin *et al.* 2010; Attayde *et al.* 2011). These characteristics suggest Nile tilapia is a hardy species and can readily sustain its stock if properly managed.

Lake Wamala and establishment of introduced Nile tilapia

Lake Wamala (Fig. 1) is one of the lakes into which Nile tilapia was introduced. Prior to the introductions, the lake harboured a fishery consisting of the African catfish, Lungfish *Protopterus aethiopicus* Heckel, 1851 and Haplochromines (Okaronon 1987). Tilapia species introduced into the other lakes also were introduced into Lake Wamala in 1956, except for *T. rendalli*, leading to the establishment of commercial fishing in 1960 (Okaronon 1987). Establishment of the tilapias resulted in increased fish catches from 1000 tons in 1960 to a peak of 7100 tons in 1967, although the catch later decreased to 6,300 tons in 1975 (Okaronon 1987). Between the years 1981 and 1988, the lake recorded the lowest catches, ranging between 300 and 500 tons (Okaronon 1995). These catches later increased to 4500–5000 tons between 1999 and 2000 (National Fisheries Resources Research Institute, NaFIRRI, unpublished data). The reasons for these changes in fish catches have not yet been readily explained.

During the years when the fish catches were high, Nile tilapia contributed >70% by weight to the total catches. The contribution of Nile tilapia increased from 10% in 1960, for example, to 78% by 1975 (Okaronon 1995) and to 90% by 1999 (NaFIRRI, unpublished catch statistics). Thus, Nile tilapia became established and was more dominant in the fishery, compared to other tilapia species in the lake. The increased lake levels, expanded lake area, nutrient influx from the catchment area and/or decaying submerged aquatic macrophytes following El Niño rains in 1961–1964 and 1997 (Uganda National Meteorological Authority, UNMA, unpublished rainfall data) could have opened more breeding and nursery grounds and enhanced food production for Nile tilapia in Lake Wamala, as had occurred in Lake Victoria and Kyoga Lake (Welcomme 1970; Ogutu-Ohwayo *et al.* 2013). Enhanced nutrient conditions are predominantly dependent on inflowing allochthonous materials, and consequently, phytoplankton biomass is closely connected with the annual floods (Kolding 1993; Ogutu-Ohwayo *et al.*

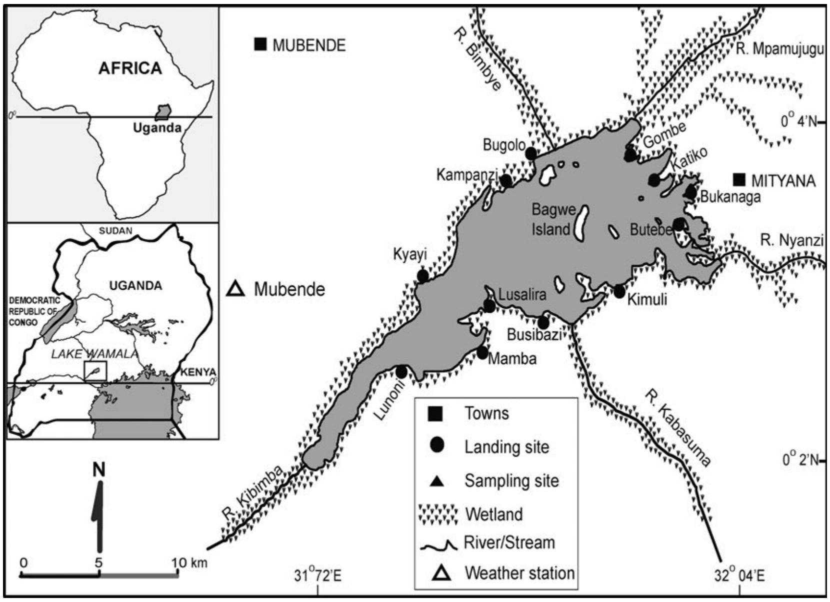

Fig. 1. Location of Lake Wamala and weather station for climate data (inset is location of Uganda within Africa).

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2013). Under such conditions, the biology of the fish communities is geared to the flood cycle, suggesting the nutrient supplies from the catchment are very important in stimulating fish production in lakes and reservoirs.

The low fish catches and low contribution of Nile tilapia to the fish catches during the period 1981–1988 were attributed to overexploitation (Okaronon 1995). This may not entirely explain the diminished contribution of Nile tilapia to fish catches; however, since the period 1981–1988 had the lowest fishing effort (150–200 boats) ever recorded for the lake (Goulden 2006). Furthermore, the cause of the recovery of Nile tilapia in fish catches during the period 1999–2000, even when the number of fishers had increased threefold (NaFIRRI, unpublished survey data), remains unclear. These changes might possibly be attributable to changes in the habitat resulting from fluctuating lake water levels as was reported for lakes Turkana (Kolding 1993; Karange & Harding 1995), Nasser (Agyapi 2000), Chilwa (Furse *et al.* 1979; Njaya *et al.* 2011) and Malawi (Tweddle & Magasa 1989). In contrast to the above-noted lakes, there were no water abstractions from Lake Wamala for such large-scale purposes as irrigation and hydropower generation. This suggests the changes in lake water levels are mainly due to fluctuations in climatic factors, especially rainfall.

Lake Wamala as a climate change hotspot

The changes in the Lake Wamala ecosystem have resulted in it being classified as one of the climate change hot spots in Africa by the United Nations Environment Programme (UNEP 2009). The highest recorded surface area of Lake Wamala is 250 km^2, with a mean depth of 4.5 m (Goulden 2006). The lake surface area was reduced by about half, and its depth by three-quarters, during the period 1984–1995 because of persistent drought (UNEP 2009). The lake regained its surface area and depth in 1999, following El Niño rains in 1997 (UNEP 2009). By 2011, however, three formerly submerged water gauges were seen on dryland (Natugonza 2015), suggesting the area and depth of the lake were reduced during the precedent decade. This is not an expected pattern, since rainfall, the major water input to the lakes of the East African rift valley region (Bootsma & Hecky 2003) was above average for most of the years around Lake Wamala since 2000 (Natugonza 2015). This suggests the persistent increase in temperature in the region (Caffrey *et al.* 2013) had driven evaporation to levels that could not be compensated for by water gains from direct rainfall, resulting in low water levels. With such a change in the lake's hydrological pattern, it is anticipated that periods of low rainfall will be accompanied by further decreases in lake depth and lake surface area. These changes have obvious implications for fish catches and the biology of fish and pose a challenge to fisheries management and the livelihoods of the communities dependent on the fisheries, as was previously observed for lakes Naivasha, Chad and Chilwa (Levèque 1995; Hickley *et al.* 2004; Allison *et al.* 2007; Njaya *et al.* 2011).

Climate variability and change, and influence on Nile tilapia fishery

Climate variability and change affects the aquatic environment by altering water inflow and outflow pattern, stratification and circulation dynamics (including nutrient loading and recycling, and dissolved oxygen concentrations) (e.g. Verburg *et al.* 2003; Vollmer *et al.* 2005; Marshall *et al.* 2013; Sitoki *et al.* 2010). Thus, climate variability and change, via its influence on water availability, limnology and habitat change, can affect fish and fisheries, including Nile tilapia (Daw *et al.* 2009). Limited work has been performed in tropical regions to demonstrate this phenomenon, compared to the extensive research conducted in temperate regions and oceans (Comte *et al.* 2013). Focusing specifically on Nile tilapia, most studies have attributed changes in the species composition, catch per unit effort (CPUE), size structure, length at 50% maturity, length–weight relationships and condition factor to such factors as overexploitation, predation and habitat degradation (e.g. Gwahaba 1973; Balirwa 1998; Bwanika *et al.* 2004; Njiru *et al.* 2006, 2008). The result is a knowledge gap on how Nile tilapia, a commercially important species in both capture fisheries and aquaculture, responds to the conditions created by climate variability and change.

In view of the observed and anticipated increased temperatures in Uganda (Caffrey *et al.* 2013) and changes in the hydrologic cycle of Lake Wamala (Natugonza 2015), it is important to better understand how Nile tilapia responds to these changes in order to make informed management decision. To this end, this study focuses on investigating the changes in species composition, CPUE, size structure, length at 50% maturity, length–weight relationships, condition factor, fecundity and diet of Nile tilapia, in relation to changes in temperature, rainfall and lake depth. This information can be used also as a basis for monitoring the impacts of climate change on fish stocks.

METHODS

Study area

This study was carried out on Lake Wamala in the Lake Victoria basin (Fig. 1). Lake Wamala lies between longitude 0° 15′ to 0° 25′ N and latitude 31° 45′ to 32° 00′ E, at

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an altitude of 1000 m above sea level. Lake Wamala is surrounded by extensive vegetation dominated by papyrus (*Cyperus papyrus* L.), ambatch (*Aeschynomene elaphroxylon*) and hippo grass (*Vossia cuspidata* Roxb), with the rest of the catchment mainly comprised of agricultural land. The lake is fed by several small rivers, including Nyanzi, Kabasuma, Mpamujugu and Bimbya. Lake Wamala is drained by River Kibimba into Lake Victoria via the Katonga wetland. The lake surface area has historically fluctuated between 100 and 250 km² and its mean depth between 1.5 and 4.5 m (UNEP 2009). This fluctuation is not attributed to water abstractions for such large-scale uses as hydroelectric power generation or irrigation, but rather to fluctuations in climate factors, especially rainfall (Goulden 2006).

Study design

Air temperature and rainfall data from the Mubende weather station (Fig. 1), the station located nearest to Lake Wamala, were used to determine changes in climate variables around the lake. As a result of gaps in fisheries data, data collected during 1976–1978, 1988–1996, 1998–2000 and 2011–2014 were used in this study. These periods were grouped into strata based on rainfall abundance (>average of 1980–2010; Ted 2011), rainfall deficit (<average of 1980–2010) and mean lake depth. The periods 1976–1978 and 1998–2000 were high rainfall (mean >1187 mm) and high lake depths (mean >4 m) periods. The period 1988–1996 was low rainfall (mean <1187 mm) and low lake depth (mean <4 m) period. The period 2011–2014 was high rainfall (mean >1187 mm), but low lake depth (mean <4 m) period. As a result of a lack of historical data, diet was only examined for different seasons during 2011–2014 to determine whether or not seasonal changes influence the abundance of prey items available for the fish. The seasons were defined as short dry (December–February), long wet (March–May), long dry (June–August) and short wet (September–November), based on the classification of Komutunga and Musiitwa (2001) for Uganda. As there were no historical data on fecundity, the number and diameter of eggs of Nile tilapia were only examined for the period 2011–2014, and compared with those from the literature (Lowe McConell 1955, Lowe-McConnell 1958; Trewavas 1983) to determine whether the number of eggs was higher, and the size smaller, as expected under conditions of increased temperature (Portner *et al.* 2001; Donelson *et al.* 2010.

Data acquisition

Monthly minimum and maximum air temperatures (1980–2013) and monthly rainfall totals (1950–2012) were acquired from UNMA, Ministry of Water and Environment (MWE). Data on monthly water inflows and outflows (2011–2013) were acquired from the Directorate of Water Resources Management (DWRM), MWE, while data on lake depth (1970–2014) were obtained from the NaFIRRI archives.

Historical data on fish catches (1960–2000) were obtained from NaFIRRI archives (NaFIRRI, unpublished data). One frame survey and two Catch Assessment Surveys were carried out between March and July 2012. Experimental fish sampling was carried out every three months, from December 2011 to April 2014, covering all four conventional seasons (defined above). Experimental fishing was carried out using three fleets of multimesh gill nets (90 m long and 26 meshes deep) of mesh sizes ranging from 25.4 to 152.4 mm, in increments of 12.7 mm. The first fleet of gill nets was set along the shoreline, the second 50 m from the shoreline and the third in open waters (200 m from the shoreline), to assure adequate and representative sampling sites in the lake. The fleets of gill nets were set in the evening between 1700 and 1800 h and retrieved at dawn between 0600 and 0700 h. After retrieval, the fish were sorted to the lowest taxon to obtain information on fish species composition. As a result of the difficulty in identifying Haplochromines to the species level, all the fish in the genus Haplochromis were merged and labelled ‘Haplochromines’. Additional specimens of Nile tilapia were obtained from commercial fishermen to improve the sample size, although these specimens were not used to determine the size structure because of the size selectivity of fishers.

The total length (TL) of each specimen of Nile tilapia was measured to the nearest 1 mm, from the most anterior part of the head (with closed mouth) to the furthest tip of the caudal fin, using a measuring board. Each specimen was weighed to the nearest 0.1 g with a digital scale (model CS-10KWP-IP65). These data were recorded in a customized biometrics data sheet (LVFO 2007), to be used in determining length frequency distribution, and for calculating length–weight relationships and condition factors. After measuring and weighing, the fish were dissected, sexed and assigned maturity stages, ranging from I to VI for males and VII for females, using a key described by Witte and Van Densen (1995). Standard operating procedures for collecting biological information on fishes of Lake Victoria (LVFO 2007) were used to define mature and immature fish. Fish in stages I–III were considered immature, while those in stages IV–VI for males and IV–VII for females were considered mature. These maturity stages were recorded on a matu-

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rity sheet (LVFO 2007 appendix 2) to be used in determining fish length at 50% maturity.

A total of 60 ripe ovaries and 314 stomachs were fixed in buffered 4% formalin for 24 h and later preserved in 70% ethanol for laboratory examination, to obtain information on fecundity and food of Nile tilapia, respectively. As a result of the variability of sizes of oocytes during gonad development, only mature ovaries in stages V and VI were used for fecundity estimates.

Laboratory analysis of fish samples for fecundity, oocyte size and diet

All the preserved ovaries were soaked in water for about one hour to wash away ethanol, and the moisture blotted off to separate the oocytes and ease the counting. All oocytes were counted with a tally counter, and the total number (absolute fecundity) recorded for each fish. The diameter of 1200 oocytes was measured to the nearest 0.1 nm, using a calibrated stage microscope (Wild Heerbrugg M3B stereomicroscope Type S) to get information on the average size of oocytes.

The preserved stomachs of Nile tilapia were split open, and the contents transferred into a Petri dish and diluted with distilled water to examine their contents under a compound microscope (model XSZ-H, ×400 magnification). The three major groups of algae (blue green algae, green algae and diatoms) were identified with the key described by Walter (2002) to determine the algal composition in the Nile tilapia diet. Insects were not classified because of inadequate detail of their body parts after digestion, with all insect remains crudely labelled as ‘insects’. Volumetric analysis (Hynes 1950) was used to quantify the different food items, and the data were recorded as the percentage contribution of each food by volume, visually assessed relative to all food items in the stomach. These data were later used to calculate the relative importance of food items ingested by the Nile tilapia.

Data analysis

Temperature

Descriptive statistics were used to determine the long-term mean of the minimum, maximum and average temperatures. A time series regression analysis was performed to determine the trend in minimum, maximum and average temperatures. The average temperature values were stratified into decades and displayed as box plots to show interdecadal temperature changes. Box plots were used because they display a full range of variation (from minimum to maximum) and a typical value (the median) which is not affected by outliers.

Rainfall

Monthly rainfall totals were summed for each year to obtain annual rainfall totals, and later used in calculating standardized precipitation index (SPI). The SPI for each year was calculated as standardized differences between annual rainfall totals and the long-term average (Tumbo 2007). SPI gives a corrected measure of rainfall abundance and deficit therefore being used to characterize wet and dry years. In calculating the SPI, the long-term average was calculated on the basis of data for the period 1981–2010, corresponding to the last three decades used in comparing climate anomalies (Ted 2011).

Water balance

The water balance was calculated as the sum of the inflows (rainfall and river inflow) minus the sum of the outflows (evaporation and river discharge). In a lake from which there are no large-scale water abstractions, the water levels are expected to remain high, as long as rainfall fluctuates within the normal pattern (Sewagudde 2009). Thus, the water balance was calculated to test whether or not there was any indication of a change in the hydrological cycle attributable to high temperatures. Lake Wamala is located in the Lake Victoria basin and, therefore, the interaction between groundwater and surface water, and its influence on other water fluxes, was assumed insignificant (Krishnamurthy & Ibrahim 1973).

Species composition and CPUE

The Nile tilapia species composition was assessed by determining the percentage contribution of each fish species to the catch during each survey period. The percentage contribution was calculated by weight, to avoid underestimating the large commercial species, which are not caught in large numbers by gill nets. This was done by year to account for temporal differences in species assemblages. The values were then related to mean lake depth to get an impression of the role of changing lake water levels attributable to fluctuating temperature and rainfall. A preliminary analysis of fish catches and fishing effort indicated the catches were strongly correlated with the number of fishers ($r = 0.927$; $n = 9$; $P < 0.001$). The CPUE was calculated and related to lake depth to account for any confounding effects of fishing effort on the correlation between catches and lake water levels. CPUE was expressed as total landed fish catch per boat per year because historical data did not encompass detailed fishing methods.

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Size structure

Fish were grouped into length classes of 30 mm (LVFO 2007), and the percentage frequency of fish in the different length classes calculated. Time-phased length frequency distributions were generated to compare the population structure of Nile tilapia over time under varying rainfall and lake depth. This approach helped visually depict differences in population characteristics, such as modal length. It also was used to assess whether the mostly exploited sizes of fish were mature or immature. The mean TL also was calculated to facilitate correlation of size structure with mean lake depth. The correlation was analysed using Pearson product–moment correlation coefficient.

Size at first maturity

The fish size at first maturity was calculated as the length at which 50% of the individual male and female fish were mature. This was performed to obtain information on the minimum size at which Nile tilapia first mature. The length at which 100% of the individuals were mature also was determined to get an indication of the length at which all the fish enter a fishery. Both the lengths at 50% and 100% maturity were determined by fitting 10-mm-length frequency classes of mature individuals, for different sexes to a logistic regression curve, using the least squares method (Sparre & Venema 1998). The correlation between length at 50% maturity and lake depth was analysed using Pearson product–moment correlation coefficient.

Length–weight relationship and condition factor

The length–weight relationship was estimated using the following equation (Wooton 1990):

$$\log W = \log a + b \log L \tag{1}$$

where, W = body weight (g), L = TL (mm), a = constant and b = slope of regression line. An independent sample *t*-test was used to investigate the difference in the length–weight coefficients between high and low lake water depth.

To facilitate the comparison of the results of this study with those of other lakes and to develop predictive models of fish condition during subsequent investigations, the relative condition factor (Kn) was calculated as a ratio of observed individual fish weight to expected weight of an individual of a given length. This was calculated with the following formula (Le Cren 1951):

$$\mathrm{Kn} = \frac{W}{aL^b} \tag{2}$$

where, W = individual body weight (g), L = individual TL (mm) and a and b = species specific constants obtained from a length–weight relationship ($W = aL^b$). The analyses used the fish weight devoid of the gonads to minimize errors from seasonal fluctuation in body weight due to spawning.

Fecundity (Absolute and Relative)

Absolute fecundity was estimated from the total counts of oocytes in the ovaries of fish in the most advanced stages of gonad development (stages V and VI). The relative fecundity (fecundity in relation to total length) was estimated with the following formula:

$$F = aL^b \tag{3}$$

where, F = fecundity, L = TL (mm), a = constant and b = slope of regression line.

Diet

The points method (LVFO 2007) was used to determine the relative importance of each food item. This method gives an indication of what is eaten, as well as the proportion of different food items. The identified food items were ranked with points, ranging from 0 to 16, depending on size and abundance. The number 0 represented empty stomach; 2 was for one quarter full stomachs; 4 for half-full stomachs; 8 for three-quarters full stomachs; and 16 for full stomachs. These points give an estimate of the index of fullness of each stomach, thereby facilitating an indication of the intensity of feeding at any time of sampling. The relative importance of each food category was determined by multiplying its percentage contribution by the points allocated to the index of fullness. The relative importance of different food categories was then compared between the four seasons (i.e. short dry, long dry, short wet and long wet).

RESULTS

Temperature

The air temperature around Lake Wamala ranged between 14.9 and 30.9 °C. The mean minimum and mean maximum temperatures around the lake were 16.0 ± 0.55 and 28.3 ± 0.46 °C, respectively, and the average temperature was 22.1 ± 0.32 °C. Time series analysis indicated a linear increase in the minimum ($R^2 = 0.145$), maximum ($R^2 = 0.094$) and average

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($R^2 = 0.199$) temperatures since 1980, although only the minimum temperature (0.02 °C year^{-1}) and average temperature (0.018 °C year^{-1}) exhibited significant trends ($P < 0.05$, Fig. 2). On the annual scale, the temperatures were higher than average during the years 1982–1984, 1993–1994 and 2005–2012. Decadal analysis indicated the increase in the temperature was much faster after 2000 (Fig. 2), with the average temperature increasing by 0.6 °C between 2000 and 2013, which translates into an annual warming rate of 0.041 °C year^{-1} (Fig. 3).

Rainfall

The long-term average annual rainfall around Lake Wamala was 1180 ± 203 mm. The rainfall increased by 525 mm year^{-1}, with maxima in 1963, 1977 and 1998. The mean annual rainfall was 1300 mm during 1976–1978, 1160 mm during 1988–1996, 1370 mm during 1998–2000 and 1350 mm during 2011–2013. The period 1988–1996 was preceded by a nine year consecutive dry spell, with rainfall averaging 970 mm. With the exception of the years 2004, 2005 and 2008, all years after 1995 were wet years, with positive SPI values (Fig. 4). Periods of low rainfall with negative SPI values were clustered between the years 1950 and 1960, 1970 and 1975, 1979 and 1987 and 1991 and 1993 (Fig. 4).

Lake depth

Except for the period 2011–2013, the mean lake depth was above 4 m during years when the rainfall was above the average of 1180 mm. The period 1979-1996 exhibited the lowest lake depth of 1.5–1.7 m, corresponding to the 11 dry years with negative SPI (Figs 4 and 5). After the El Niño event of 1997, the lake regained its normal depth of 4.5 m. During the period 2011–2013, however, the average depth was only 3.4 m, despite average rainfalls exceeding 1300 mm (Fig. 5).

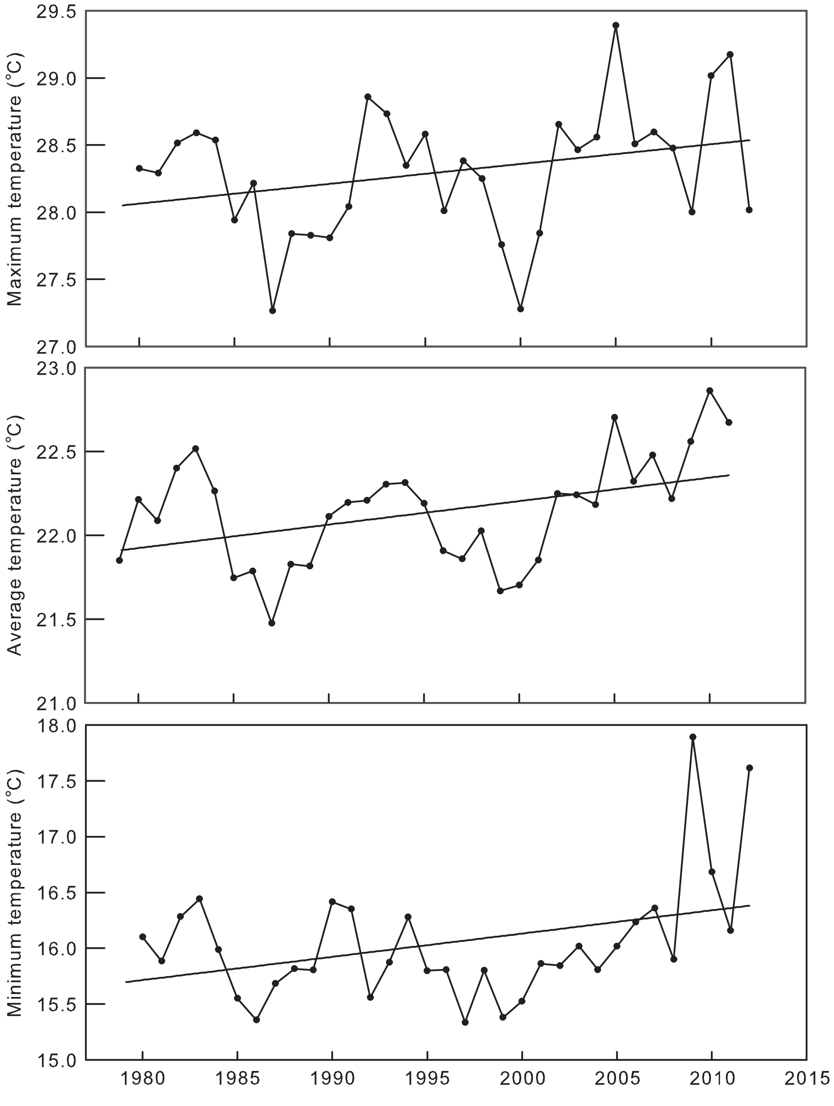

Fig. 2. Trends in minimum, maximum and average air temperatures around Lake Wamala, 1980–2013 (data from Uganda National Meteorological Authority, Ministry of Water and Environment).

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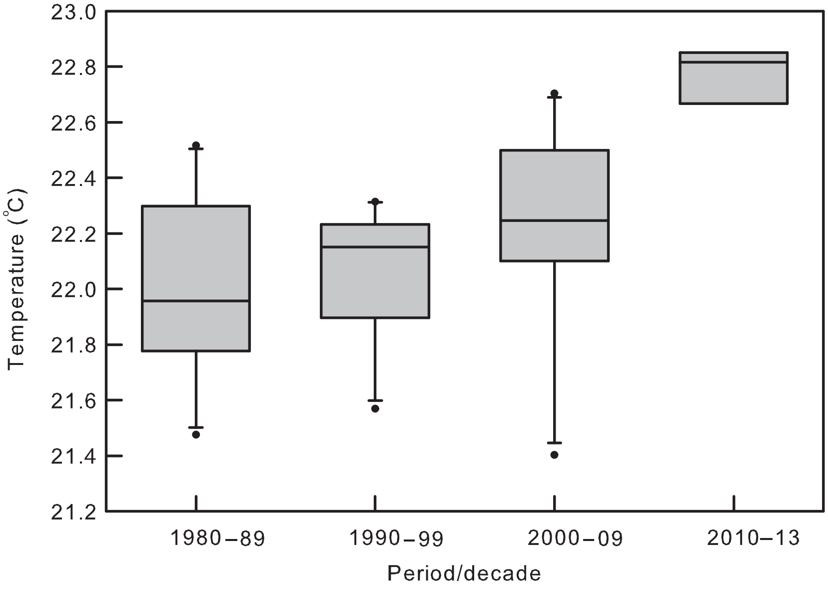

Fig. 3. Decadal air temperature averages around Lake Wamala, 1980–2013 (data from Uganda National Meteorological Authority, Ministry of Water and Environment).

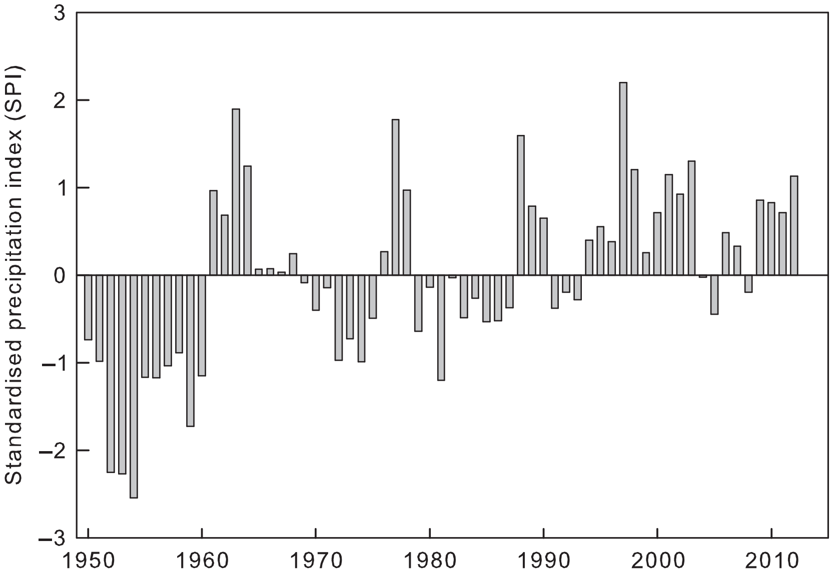

Fig. 4. Annual standardized precipitation indices of Lake Wamala, 1950–2013 (data from Uganda National Meteorological Authority, Ministry of Water and Environment).

Water balance

Rainfall and evaporation were the most important factors in the water balance of the lake (Table 1). Rainfall contributed 79.5% of the total water input into the lake and the remainder from catchment inflow. More water (86.2%) was lost through evaporation, however, resulting into to a negative water balance.

Fish species composition

Except for the years 2012 and 2013, the contribution of Nile tilapia to commercial catches was >60% during the years that rainfall was above average. The contribution of Nile tilapia to the total catches was only 10% and 2%, respectively, during 2012 and 2013, despite high rainfall averaging 1300 mm since 2011. Similarly, the contribution of Nile tilapia to commercial catches was >50% during the years the lake depth was high (>4 m) (Fig. 6). In experimental catches, the contribution of Nile tilapia decreased from 67 to <1% between 1975 and 2013 with the decreased lake depth, although the time series relationship did not indicate any distinct trend (Table 2).

CPUE

The annual CPUE increased from 0.4 tons per boat in 1960 to 4.8 tons per boat by 1975, but then decreased to as low as 0.2 tons per boat by 1988. The increased CPUE

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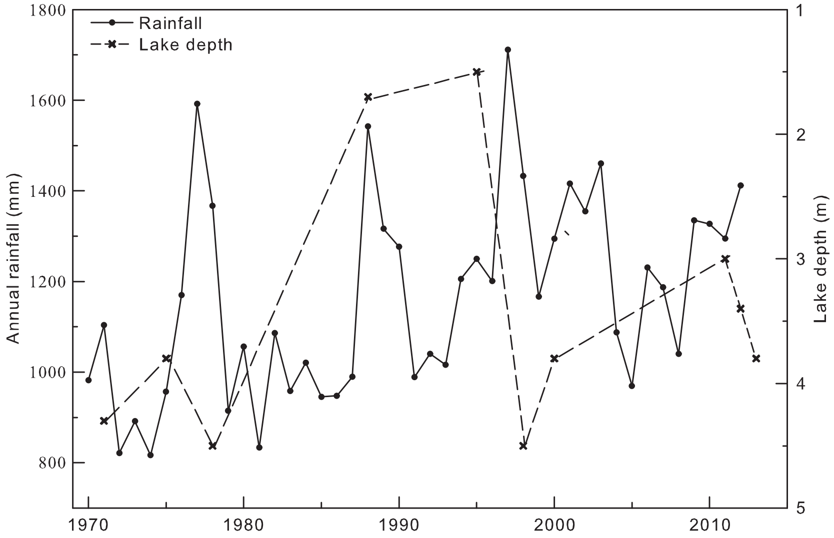

Fig. 5. Changes in annual rainfall and lake depth of Lake Wamala, 1970–2013 (rainfall data from Uganda National Meteorological Authority; lake depth data from NaFIRRI Unpublished).

Table 1. Average annual water balance of Lake Wamala, 2011-2013 (data from Uganda Directorate of Water Resources Management, Ministry of Water and Environment)

	Flow ($\times 10^{-14}$ m^3 s^{-1})	Volume ($\times 10^{-15}$ km^3 year^{-1})	%
Gains			
Rainfall	4.29	1.37	79.5
Inflow from catchment	1.10	0.35	20.5
Total	5.39	1.72	
Losses			
Lake evaporation	4.82	1.54	86.7
River Kibimba	0.77	0.24	13.3
Total	5.59	1.78	
Storage	−2.04	−0.06	

coincided with rainfall maxima at the beginning of 1960s (Fig. 7). The decrease in the average rainfall to as low as 960 mm during the first half of 1980s, however, accompanied by a drop in lake depth from 4.5 m to 1.7 m, were followed by the lowest CPUE of 0.2 tons per boat. The CPUE increased again to 10.6 tons per boat by 1999, corresponding to rainfall maxima of 1997 mm and an increase in lake depth back to 4.5 m (Fig. 7). By 2012, the CPUE was as low as 0.3 tons per boat, despite the continued increase in rainfall above average in the precedent decade.

Population structure

The modal TL of Nile tilapia was 190–249 mm, except during the period 1988–1996, when the fish were smaller, with a modal TL of 130–159 mm. The decrease in TL from 190–249 cm during the 1976–1978 to 130–159 mm during the period 1988-1996 coincided with a decreased lake depth, which fell from 4.5 m to 1.5 m (Fig. 8). When the lake depth increased back to 4.5 m following the El Nino rains of 1997, the mean TL increased to 220–249 cm during 1998–2000, remaining in the same range between the years 2011 and 2014 (Fig. 9).

Size at first maturity

The length at 50% maturity was 200–220 mm TL for males and 190–200 mm TL for females, with all fish >240 mm TL being mature, except during 1988–1996. During the period 1988–1996, the length at 50% maturity was 135 mm TL for males and 115 mm TL for females, with all fish >170 mm TL being mature. The decreased length at 50% maturity between 1976–1978 and 1988–1996 coincided with a decreased depth of the lake by 3.0 m. When the lake level increased to 4.5 m by 1998, the length at 50% maturity increased to 200–220 cm TL during the period 1998–2000. The average length at 50% maturity was 180–200 cm TL during the period 2011–2014, following a decrease in the average lake depth to 3.5 m (Fig. 9).

Length–weight relationships and condition factor

The slopes of the length–weight relationships for high and low lake depths were significantly different [$t_{(6)} = 3.225$, $P < 0.05$], with the slopes being higher at the high lake depth than at lower depths (Table 2). The Kn also increased from 0.9 during the period 1988–1996, when lake depth was low (1.6 m) to 1.1 during 1998–2000 when lake

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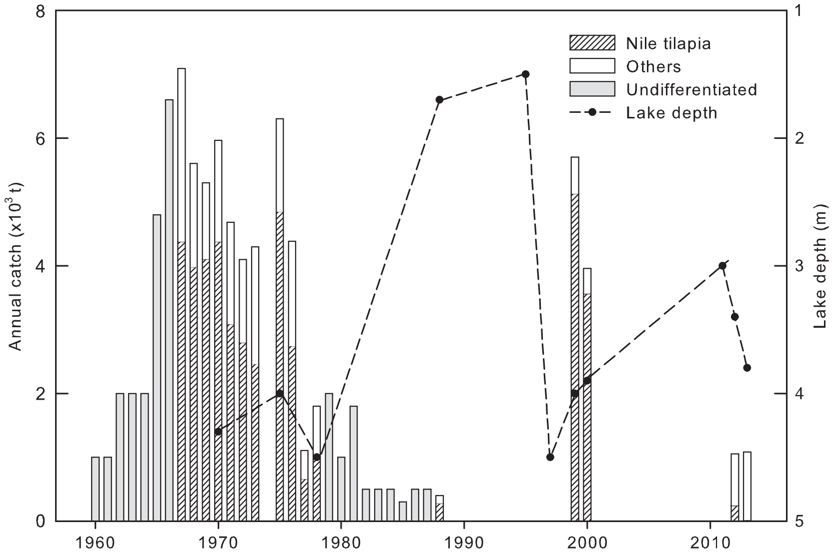

Fig. 6. Changes in fish catches and mean lake depth in Lake Wamala, 1960–2013 (other fish refer to African catfish and lungfish; fish catch data for 1960–2000 from Department of Fisheries Resources; data for 2012–2013 from Catch Assessment Survey carried out by NaFIRRI; lake depth data obtained from NaFIRRI archives).

Table 2. Percentage contribution of species by weight in experimental catches from Lake Wamala, 1975–2013 (Data for 1975–2000 from Department of Fisheries Resources and for 2012–2013 from experimental fishing)

Species/lake depth	1975	1988/9	1996	1998	1999	2000	2011	2012	2013
Lake depth (m)	4.5	1.7	1.5	4.5	4.0	3.9	3.0	3.4	3.8
Oreochromis niloticus	67	45	34	21.9	37	18.1	2.9	1.03	0.3
Clarias gariepinus	17	14.0	13.7	43.3	17.8	54.9	69.1	33.4	73.4
Oreochromis leucostictus	0.9	2.4	10.2	14	14.1	1.7	4.9	6.6	1.7
Protopterus aethiopicus	15.1	38.6	16	10.7	16.4	13.6	10.7	5.9	17.9
Haplochromines	–	–	25.7	5.8	14.1	11.7	10.4	47.7	6.4
Tilapia zillii	–	–	0.4		–	–	1.5	4.8	0.3
Clarias liocephalus	–	–	–	4	0.6	–	0.2	0.6	–

depth was high (4.1 m). The Kn remained the same throughout 2011–2014, however, despite a decreased lake depth (Table 2).

Fecundity and size of oocytes

The total number of oocytes ranged from 735 to 1050, with a mean absolute fecundity of 837 oocytes. Fecundity in relation to TL was described by the following equation (Fig. 10):

$$F = 6.12L^{0.902}. \quad (4)$$

where, F = fecundity and L = TL (mm). The mean diameter of oocytes was 2.44 ± 0.28 mm.

Diet

During the different seasons of the year comprising the period 2011–2014, Nile tilapia was omnivorous, feeding on algae, insect larvae, fish, higher plant material and detritus. A shift from an algal-dominated diet during the wet season, however, was observed to include more insects during the dry season (Fig. 11).

DISCUSSION

Temperature and rainfall changes and their effects on water balance and lake depth

Most of the water in East African great lakes is contributed by direct rainfall (Bootsma & Hecky 2003). Thus, for lakes that do not experience significant water abstractions for large-scale water uses (e.g. irrigation; hydroelectricity power generation), lake water levels typically remain high as long as the rainfall fluctuates within normal pattern (Sewagudde 2009). The findings of the present study are in agreement with the above observation, noting the depth of Lake Wamala was above 4 m for all the years in which the rainfall was above average, except for the period 2011–2014 (Fig. 5). The low average lake depth of 3.5 m during 2011–2014, even when the rainfall

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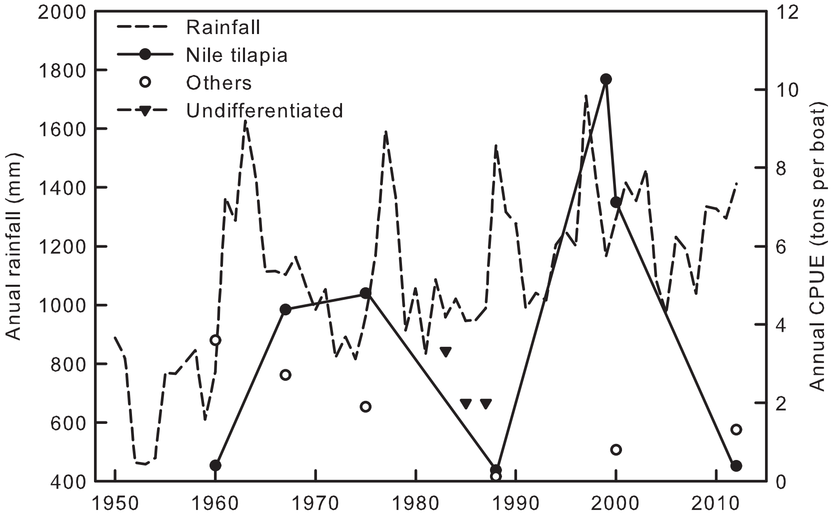
Fig. 7. Changes in annual catch per unit effort (CPUE) and annual rainfall around Lake Wamala, 1950–2012 (other fish refer to African catfish and lungfish; rainfall data from Uganda National Meteorological Authority, Ministry of Water and Environment; data on fish catch and number of boats for 1960–2000 period obtained from Department of Fisheries Resources, and for 2012 from Frame Survey and Catch Assessment Survey by NaFIRRI).



was above average since 2006, was unexpected for a small lake like Lake Wamala, which experiences no significant water abstractions. This observation suggests there might have been a change in the hydrological pattern of the lake. Although most of the water input into East African Rift Valley lakes is through direct rainfall, a similar or even greater quantity is lost through evaporation (Bootsma & Hecky 2003). Thus, the current low depth of Lake Wamala can be attributed to higher evaporation rates (Table 1) associated with increased temperatures after 2000 (Figs 2 and 3). These observations imply there may be an increase in rainfall associated with climate variability and change, but that the water gain may be offset by increased evaporation associated with an increased temperature.

The situation in Lake Wamala is similar to that observed for other East African lakes. Approximately 83% of the water in Lake Victoria, for example, is contributed through direct rainfall, with a similar quantity lost through evaporation (Sewagudde 2009). Lake Victoria, however, does not suffer large annual water level fluctuations because of its large size (68 800 km^2) and maximum depth (80 m) sufficiently high to buffer the effects of evaporation (Sewagudde 2009). This is not the case for small shallow lakes such as Lake Wamala, with a small surface area of 250 km^2 and a low mean depth of 4.5 m. The fact that the rate of water loss from Lake Wamala attributable to evaporation currently exceeds the rate of water gain from direct rainfall (Table 1) suggests that any period of lower than average rainfall will be accompanied by a corresponding decrease in lake depth and lake surface area. This happened between the years 1984 and 1995 (UNEP 2009) and is expected to worsen in the future if the observed temperature trend (Fig. 1) continues, or if the predicted increase in rainfall in the region (IPCC 2014) is not sufficiently high to compensate for evaporation losses associated due to increased temperature. These changes have implications for the lake fish stocks.

Changes in fish species composition and CPUE

The contribution of Nile tilapia to commercial catches was highest during the periods of above average rainfall and high lake depths (Fig. 6). When the lake level rises, the terrestrial vegetation is submerged and nutrients leaching from decomposing organic matter, and directly from inflowing water, result in increased plankton food and fish production (Kolding 1993; Ogutu-Ohwayo *et al.* 2013). Additionally, flooded marginal areas and increased river flows result in better spawning conditions and excellent conditions for the growth and survival of juvenile inshore fish species, including Nile tilapia (Ogutu-Ohwayo *et al.* 2013). This explains why the contribution of Nile tilapia to commercial fish catches, and ultimately to the CPUE, was low during dry years when the lake depth was low, implying limited breeding and nursery space and high mortality rates (Ogutu-Ohwayo *et al.* 2013). In many studies, however, the decreased CPUE has largely been attributed to overexploitation due to an increased number of fishers (e.g. Bwanika *et al.* 2004; Marshall 2012). Whereas this is a possible scenario for many aquatic systems, including Lake Wamala, there is no sufficient evidence to suggest the decreased CPUE in Lake Wamala from 4.8 tons per boat in 1975 to 0.2 tons per boat by 1988 (Fig. 7) was largely driven by overfishing. In fact, the number of fishers on the lake decreased from 750 in 1975, to a record low of 150–200 between 1981 and 1988 (Goulden 2006). Overfishing as a sole determinant of the decreased CPUE is further weakened by the fact that the CPUE in Lake Wamala increased to a record high of 10.2 tons per boat in 1999

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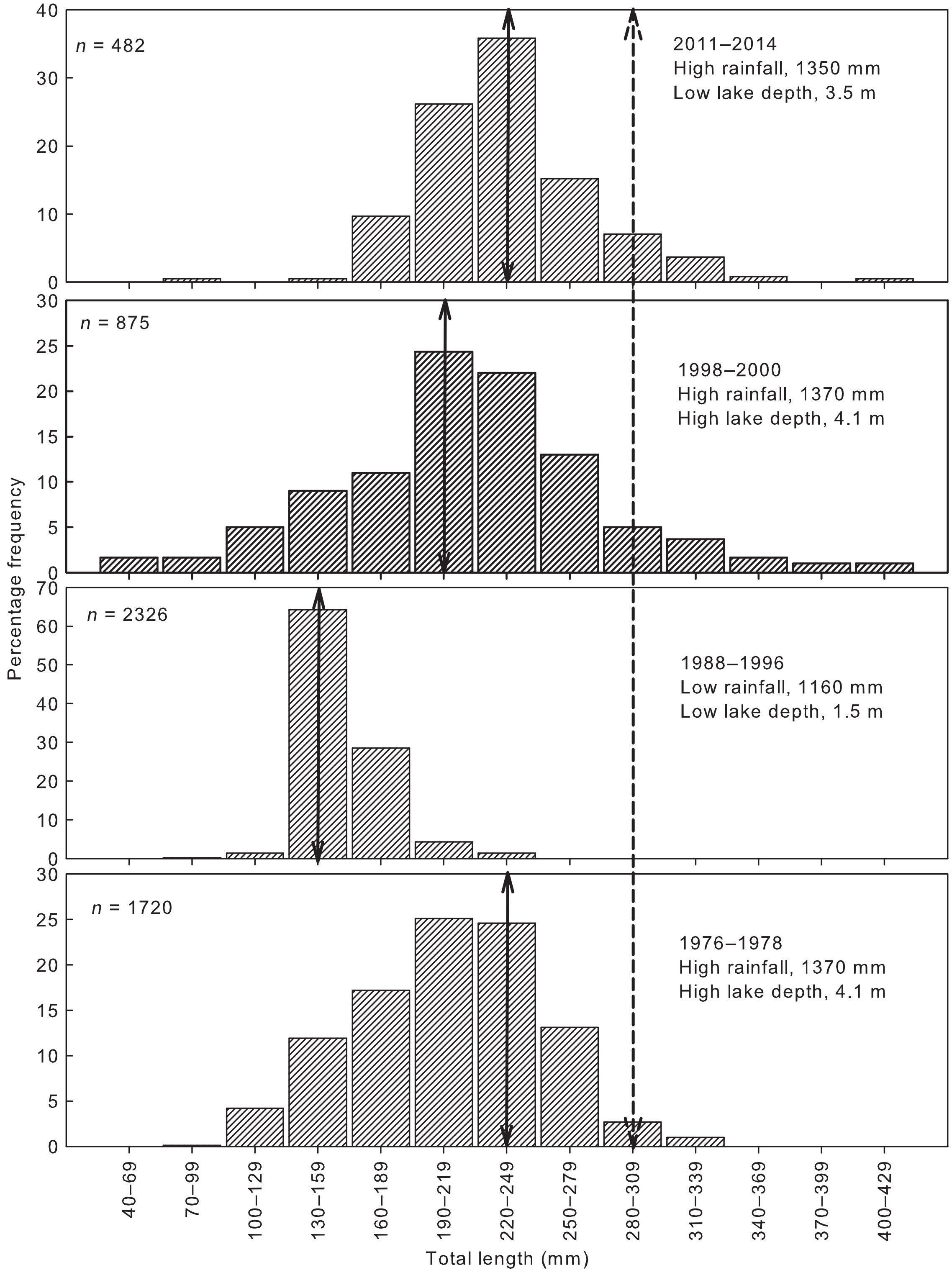

Fig. 8. Length frequency distribution of Nile tilapia in Lake Wamala at varying rainfall and lake depths (Periods; *a* = 2011–2014; *b* = 1998–2000; *c* = 1988–1996; *d* = 1976–1978; vertical solid lines indicate length at which 100% of fish are fully mature; vertical broken line indicates legal minimum length permitted in Uganda ((GoU) 2000); during periods a, b, c and d, 73.7, 75, 67 and 83.2, respectively, of harvest fish were 100% mature, although less than the minimum length required by the law; data for periods *b, c* and *d* from NaFIRRI archives; data for *a* from experimental fishing; rainfall data from Uganda National Meteorological Authority, Ministry of Water and Environment; lake depth data from NaFIRRI archives)

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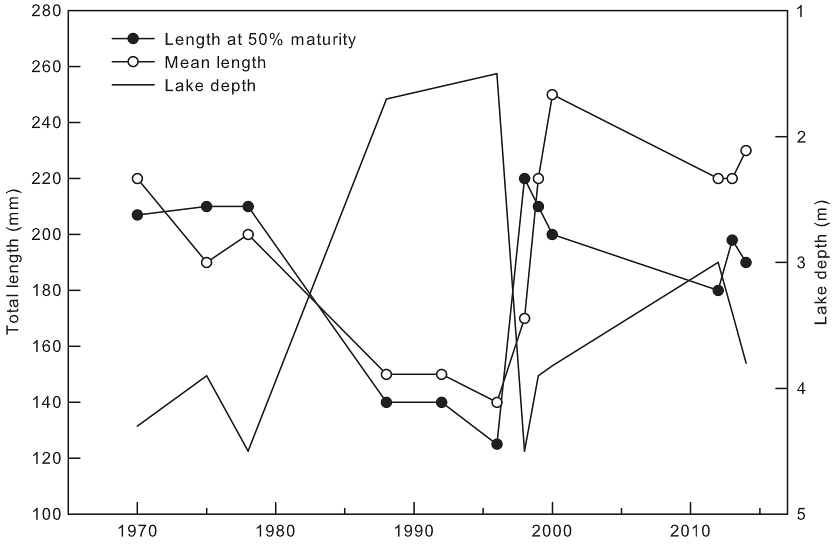

Fig. 9. Changes in mean total length and length at 50% maturity of Nile tilapia in relation to lake depth in Lake Wamala between 1970 and 2014 (correlation between lake depth and mean total length ($r = 0.991$, $P < 0.001$) and between lake depth and length at 50% maturity ($r = 0.726$, $P < 0.001$) was strong and significant; data on total length and length at 50% maturity for 1970–1975 from Okaronon (1987), 1978–2000 from NaFIRRI archives and 2011–2014 from experimental fishing; lake depth data from NaFIRRI archives).

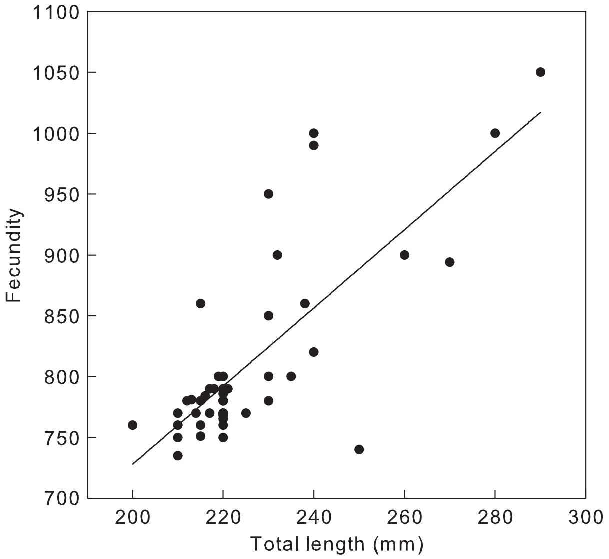

Fig. 10. Relationship between absolute fecundity and total length of Nile tilapia from Lake Wamala between 2011 and 2014 (data obtained from experimental fish samples).

(Fig. 7), even when the number of fishers had increased threefold since 1988 (Goulden 2006). Thus, the decrease could have been driven largely by desiccation, because the rainfall was below average for all the years between 1979 and 1987 (Fig. 4), with a reduced lake depth from 4.5 to 1.7 m (Fig. 5).

The results of the present study indicate changes in the contribution of the Nile tilapia to commercial and experimental catches in Lake Wamala, and ultimately to the CPUE, varied with rainfall only up to the year 2000. After 2000, both the CPUE and the contribution of Nile tilapia to total catches decreased, despite high rainfall (above average) for most of the years. The cause of this situation is not clear. Conjectures include overfishing or environmental stresses due to desiccation associated with increasing temperatures and low lake levels. During the 2012 frame survey, the number of fishers was estimated at 640, translating into an increase of 90 fishers since 2000 (Goulden 2006). Based on these data, the suggestion that an increase in fishing effort by 90 fishers exclusively led to a reduction in catches by 87.1% between 2000 and 2013 is not supported (Fig. 6). Rather, the decrease could have been attributable to a combination of fishing pressures, desiccation due to the highest temperature increase between 2001 and 2013 (Fig. 3), and the continued decrease in lake depth after 2000 (Fig. 5). This is consistent with the findings of Jul-Larsen *et al.* (2003a,b) who analysed the combined effects of fishing effort and water levels on catch rates in the three African lakes (Kariba, Malombe and Chilwa) and found that environmental variability in all cases explained as much of the variance in catch rates as did fishing effort and that these two factors often interacted.

Average size and size at first maturity

Nile tilapia is known to grow to a smaller TL and to mature faster sexually in response to overexploitation, to predation, especially by Nile perch, and to habitat degra-

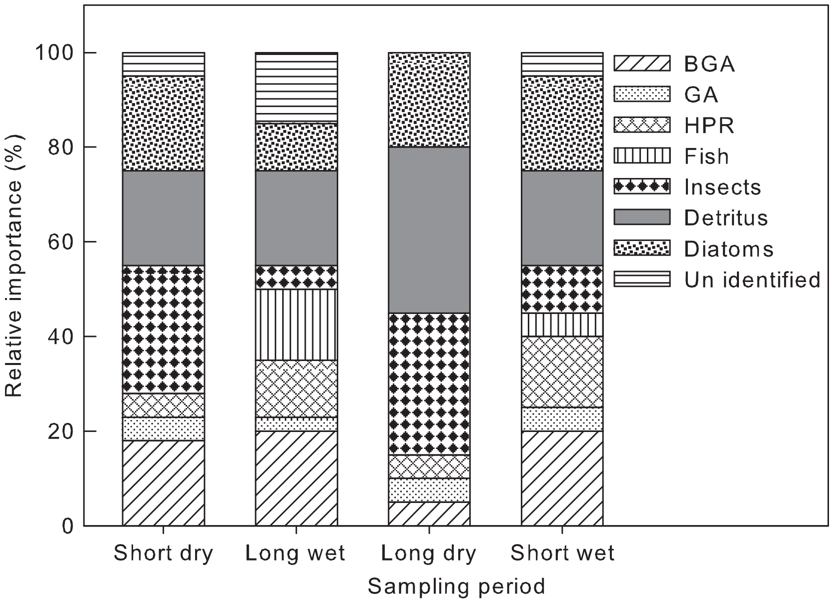

Fig. 11. Seasonal changes in food categories ingested by Nile tilapia in Lake Wamala between 2011 and 2014, BGA = Blue green algae, GA = Green algae, HPR = Higher plant remains (data from preserved stomachs of experimental fish samples).

dation (Gwahaba 1973; Kolding 1993; Okaronon 1995; Bwanika *et al.* 2004; Njiru *et al.* 2007). The decrease in mean TL and length at 50% maturity between the periods 1976–1978 and 1988–1996 coincided both with a decrease in lake depth from 4.5 m to 1.5 m (Fig. 9), and fishing effort from 750 to 150 fishers (Goulden 2006). However, the average TL and length at 50% maturity later increased during 1998–2000, corresponding to increased lake depth from 1.5 m to 4.5 m (Fig. 9), and an increased number of fishers from 150 to 550 between 1996 and 2000 (Goulden 2006). These observations suggest changes in mean TL and length at 50% maturity of Nile tilapia, in Lake Wamala, are largely driven by lake water levels, as opposed to fishing pressure.

Lake depth and lake volume determine the area of the productive lake bed in which fish breed and find most of their food (Welcomme 1970; Kolding 1993). This means that when the lake depth is high, habitat space and food resources are optimal, and competition is minimal. Nile tilapia invests more energy in somatic growth and grows to a larger size before reproduction (Welcomme 1970; Lowe-McConnell 1982). Conversely, with decreasing lake depth, breeding and nursery areas are reduced, with Nile tilapia adapting by growing to a smaller size, and maturing at a smaller size, as survival strategies, and means of avoiding high mortality rates associated with overcrowding and competition (Iles 1973; Lowe-McConnell 1982).

According to Welcomme and Merona (1988), the major causes of mortality especially in shallow lakes include the following: (i) isolation and desiccation; (ii) deoxygenation and high temperatures; and (iii) predation. Except for predation (unless it is from birds, which is not a significant factor for Lake Wamala; Sekiwunga personal communication), all the other factors prevail. Climate variability and change, manifested by persistent increased temperature, has begun disrupting the hydrological pattern of the lake (Table 1; Fig. 5). Nile tilapia in the lake is now adapting to reduced breeding and nursery areas attributable to desiccation resulting from reduced lake depth, increased temperature and possibly de-oxygenation (Welcomme & Merona 1988; Kolding 1993).

Length–weight relationships and relative condition

According to Witte and Van Densen (1995), fish species in Lake Victoria are known to exhibit peak breeding during the rainy period. This observation, similar to that of Dadzie *et al.* (2000), prompted Njiru *et al.* (2006) to conclude that the increases condition factor of Nile tilapia at the onset of rains is due to the development of the gonad tissue during the breeding season. The present study used fish weight devoid of gonads in calculating Kn and found the Kn to be higher during wet years than dry years (Table 2), thereby deviating from this notion. The findings of the present study suggest fish condition is largely driven by rainfall and associated increased lake levels, which increase habitat space and reduce intraspecific competition (Vila-Gispert & Moreno-Amich 2001; Bwanika *et al.* 2004), and enhances plankton availability, which is the major food for tilapia in the lake (Magadza 2008).

Diet

An issue still unresolved by the recent literature (e.g. Balirwa 1998; Njiru *et al.* 2002, 2007; Bwanika *et al.* 2006)

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about the diet of Nile tilapia concerns what caused Nile tilapia, originally known to be herbivore feeders on phytoplankton (Fish 1955; Moriarty & Moriarty 1973) to include invertebrates in their diet. The authors of most recent studies argue that Nile tilapia, especially in Lake Victoria, diversified its diet to fill niches previously occupied by other cichlids, most especially the insectivorous Haplochromines that were exterminated by the Nile perch (Njiru *et al.* 2002, 2007; Bwanika *et al.* 2006). The fact that this diversification has occurred in Lake Wamala, which contains no Nile perch, and where Haplochromines were not abundant (Table 3), suggests another cause. Several studies have demonstrated a decreased phytoplankton biomass over the last three decades, associated with warming of lake surface waters (e.g. O'Reilly *et al.* 2003; Verburg *et al.* 2003; Ndebele-Murisa *et al.* 2012). This suggests the inclusion of invertebrates in Nile tilapia diet, as observed in Lake Wamala, could be an adaptation response to widen the food resource base, particularly since the preferred phytoplankton sources could be declining because of increasing temperatures observed for the lake, a suggestion that needs further investigation.

The present study showed Nile tilapia shifted from an algal-dominated diet during the wet season to include more insects during the dry season. This provides additional rationale for suggesting that temperature and rainfall influence the type of prey items available for the fish. Ndebele-Murisa *et al.* (2012) reported a distinct seasonal trend in phytoplankton biomass, with the peaks coinciding with wet season, which they attributed to local floods discharging nutrient-rich waters into the lake. Similarly, the low biomass observed during the dry season was attributed to the possibility of photoinhibition of algal photosynthesis because of higher temperatures at the water surface (Ndebele-Murisa *et al.* 2012). This suggests rainfall and temperature catalyse ecological changes that drive primary productivity processes and determine which prey is abundant. Accordingly, phytoplankton dominates during the wet season and insects during the dry season. This means the seasonal shift in the Nile tilapia diet observed in Lake Wamala is a reflection of the differences in the relative abundance of different food items in the system during different seasons of the year. It also implies that the diet of Nile tilapia would be affected if there was a change in the length of a given season because of climate variability and change. The extent and direction of such effects also merit further investigation.

Table 3. Correlation between log *L* (TL, mm) and log *W* (weight, g) of Nile tilapia in Lake Wamala for varying lake depths during periods 1988–1996, 1998–2000 and 2011–2014 (R^2 = adjusted *R* square; data for 1988–1996 and 1998–1999 from NaFIRRI and for 2011–2014 from experimental and commercial fish samples)

Period	Lake depth	Length-weight relationship	R^2	Kn
1988–1996	1.6	$\log_{10} W = 2.4\log_{10} L$-0.9	0.93	0.9
1998–2000	4.1	$\log_{10} W = 3.15\log_{10} L$-4.7	0.96	1.1
2011–2014	3.5	$\log_{10} W = 2.47\log_{10} L$-3.5	0.94	1.1

Fecundity and oocyte size

The minimum number of oocytes of 735 observed in the present study suggests the fecundity of Nile tilapia in Lake Wamala is high, compared to those of the same size class in other water systems. An example was documented by Lowe-McConnell (1958), who reported a minimum absolute fecundity of 340 oocytes for Nile tilapia of similar size class. Similarly, the mean diameter of oocytes was small, compared to that reported by Lowe-McConnell (1958) and Trewavas (1983). Thus, Nile tilapia in Lake Wamala could be exhibiting an 'r' selected reproductive strategy (Pinka 1970; Mann & Mills 1985) by adjusting its fecundity to maximize reproductive success under unfavourable conditions associated with increasing temperatures (Portner *et al.* 2001; Donelson *et al.* 2010).

CONCLUSIONS

Lake Wamala represents a classical example for monitoring the effects of climate change on lake water levels and fish production. There is evidence to suggest that an increased temperature around the lake, especially over the past decade, has disrupted the hydrological pattern of the lake, with high rainfall no longer being sufficient to sustain normal lake water levels during high temperature periods. Thus, Lake Wamala is not likely to regain its normal mean depth of 4.5 m if the observed increase in temperature does not slow down, or if the predicted increased rainfall within the region (IPCC 2014) does not outmatch the water losses attributable to evaporation.

The lake water level changes, and the fluctuations in temperature and rainfall from the normal pattern play an important role in determining the fish species composition, CPUE, population structure, length at 50% maturity, length–weight relationship and condition factor for Lake Wamala. The results of the present study suggest that Nile tilapia in Lake Wamala is displaying a typical 'r' selected reproductive strategy, by growing to a small size, maturing faster, becoming more fecund and feeding on different food items to survive high mortality rates under unfavourable conditions caused by higher temperatures,

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low rainfall and low lake water levels. All these changes determine how abundant the species will be, relative to others, at any time period. Under high rainfall and lake depth, the normal lake area is wide, breeding and nursery space are optimal, food resources are abundant, and competition is minimal (Welcomme 1970). This largely explains why Nile tilapia in Lake Wamala dominates the catches, grows to a large size and delays sexual maturation when the rainfall and lake water levels are high.

RECOMMENDATIONS

Given that temperature and rainfall interact and affect lake water levels, and ultimately fish catches, in Lake Wamala, it is not advisable to establish a permanent fishing effort. The fishing effort can either be too high or too low, depending on the prevailing climatic conditions, making the regulation of such an effort hard to implement. Thus, it is important to determine the optimal fishing effort under different case scenarios (low/high fish abundance) that could be implemented synchronously, depending on the fish abundance.

The results of the present study indicate it may be necessary to periodically review Ugandan law (GoU, 2000) regarding the minimum size of fish that should be harvested, and it would vary depending on prevailing conditions at different times for different water bodies. According to the law, the size at which fish should be harvested is normally set above the length at 50% maturity. Based on this delineation, the minimum size of Nile tilapia that should be harvested from Lake Wamala was set at 280 mm TL, corresponding to the minimum mesh size of gill nets 114.3 mm that should be used. Nile tilapia in Lake Wamala, however, adjusts its length at 50% maturity between 120 and 220 mm TL, depending on lake water levels (Fig. 9), rendering this minimum mesh size inappropriate, especially with low lake levels. To avoid fishing overexploitation, the minimum mesh size can be adjusted to 101.6 mm (4 inches), translating into a minimum size of 220 mm TL (maximum length at 50% maturity of Nile tilapia in Lake Wamala, attained under high lake water levels; Fig. 9) that can be harvested.

The present study has provided some insights into possible changes in the fish stocks in Lake Wamala associated with climate variability and change. There is a need, however, for further studies to determine the actual impact of increasing variability and change in Lake Wamala, and other water systems, with intensifying climate changes.

ACKNOWLEDGEMENTS

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