



Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Review

Implications of climate variability and change for African lake ecosystems, fisheries productivity, and livelihoods

Richard Ogutu-Ohwayo, Vianny Natugonza *, Laban Musinguzi, Mark Olokotum, Shamim Naigaga

National Fisheries Resources Research Institute (NaFIRRI), P.O. Box 343, Jinja, Uganda

ARTICLE INFO

Article history:

Received 27 August 2015

Accepted 4 March 2016

Available online xxxx

Communicated by Tom Hrabik

Keywords:

Adaptation

Aquatic productivity

Climate change

Fisheries

Livelihoods

ABSTRACT

Inland fisheries are important for nutrition, employment, and income, but climate variability and change are adding to other stressors, such as overexploitation, pollution, habitat degradation, and invasive species, to threaten their productivity as well as livelihoods of fisheries-dependent communities. Understanding the whole socio-ecological system to enable communities to adapt and build resilience is therefore vital. Here, we present results from a review of the responses of African lakes, fisheries productivity, and livelihoods to climate variability and change, and provide suggestions on required policy interventions to promote adaptation and build resilience. Changes in climate variables, especially temperature, wind speed, and rainfall have contributed to changes in lake water levels, loading, and recycling of nutrients. In some lakes, such disruptions in physical and chemical conditions have triggered changes in water quality, algae and invertebrate productivity, life history of fish, and contributed to shifts in fish community composition, proliferation of invasive aquatic weeds, and changes in parasite–vector–host interactions. Fish yield has either increased or decreased depending on climatic events, with the latter negatively affecting livelihoods, and forcing affected communities to adapt. Because adaptation strategies are location specific, and influenced by local conditions, many adaptation strategies have been unguided and have negatively affected fisheries. The responses of fisheries to climate change vary among lakes of different morphometric characteristics. There is need for consistent data to examine the direction and consequences of climate variability and change on fisheries and livelihoods of specific aquatic systems, and promote location specific adaptation and mitigation measures.

© 2016 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

Contents

Introduction	0
Climate variability and change	0
Temperature	0
Wind speed	0
Rainfall	0
Abiotic responses of lakes to climate variability and change.	0
Water balance, lake levels, and surface area	0
Nutrient loading and recycling	0
Water quality	0
Biotic responses to changes in climate and lake physicochemical attributes	0
Algal biomass and primary productivity	0
Invertebrate productivity	0
Life history of fish, composition, and catches	0
Parasite–vector–host interactions	0
Invasive aquatic weeds	0
Human responses to changing lake ecosystems	0
Livelihoods	0
Adaptation and mitigation strategies	0
Policy interventions	0

* Corresponding author. Tel: +256 783 880 777.

E-mail address: viannynatugonza@yahoo.com (V. Natugonza).

Conclusions	0
Acknowledgments	0
References	0

Introduction

Inland fisheries are important livelihood sources, especially for the rural poor in most low-income countries who suffer disproportionately from undernutrition, including micronutrient deficiencies (Traoré et al., 2012). Inland fisheries contribute >6% of the world's annual animal protein supplies for human consumption, and about 94% of all freshwater fisheries are in developing and underdeveloped countries (FAO, 2010). In Africa, inland fisheries generate about US\$4,676 million from local, regional, and international trade, employ >600,000 fishers (de Graaf and Garibaldi, 2014), and contribute at least 30% of total animal protein intake in some landlocked countries (Table 1).

Despite the economic and nutritional benefits, especially for the landlocked countries that derive most of their fish protein from lakes, inland fisheries are under pressure from overexploitation, pollution, invasive species, and habitat degradation, all of which have been accelerated by the rapidly increasing human population. Some of the fastest human population growth rates in the world, and highest population densities in Africa, are found around the African Great Lakes (Kolding et al., 2008). The Lake Victoria basin, for instance, has over 25 million people, with a population density of about 500 persons/km², which is much greater than the average for the continent (Kolding et al., 2014), and whose activities directly or indirectly affect the lake ecosystem. About 30 million people depend on Lake Chad and the floodplains of the Chari River for agriculture, livestock, and fisheries (FAO, 2012). This high population is putting pressure on critical habitats, including wetlands, by converting them to agriculture and livestock production, which increases the degradation of the lake habitats. Most urban areas are also located in the proximity of the lakes, where municipal and industrial effluents are released into lakes. Many areas along the northern shores of Lake Victoria in Kenya and Uganda, for instance, will become urbanized by 2030 (Seto et al., 2012), and this urban growth poses additional threats to the lake.

Climate variability and change, which have intensified since the 1970s (IPCC, 2014), are adding to these challenges and will complicate the sustainability of fisheries resources and the livelihoods of people depending on the resources. Climate variability and change have contributed to a change in composition and sizes of marine fishes, sometimes with a significant loss of revenue and household income (Tseng and Chen, 2008), and the same might occur in inland fisheries. The poor and marginalized members of riparian societies, who depend on fisheries for their livelihood but have limited capacity to adapt, are most vulnerable to such changes (Cinner et al., 2011). This is especially apparent in Sub Saharan Africa, where about 240 million people are poor, with 60–70% of the population depending on natural resources, including fisheries (FAO, 2010). This makes Africa one of the most vulnerable continents to climate change (Allison et al., 2009).

Table 1

Fish consumption, its contribution to animal protein, and population growth in some landlocked African countries that derive their fish protein virtually from lakes. Data on fish consumption from FAO (2009), and that of population growth from PRB (2014).

	Consumption (kg per person)	Animal protein (%)	Population growth (% per annum)
Burundi	3.2	29.6	3.2
Democratic Republic of Congo	5.3	43.1	3.0
Malawi	4.6	35.9	2.9
Uganda	11.5	35.9	3.4

Optimally managed fisheries, with abundant stocks, are better able to adapt to climate change compared to ones that are less efficiently managed (Cheung et al., 2008; Sumaila et al., 2011), but, as in many parts of the world, management of lakes in Africa has not yielded sustainable fisheries that potentially yield high value fishes. Examples of historical collapses of highly valued fisheries include *Labeo* spp. (e.g., *Labeo victorinus* in Lake Victoria, *L. altivelis* in Lake Mweru, and *L. mesops* in Lake Malawi); the endemic *Oreochromis* spp. in Lakes Victoria, Kyoga, and Malawi; all species in Lake Malombe; and the sardine fishery of Lake Kariba (Ogutu-Ohwayo, 1990; FAO, 2003). In other lakes, stocks of high valued species have decreased and been replaced by low-valued fishes (e.g., in Lakes Albert, Victoria, and Kyoga, MAAIF, 2012). Such changes have mostly been attributed to fishing pressure; but there is evidence, also, that fresh water fisheries have either declined and/or collapsed for environmental reasons, e.g., Lakes Chad (FAO, 2012), Ngami and Liambezi (Moyle et al., 2009), Rukwa (Mbungu, 2015), Chilwa (Njaya et al., 2011), and Wamala (Natugonza et al., 2015) or shifted in composition to smaller opportunistic species due to climate change (FAO, 2010). Understanding the influence of climate variability and change will therefore be important for managing these lakes and their fisheries, and for development of appropriate adaptation strategies.

Aquatic productivity is linked to climatic variables, such as wind strength, temperature, and rainfall, which affect nutrient dynamics, stratification and mixing regimes, primary productivity, fish yield, and, ultimately, livelihoods (Talling and Lemoalle, 1998; Allison et al., 2009; MacIntyre, 2012). How aquatic ecosystems respond to such changes depends on morphometric characteristics of individual systems (Kraemer et al., 2015a). Deep African lakes, >100 m, are permanently stratified while shallow lakes and shallow bays of deep lakes, such as Pilkington Bay and Winam Gulf of Lake Victoria, mix daily (MacIntyre et al., 2014). Shallow lakes have a high area to volume ratio and are therefore more influenced by wind intensity that induces diel mixing and increases sediment–water interactions that alter turbidity, nutrient cycling, and dissolved oxygen concentrations (MacIntyre, 2012). Climatic change is expected to affect these processes, and there is a need to understand how this might affect fisheries production and, ultimately, the livelihoods of fishery-dependent communities.

The tropics absorb about twice the solar energy that the higher latitudes absorb, creating a meridional gradient in temperature and potential energy which is converted into kinetic energy that is manifested as wind (Reichler, 2009). Increasing global temperatures will change wind speed as well as rainfall patterns in different parts of the world (IPCC, 2014). In large parts of Africa (including the Great Lakes region), wind speed (at 10 m above ground level) is expected to increase by 10% relative to a 1981–2100 control period (McInnes et al., 2011), and rainfall in the region is also projected to increase over the next few decades (IPCC, 2014). These changes will affect river flows and nutrient loading into lakes (MacIntyre, 2012) and will be exacerbated by land use and land cover change because of the rapid increases in human population in many parts of Africa, estimated at 3–4% per annum (PRB, 2014). An increase in temperature is also expected to change internal processes, including water column stability, distribution of planktonic organisms, and the species that feed on them (Cochrane et al., 2009). The responses of fish to these changes, in turn, will affect fisheries and their sustainability as climate change intensifies. This paper draws from examples and experience on the African lakes to present the likely impacts of climate variability and change on some African inland fisheries (Fig. 1),

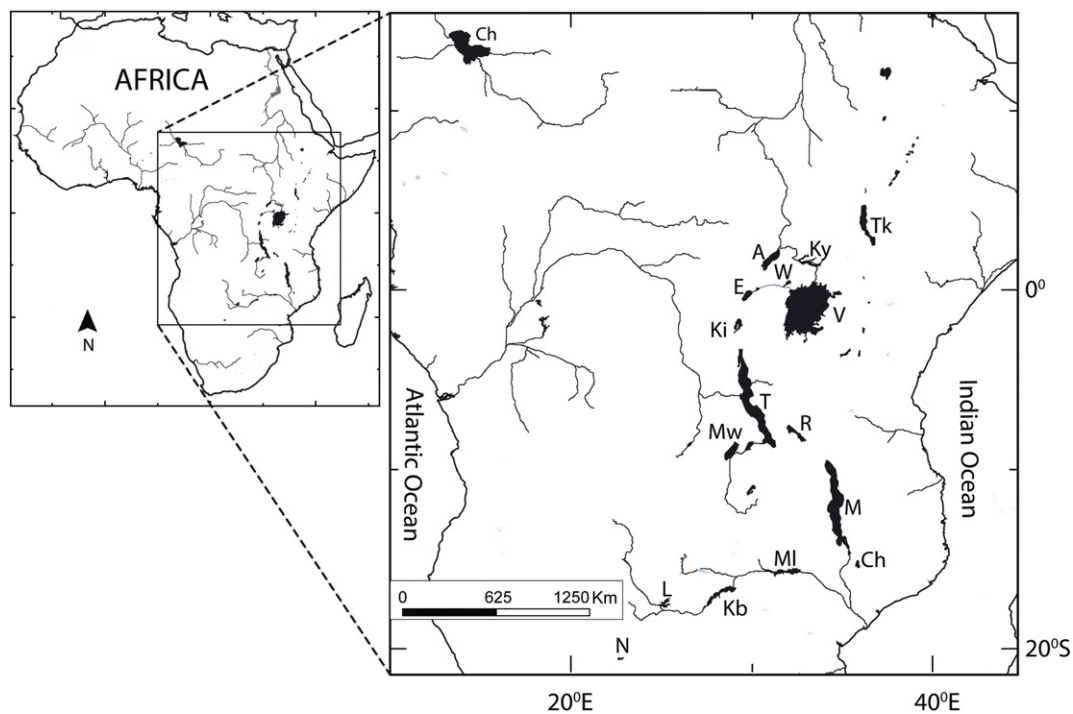


Fig. 1. Location of lakes that were reviewed within Africa. Letters denote: A, Albert; Ch, Chad; Cw, Chilwa; E, Edward; Kb, Kariba; Ki, Kivu; Ky, Kyoga; L, Liambezi; M, Malawi, MI, Malombe, Mw, Mweru, N, Ngami; R, Rukwa, T, Tanganyika, Tk, Turkana; V, Victoria; and W, Wamala.

and the information that will be needed to improve management to build resilience and allow adaptation.

Climate variability and change

Temperature

Global warming has been rising since the 1970s, and by 2013, global temperatures had increased by 0.62 °C above the 20th century average (NOAA, 2013). Although warming in Africa started at the beginning of the 20th century, the increase in temperature after 1970 exceeded the previous natural variability (IPCC, 2014). Africa became warmer on average by 0.5 °C during the last three decades of the 20th century, and temperature over the continent is expected to increase by 1.4–5.8 °C by 2050. The effect of this regional increase in temperature has been detected in many African lakes, especially within the Great Lakes region. The temperatures of Lakes Albert (Lehman, 1998), Edward (WWF, 2006), Kivu (Lorke et al., 2004; Katsev et al., 2014), Tanganyika (O'Reilly et al., 2003; Verburg et al., 2003; Verburg and Hecky, 2009; Kraemer et al., 2015b), Malawi (Vollmer et al., 2005), Victoria (Sitoki et al., 2010; Marshall et al., 2013), Kariba (Mahere et al., 2014), and Nkuruba (Saulnier-Talbot et al., 2014) have all increased by 0.2–1.5 °C since 1900. The trend toward higher temperatures than the longterm regional average for these lakes, however, became more prominent after 1970s, coinciding with regional and global changes in climate (IPCC, 2014). Data from a global database of lake surface temperatures (Sharma et al., 2015) show that temperatures around these lakes have been rising (Fig. 2), coinciding with regional climate warming (Hulme et al., 2010; IPCC, 2014).

Water temperatures of other quite shallow lakes, such as Chad, Chilwa, and Wamala, have not been monitored as frequently in the past as those of deep lakes. However, analysis of air temperature around these systems shows that Lake Chilwa has warmed by 0.021 °C yr⁻¹ between 1982 and 2009 (Foli and Makungwa, 2011), Lake Chad by 0.02 °C yr⁻¹ between 1975 and 2009 (Funk et al., 2012), and Lake Wamala by 0.018 °C yr⁻¹ between 1980 and 2012 (Natugonza et al.,

2016). These trends are consistent with the regional warming averages reported for the last three decades of the 20th century (IPCC, 2014).

Wind speed

The strength, direction, and steadiness of the prevailing winds are crucial aspects of climate. Winds resulting from atmospheric circulation lead to transport of heat and moisture from remote areas and thereby modifying the local characteristics of climate. This, in aquatic systems, can affect water column stability, and have implications for mixing dynamics (MacIntyre, 2012; MacIntyre et al., 2014) and primary productivity (O'Reilly et al., 2003; Tierney et al., 2010).

Within the African Great Lakes region, lakes that have fairly consistent meteorological records show that wind speed has decreased, especially after 1970, except for Lake Victoria. Wind speed around Lake Victoria increased from about 2.5 m s⁻¹ during 1970s and 1980s to about 4 m s⁻¹ by 2000, after which it decreased slightly (MacIntyre, 2012). This trend is consistent with the one of Lake Wamala, which lies within the same watershed (Natugonza et al., 2016). By contrast, wind speed in the north of Lake Tanganyika decreased from about 8 ms⁻¹ to 4 ms⁻¹, and in south from 2.5 ms⁻¹ to about 1 ms⁻¹ between 1970 and 1995 (O'Reilly et al., 2003), although other researchers found no significant trends in wind speeds over Lake Tanganyika from 1998 through 2003 (Verburg and Hecky, 2009). Historical wind-speed measurements collected near the southeastern shore of Lake Malawi between 1980 and 1993, although sparse, are also suggestive of a decrease in wind speed (Patterson and Kachinjika, 1995).

Rainfall

Rainfall has been variable across many parts of the African continent and has had profound effects on lake water levels. Rainfall data around Lake Victoria since 1960 show a high level of inter-annual variability characterized with episodic floods (1962, 1978, and 1998) and droughts (1973, 1984, and 1997), but with an overall downward trend (Awange et al., 2008; Nsubuga et al., 2014). Around lakes Tanganyika and Rukwa,

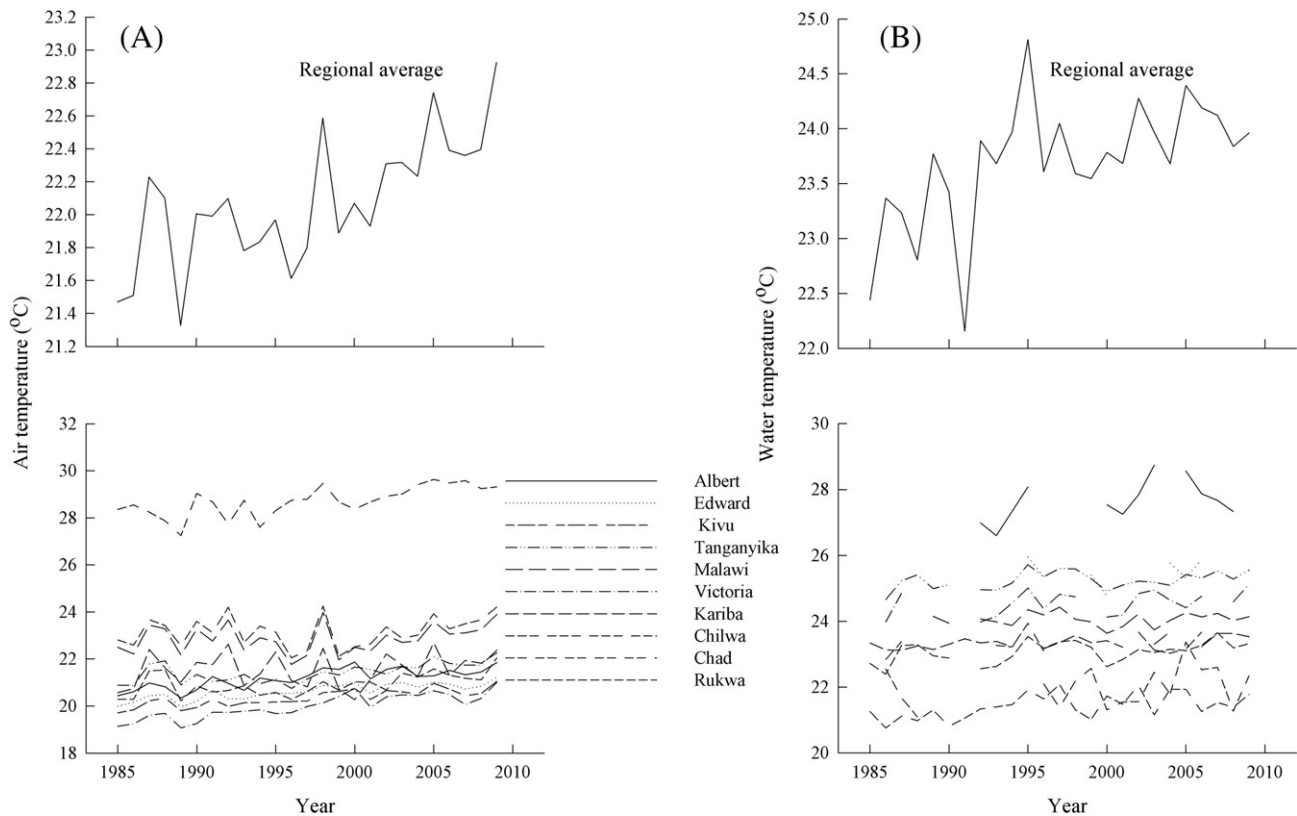


Fig. 2. Mean annual air temperature (°C) (panel A) and summer lake water temperature (°C) (panel B), with respective regional averages, for some inland lakes in Africa between 1985 and 2009. Data were obtained from Sharma et al. (2015). Note that not all lakes in panel A have water temperature records.

there has been a superficially increasing trend of annual rainfall since the beginning of the 20th century, with reduced incidences of drought after 1970 (Nicholson, 1999). The inter-annual rainfall variability (coefficient of variation = 41%) at Mangochi weather station on the shores of Lake Malawi for the period 1960–2000 has been higher than any other location across Malawi (Ngongondo et al., 2011; Kumbuyo et al., 2014). This weather station is one of two stations across the whole country that have had significant declining trends in annual rainfall over the same period. The effect of this is evident in the water levels of Lake Malawi, which have dropped since a high in 1980 (Kumambala and Ervine, 2010; Vollmer et al., 2005). Similar decreasing trends in rainfall have been reported for Lakes Chad (Zilefac, 2010), Kariba (Ndebele-Murisa et al., 2011), Chilwa (Njaya et al., 2011), Albert, Edward, and Kyoga (Nsubuga et al., 2014; USAID, 2013). Unlike these lakes, rainfall around Lake Wamala has been increasing since 1950 and has been above the long-term average (1180 mm) since 1995, except in 2005 and 2008 (Natugonza et al., 2016).

Abiotic responses of lakes to climate variability and change.

Water balance, lake levels, and surface area

Most of the larger natural lakes in Africa gain most of their water through direct rainfall on their surface, and lose similar quantities through evaporation (Bootsma and Hecky, 2003). This means that temperature and rainfall are important in regulating the water balance of these water bodies, and fluctuations in either variable can significantly change their water levels and surface area. For instance, the average depth of Lake Chad decreased from about 7 m to 1.5 m, resulting in a >90% decrease in the lake surface area since the 1960s, with climate variability and change accounting for 83% of the decrease (Zilefac, 2010). The mean depth of Lake Chilwa has fluctuated between 0 and 12 m between 1960 and 2000, depending on temperature and rainfall, and the

lake has periodically dried up every 10–20 years (Njaya et al., 2011), while that of Lake Naivasha has decreased by about 4 m between 1965 and 2001, although part of the decline is attributed to withdrawal of water for human activities (Mekonnen et al., 2012).

The impact of climate variability and change on water levels of Lakes Chad, Chilwa, and Naivasha is exacerbated by withdrawal of water for irrigation, forest degradation, conversion of wetlands for rice cultivation, and cultivation up to the edge of the lake that increase siltation (Njaya et al., 2011; Zilefac, 2010; Mekonnen et al., 2012). Unlike Lakes Chilwa, Chad, and Naivasha, there is no withdrawal of water for either irrigation or urban use from Lake Wamala, but the mean depth of the lake has continued to decrease since 2000 even when rainfall, which accounts for ~80% of the total water input, has been above the long-term average (Natugonza et al., 2016). This is suggestive of a change in the lake's hydrological cycle, where rainfall is no longer sufficient to maintain normal lake levels because evaporative losses resulting from an increased temperature (Fig. 2) now exceed inflow. This may also apply in large and deep lakes where lake water levels have continued to decrease despite an upward trend in rainfall (Table 2).

Fluctuations in water levels with rainfall have also been observed in large lakes although they are less pronounced compared to small shallow lakes and especially endorheic lakes like Chad and Chilwa. The level of Lake Victoria, for instance, rose by about 2 m in 1961–1962 but has since been decreasing with at least 50% of the decline attributable to climate variability and change, and the remainder to excessive discharges for hydroelectric power generation (Awange et al., 2008; Swenson and Wahr, 2009). Similarly, the water level of Lake Kariba decreased by a large magnitude between 1984 and 1996, concurring with an upward shift in temperature and evaporation and a drop in annual rainfall (Ndebele-Murisa et al., 2011). Other researchers, however, claim that the lake-level fluctuation in Lake Kariba is largely influenced by activities at the dam (Marshall, 2012). Unlike Lakes Victoria and Kariba, Lakes Tanganyika, Malawi, and Rukwa are not regulated for

Table 2
Summary of reported trends in climate variables, and lake water levels of African major lake ecosystems.

Lakes	Climate variables and lake water level				
	Air temperature	Water temperature	Wind speed	Rainfall	Lake water level
Albert	Increasing	Increasing		Decreasing	Declining
Edward	Increasing	Increasing		Decreasing	Declining
Kyoga	Increasing			Decreasing	Declining
Kivu	Increasing	Increasing			
Tanganyika	Increasing	Increasing	Decreasing	Increasing	Declining
Malawi	Increasing	Increasing	Decreasing	Variable but declining	Declining
Victoria	Increasing	Increasing	Decreased after 2000	Variable but declining	Declining
Kariba	Increasing	Increasing		Variable but declining	Fluctuates with rainfall
Chilwa	Increasing	Increasing		Variable but declining	Fluctuates with rainfall
Wamala	Increasing		Increasing	Increasing	Declining
Chad	Increasing	Increasing		Variable but declining	Declining
Rukwa	Increasing	Increasing		Mild decreasing trend	Sensitive to rainfall
Naivasha				Decreasing	Declining

hydropower production but have also experienced similar decline in lake water levels, associated with climate variability (Nicholson, 1999; Kumambala and Irvine, 2010). Although water regulatory activities at the dams may significantly affect water levels, climate variability and change have played a major role, especially during the last three decades of the 20th century.

Nutrient loading and recycling

Nutrients are one of the major factors that drive ecosystem changes in inland waters through their influence on primary and secondary productivity. The combined effect of increasing temperature and decreasing wind speed is to increase density stratification and enhance the stability of the water column (Verburg and Hecky, 2009). Consequently, vertical mixing is greatly diminished and thereby limiting nutrient fluxes to the phototrophic zone resulting in declining productivity (O'Reilly et al., 2003; Verburg et al., 2003; Verburg and Hecky, 2009).

However, the implication of increasing temperature for density stratification and stability of the water column is not readily apparent for Lakes Victoria and Kariba. Lakes Victoria and Kariba are shallow lakes compared to Tanganyika and Malawi, and therefore the effects of density stratification are expected to be less pronounced compared to the deep lakes. Also, because Lake Victoria is close to the equator, the temperature gradient between surface and bottom waters is small, resulting into cooling-induced mixing, as a result of high evaporation rates, to extend to deep depths (MacIntyre et al., 2014). After the breakdown of seasonal stratification, which is enhanced by the offshore flow of cooler water produced in the shallow regions (Talling, 1966), nutrients are quickly replenished in the water column. Such events could explain the rapid nutrient enrichment of Lake Victoria, where a reduction in the volume of the mixed layer and increased anoxia in the hypolimnion that occurred during 1970s concurrent with climate warming and low wind speed, allowed mobilization of previously deposited sedimentary phosphorus and increased rates of primary production (Hecky et al., 2010).

Some researchers, however, have suggested that eutrophication in Lake Victoria was triggered by introduction of Nile perch, *Lates niloticus* (Linnaeus, 1758), increased surface runoff, and atmospheric input of phosphorus (Scheren et al., 2000; Tamatamah et al., 2005; Kolding et al., 2008). Whereas these causes are fairly substantiated, they are weakened by the timing of events, where Nile perch became well established in the lake in 1980s, while land degradation started back in mid-20th century (Hecky, 1993; Verschuren et al., 2002). The signs of eutrophication became manifest at the beginning of 1970s before the upsurge of the Nile perch, and was concurrent with the period of warming and low wind stress (Hecky et al., 2010). This is also consistent with the diatom paleolimnologic evidence (Stager et al., 2009).

Comparative information from small and shallow lakes, such as Chilwa, Chad, and Rukwa, are sparse. However, available data show that between 1998 and 2013, Lake Wamala shifted in status from a mesotrophic state to hypertrophic state (NaFIRRI, 2014), concurrent with 0.65 °C increase in temperature, increased surface run off because of higher rainfall than the long-term average, and an upward trend in wind speed (Natugonza et al., 2016). The mean conductivity of the lake increased from 160 to 380 $\mu\text{S cm}^{-1}$, total phosphorus (TP) from 137 to 303 $\mu\text{g L}^{-1}$, nitrate nitrogen ($\text{NO}_3\text{-N}$) from 11 to 32 $\mu\text{g L}^{-1}$, and soluble reactive silicon (SRSi) from 1960 to 6450 $\mu\text{g L}^{-1}$, while water transparency remained low (Secchi depth < 0.7 m) because water turbidity (~20 NTU), which is also linked to wind stress, was high (NaFIRRI, unpublished data). Increased rainfall, coupled with cultivation of the near shore wetland and use of organic fertilizers by riparian communities to diversify the single declining fishery livelihood (Musunguzi et al., 2015), could have accelerated allochthonous fluvial nutrient input from the surrounding agricultural catchment. The increase in concentration of some nutrients, especially phosphorus, however, can also be attributed to the declining lake water level that exposes the sediment-bound phosphorus from which, under low dissolved oxygen concentrations during certain seasons of year, phosphorus is released into soluble forms (Seitzinger, 1988).

Water quality

The changes in temperature and wind speed, and their associated impacts on circulation, internal wave motions, and evaporation rates, are also reflected in water quality status. The high density differentials in the water column increase the intensity and duration of deoxygenation (MacIntyre, 2012). This, however, has only become more apparent in the deep rift valley lakes, e.g. Tanganyika (O'Reilly et al., 2003; Verburg et al., 2003; Verburg & Hecky, 2003), Malawi (Vollmer et al., 2005), Albert (Lehman, 1998), and Kivu (Lorke et al., 2004), compared to relatively shallow lakes such as Victoria and Kariba. In Lake Tanganyika, for example, the stability of the lake, measured as work required to mix the water column to uniform density, increased by 97% between 1913 and 2003, while the depth of the oxygenated zone, an indicator for reduced mixing, showed a significant shallowing trend since 1939 (O'Reilly et al., 2003). This, however, has not happened in Lakes Victoria and Kariba, which further attests that the effects of climate change are not symmetrical across the lakes (Butcher et al., 2015; Kraemer et al., 2015a).

Changes in stratification and mixing dynamics of lakes induced by climate change, and their effect on water quality, in tropical Africa are influenced by the lake's geological setting particularly as it influences their depth, temperature gradient between surface and bottom waters, evaporation rates, and overall cooling (Kraemer et al., 2015a). Around the African Great Lakes, decadal scale climate variability is induced by

the El Niño Southern Oscillation (ENSO) (depending on the latitudinal position of the Inter Tropical Convergence Zone, ITCZ), and the rates of warming over the Indian Ocean (MacIntyre, 2012; Loiselle et al., 2014). Thus, high solar insolation, air temperatures, net long wave radiation, wind speeds, and lower relative humidity tend to be greatest during La Niña years. These changes, especially for lakes near the equator, such as Lake Victoria, can occasionally result in greater cooling-induced mixing, thereby alleviating the incidences of prolonged anoxia.

The water temperature of Lake Victoria increased by about 0.7 °C between 2000 and 2008 (Sitoki et al., 2010). Theoretically, this increase in temperature was expected, as was the case for neighboring Great Lakes, such as Tanganyika and Malawi, to stabilize the water column, restrict nutrient fluxes, and enhance anoxia (Verburg et al., 2003; Vollmer et al., 2005). On the contrary, the warming of surface waters coincided with reduction in thermal discontinuities, and a general improvement in water quality (improved dissolved oxygen concentrations and improved water transparency) (Sitoki et al., 2010; Marshall et al., 2013). These data give an implication that water quality of some African lakes would improve with climate warming and, therefore, lessen the threat of climate change to fisheries production. This, however, only has to be taken cautiously as more data become available because such changes do not preclude the fact that low wind stress, especially when the Indian Ocean Dipole is positive, and a rise in temperature over the Indian Ocean can deepen stratification and anoxia (MacIntyre, 2012).

During 1970s and 1980s, a shift toward higher temperature in Lake Victoria was accompanied by doubling of phosphorous concentration, a fivefold increase in chlorophyll *a* concentration, and a reduction in water transparency (Hecky et al., 2010). Currently, a positive decadal (2002–2011) correlation between water temperature and chlorophyll *a* concentration has been observed in the central and southern portions of Lake Victoria (Loiselle et al., 2014). This suggests that some sections of the lake might be moving toward a higher trophic status with climate warming. The reduction in density stratification and a general improvement of water quality (Sitoki et al., 2010; Marshall et al., 2013) could only have been a result of increase in wind speed after 1990s, low relative humidity, more La Niña years (characterized by low rainfall and continuous decline of lake water level), cooling-induced mixing that extends to high depths, and thermocline tilting, all of which have potential for alleviation of anoxia (MacIntyre, 2012). This, also, applies to Lake Kariba, and the current instability of the seasonal thermocline (Mahere et al., 2014) cannot disqualify the fact that Lake Kariba is highly vulnerable to stratification and deoxygenation (Ndebele-Murisa et al., 2012), considering the current trend of water temperature (Fig. 2).

Biotic responses to changes in climate and lake physicochemical attributes

Algal biomass and primary productivity

In the deep meromictic lake, the stability of the water column that is associated with climate variability and change is expected to result into

less nutrient transport from the permanently anoxic hypolimnion into the upper seasonally mixed phototrophic zone. In consequence, primary production would be greatly altered, with the composition of phytoplankton shifting to species that can readily persist or adapt to reduced nutrient conditions. This has become evident in all deep lakes in Africa but also a few shallow lakes (Table 3). In Lake Tanganyika, this led to a decline in algal abundance (Verburg et al., 2003) and fish production (O'Reilly et al., 2003). A similar declining trend in phytoplankton productivity in relation to increasing temperature has been reported for Lakes Malawi (Guildford et al., 2007), Nkuluba (Saulnier-Talbot et al., 2014), and Kariba (Ndebele-Murisa et al., 2012). In Lake Kariba, however, the decline in phytoplankton and primary productivity by 95% and 50%, respectively, (Ndebele-Murisa et al., 2012), concurrent with a 1.9 °C rise in temperature and a 50% reduction in the depth of the euphotic zone, is still debatable as new evidence suggests that the depth of upper mixed layer has increased despite climate warming (Mahere et al., 2014).

In contrast to the deep lakes discussed above and a few other lakes that have likely suffered declines in nutrients and primary productivity, primary productivity in Lake Victoria has increased and is now light limited rather than nutrient limited because of self-shading by high phytoplankton biomasses (Silsbe et al., 2006). Unlike other deep African Great Lakes whose primary productivity decreased with climate warming, Lake Victoria registered a twofold increase in primary production between 1960s and 1990s, concurrent with a twofold increase in TP (Hecky, 1993; Mugidde, 1993). Consequently, phytoplankton biomass increased, but the composition shifted from dominance of diatoms to blue green algae (cyanobacteria), which caused massive algal blooms in some lake embayments, because blue green algae could fix atmospheric nitrogen and were not nitrogen-limited (Mugidde, 1993). The composition of the remaining diatoms shifted from the large *Aulocoseira* spp. to small thinly silicified forms, such as *Nitzschia* spp., which can grow at lower concentrations of silicon (Stager et al., 2009; Hecky et al., 2010).

The increase in wind strength in Lake Victoria, coupled with reduced thermal discontinuities (Sitoki et al., 2010; Marshall et al., 2013), might have changed the diurnal dynamics, e.g., reduced shallower diurnal stratification, and increased mixing intensity, and such changes can favor more buoyant phytoplankton taxa (Reynolds, 2005). Cyanobacteria, in this case, are favored because of their buoyancy and capacity to migrate vertically to seek light or nutrients, and their ability to fix atmospheric nitrogen (Mugidde, 1993; Gikuma-Njuru and Hecky, 2005). Climate warming, as manifested by the continuous rise in water temperature (Fig. 2b) would exacerbate the proliferation of cyanobacteria and enhance algal blooms (Paerl and Huisman, 2009), and this is consistent with the changes in Lake Victoria (Mugidde, 2001).

The increase in cyanobacteria, also, has major implications for the quality of water and aquatic organisms as some cyanobacteria produce toxins, which can cause serious animal and human health problems such as liver, digestive, and skin diseases, neurological impairment, and death (Van Dolah, 2000; Landsberg, 2002). The levels of these toxins have been observed to exceed those recommended by the

Table 3

Summary of reported trends in water quality parameters for major African lake ecosystems. PB is phytoplankton biomass and PP is primary productivity.

Lakes	Physicochemical parameters, algae, and invertebrate productivity			
	Nutrients	Water quality and stability	PB and PP	Invertebrate productivity
Albert		Enhanced stratification and anoxia		
Kivu		Enhanced stratification and anoxia	Declined	
Tanganyika	Restricted nutrient fluxes	Enhanced stratification and anoxia	PP decreased	
Malawi	Restricted nutrient fluxes	Enhanced stratification and anoxia	PP decreased	
Victoria	Increased	Reduced stratification and anoxia	Composition changed	Declined
Kariba	Increased conductivity	Upward shift in thermocline and reduction of euphotic depth, but this is still questioned	Declined	Decline in zooplankton diversity and abundance
Chilwa				Declined
Wamala	Increased		Increased PB	Decreased

World Health Organization in some lakes associated with warming climate (Poste et al., 2011). Therefore, environmental effects of global warming should be incorporated in water quality management measures to advise consumers of water and fish as algal communities shift to types that produce toxins following nutrient enrichment and climate change.

Comparative information from small and shallow lakes shows a situation that is consistent with the observations from Lake Victoria. Between 1998 and 2013, a total of 40 phytoplankton genera were recorded in Lake Wamala but, out of these, only 21 genera were recorded during 1999–2000 period, while 35 genera were recorded during 2011–2013 period (NaFIRRI unpublished data). Four of the new genera that emerged belonged to cyanobacteria. The overall algal biovolume increased by >70%, but unlike Lake Victoria, the phytoplankton composition slightly changed from the dominance of cyanobacteria during the 1999–2000 period to diatoms during 2011–2013 period. Among the diatoms, the genus *Aulocoseira* was never observed in Lake Wamala during 1999–2000 period but emerged during 2011–2013. This can be attributed to the threefold increase in SRSi (NaFIRRI unpublished data), as a result of increased rainfall and surface runoff from the agriculture-dominated catchment. In addition, the dominance of diatoms over cyanobacteria can be accounted for by the intolerance of the latter to poor light conditions arising from complete mixing, and resulting high turbidity due to increased wind strength (Natugonza et al., 2016). Because Lake Wamala is a small shallow lake (mean depth = 4.5 m), frequent mixing could also account for the low primary production ($806 \pm 258 \text{ mg O}_2\text{m}^{-2} \text{ h}^{-1}$) countering nutrient enrichment (NaFIRRI, 2014) because of light limitation due to high mineral turbidity.

Invertebrate productivity

The changes in physical and chemical conditions associated with climate variability and change can impose stressful conditions that only certain invertebrate types are able to tolerate. The warming of Lake Kariba, for instance, was accompanied by a decline in zooplankton productivity, especially for the large calanoid copepods and cladocerans (Magadza, 2011). This, however, observation was challenged on grounds that the decline of the two zooplankton groups was a result of size-selective predation by the introduced Lake Tanganyika planktivorous sardine, *Limnothrissa miodon* (Boulenger, 1906), called Kapenta locally, because the zooplankton declined around 1970 when Kapenta, became well established (Marshall, 2013). Analogously, this would imply that the increase in abundance of the silver cyprinid, *Rastrineobola argentea* (Pellegrin, 1904) (locally dagaa), another size-selective planktivorous fish, in Lake Victoria caused a decline in large calanoid copepods and cladocerans, and allowed small cyclopoid copepods to flourish. However, this notion was earlier dismissed on grounds that increased eutrophication and the decrease in silica concentration, which were preceded by climate warming, resulted in a shift in predominance from diatoms, the preferred diet for herbivorous cladocerans and calanoids, to the less desired cyanophytes (Wanink et al., 2002). The impact of kapenta on zooplankton in Lake Kariba (Marshall, 2013), therefore, could have been overstated, especially when the zooplankton types decreased with undoubted warming of the lake, given a similar change as in Lake Victoria.

In Lake Chilwa, the number of invertebrate species decreased from 45 species, when the lake volume was high, to only one species during the drying up phase (Njaya et al., 2011). When conditions improved and water levels increased, smaller zooplankton with shorter hatching and generation turnover time, e.g., rotifers recovered first followed by crustaceans with *Mesocyclop* spp. appearing first and feeding on the growing rotifer populations. A similar situation was observed in Lake Wamala. Although rotifers declined from about 1100 to 60 individuals/m² between years 1999 and 2013, they remained two times and six times higher than the cladocerans and copepods, respectively

(NaFIRRI, 2014). The decrease can be attributed to the shrinking of the lake, with an exacerbation of eutrophication, which are all known to lengthen the spawning time of most zooplankton, and affect their reproductive success (Yildiz et al., 2007). The observation in both shallow lakes supports the prediction that climate warming can shift organisms to smaller opportunist species with short reproductive turnover rates (FAO, 2010).

The change in zooplankton communities have also been accompanied by that in benthic macroinvertebrates. In Lake Victoria, both eutrophication and climate warming during the 1980s enhanced anoxia and was accompanied by changes in the composition of benthic invertebrates to the dominance of the midge larvae, such as *Chironomus* spp. and *Chaoborus* spp., although at reduced densities (Sekiranda et al., 2004), and this is consistent with changes in benthic community in other shallow lakes within the same basin such as Lake Wamala (NaFIRRI, 2014). Before the intensification of climate warming in 1970s, the lake fly larvae in Lake Victoria were estimated at 3000–4000 individuals/m² (75% of them were *Chaoborus* spp.) (MacDonald, 1953), but most recent data give densities at 89–286 individuals/m² in Hannington Bay, 136–2262 individuals/m² in Fielding Bay, and 72–1629 individuals/m² in Murchison Bay (Sekiranda et al., 2004). Although the densities of these organisms have decreased, *Chaoborus* spp. are still one of the dominant benthic invertebrates in both Lakes Victoria and Wamala because they can tolerate low oxygen conditions that characterize the hypolimnion during episodic stratified conditions (Lehman et al., 1994; Verschuren et al., 2002).

Life history of fish, composition, and catches

The influence of climate warming on water levels, stratification, loading and recycling of nutrients, and dissolved oxygen in lakes directly affects the physiology, growth, and reproduction of fish, whereby fish in warmer waters are likely to become smaller and reach maturity at a smaller size than those in cool waters. These attributes are well documented in marine ecosystems (Portner et al., 2001; Dembski et al., 2006; Daufresne et al., 2009; Donelson et al., 2010; Jeppesen et al., 2010), but tropical lakes could also be vulnerable. Decreasing water levels, either in shallow lakes or shallow areas of deep lakes, have been linked to disappearance of vegetation and interference with fish reproduction through loss of breeding areas (Hickley et al., 2004; Njaya et al., 2011; Luxereau et al., 2012). In Lake Wamala, decrease in total length and size at first maturity of Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), has been recorded during prolonged drought, with increase in the growth parameters during the wet periods (Natugonza et al., 2015). Because these responses are often confounded by other factors, notably fishing, the exact impacts of climate change on life history and composition of fish are still less appreciated and understood.

In Lake Tanganyika, it was suggested that a 20% decrease in algal productivity due to climate warming contributed to a 30% reduction in fish production (O'Reilly et al., 2003). Similarly, the decline in catch per unit effort of both kapenta and inshore fishes in Lake Kariba between 1986 and 1997 was attributed to increase in temperature, a reduction in rainfall, declining lake water levels, and a reduction in the depth of the euphotic zone with increased incidences of prolonged deoxygenation (Ndebele-Murisa et al., 2011). These explanations, however, have faced criticism because the effects of fishery practices, including the eminent threat from overexploitation, were not accounted for (Sarvala et al., 2006; Marshall, 2012). Such disputes arise because isolating the possible role of complex interaction between climate change and fishing requires a continuous record, at least with annual resolution, of physical mixing dynamics and primary productivity, which can be compared with the changes in fish community. Unfortunately, such data do not exist for most of the lakes that have warmed due to climate warming. High-resolution palaeolimnological studies, therefore, are required to reconstruct a temporal record of primary productivity and

Table 4
Reported changes in fishes and livelihoods that may be climate related in major African lake ecosystems.

Lakes	Impact on fishes and livelihoods				
	Life history of fish	Composition	Catches	Parasites and weeds	Livelihoods
Albert		Shifted to small pelagic species	Increased		
Tanganyika			Decreased		Affected
Malawi			Decreased		Affected
Victoria	Affected	Shifted to small pelagic species	Decreased	Establishment of water hyacinth	Affected forcing fishers to use undersized gear
Kariba	Kapenta affected		Decreased		
Chilwa	Loss of breeding areas	Changed	Variable		Loss of income
Wamala	Affected	changed	Decreased	Shift in parasite host	Reduced income
Chad	Loss of breeding areas	Changed	Decreased		Affected
Naivasha	Reduced size at maturity	Changed	Decreased		

water chemistry, which can be related to the changes in fish productivity, whose data are readily available for most lakes.

Although most studies have not shown a conclusive cause–effect relationship between climate change and fishery productivity, past events in some lakes do show a link between climate extremes (droughts and floods) and fish yield (Table 4). The shrinking of Lake Chad by about 90% of its size, following frequent droughts between 1970 and 1990, was accompanied by a decrease in the number of fish species from 41 to 16 species (Lévéque, 1995), and catches from 220,000 t to 100,000 t (FAO, 2012). In Lakes Wamala and Chilwa, fish production has fluctuated between 300 and 7100 t and 0–24,000 t per year, respectively, depending on rainfall and water level (Njaya et al., 2011; Natugonza et al., 2015). The fisheries of both lakes, however, are able to recover from remnant populations that survive in rivers and pools in wetlands during prolonged drought. Normally, *Clarias* spp. are the first to recover, followed by *Barbus* spp. and then *Oreochromis* spp. (Njaya et al., 2011).

These changes highlight the need to understand differences in the ability of fish species to survive under changing climatic conditions and the importance of refugia in conserving fish diversity during periods of desiccation. More tolerant fishes, such as *Clarias* spp. and *Protopterus* spp., which can tolerate low lake levels and anoxic conditions, and can survive in wetlands (Greenwood, 1986; Van der Waal, 1998), are expected to persist while the less tolerant ones may disappear. An example is silversides, *Alestes baremose* (Joannis, 1835), which was an important component of the fisheries of the Lake Chad basin in 1970s but disappeared with the shrinking of the lake and was replaced by the *Clarias* spp. (FAO, 2012), which are well adapted to the new swampland conditions. The *Clarias* spp. can breathe atmospheric air, through auxiliary gills, under hypoxic conditions, and when the lake starts drying, *Clarias* spp. and other fishes that are able to persist or adjust their life history to extreme anoxia and reduced lake levels, have a better chance of surviving. A single management strategy, therefore, may not be ideal for fishes that have different capabilities for adapting to changing climatic conditions. Researchers will need to identify different management mechanisms that suit fishes with different adaptation capabilities in order to enhance the resilience of all fisheries under changing climatic conditions.

Climate warming is expected to shift fisheries to small opportunistic species that can rapidly exploit the changed conditions (FAO, 2010). This shift in composition of fish communities to those that are tolerant to the changed conditions would result in gains and losses of some fish species, and changes in fish community structure. This has begun to manifest in some African lakes. The total fish production in Lake Malawi, for instance, has increased since 2003 due to increasing contribution of small zooplanktivorous fish such as Lake Malawi sardine, *Engraulicypris sardella* (Günther, 1868), and pelagic haplochromines (Jamu et al., 2011). Also, the stocks of dagaa in Lakes Victoria and Kyoga, and ecologically similar *Neobola bredoi* (Poll, 1945) and *Brycinus nurse* (Rüppell, 1832) in Lake Albert, have increased to contribute 40–80% in the total catches (Fig. 3). Although these changes have occurred in concurrence with climate warming, which is now apparent in all

African lakes, there is still need for meta-analyses to separate the effects of other factors such as changes in fishing gear, market demands, and overfishing of target species.

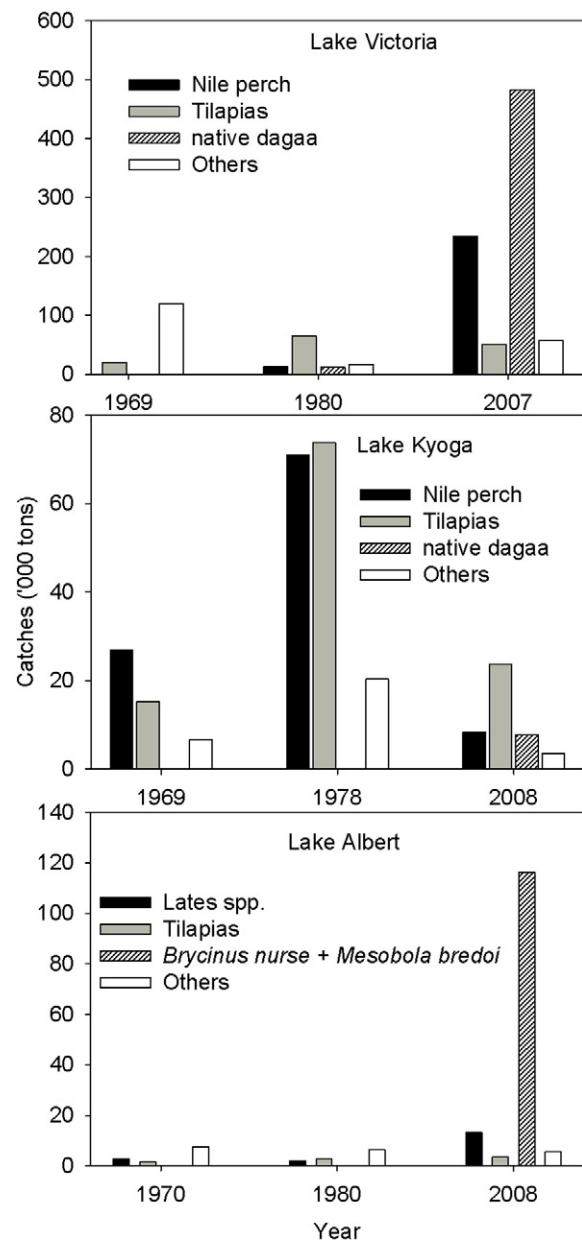


Fig. 3. Contribution of fish species to total landed catches on Lakes Victoria, Kyoga, and Albert (Uganda) during the different climatic periods (i.e., 1970s, 1980s, and 2000s). Data from MAAIF (2012). The shift to small pelagic species occurred from 1980s onward.

Parasite–vector–host interactions

Parasite transmission depends on host condition, the presence of intermediate hosts necessary for the parasite life cycle, water quality, and temperature (Marcogliese, 2001; Cochrane et al., 2009). Because changing water quality, and the resultant osmotic stress can weaken the immune system of fish, there is high risk that increasing water temperature can increase the susceptibility of fish to diseases, particularly vector-borne fish diseases (Marcogliese, 2008). This has been proven in temperate waters, where warming waters in the Upper Colorado River, Colorado, were accompanied by increase in gill ectoparasites in juvenile rainbow trout and brown trout (Schisler et al., 1999). In a similar, but laboratory based experiment, plerocercoid infestation rate in sticklebacks increased by 67% when water temperature was raised by 5 °C (Macnab and Barber, 2012). Similar incidences of increased parasite prevalence with increased temperature could also happen in tropical systems.

Although there are limited documented examples of climate change-induced parasite and diseases in African lakes, available data from Lake Wamala show that the prevalence of helminth parasites, especially *Contracaecum* spp., decreased from 15% to 0% in Nile tilapia, but increased from 10% to 82% in the North African catfish, *Clarias gariepinus* (Burchell, 1822), between 1999–2000 and 2011–2013 periods (NaFIRRI, 2014). Interestingly, during the period 2011–2013, 11 new helminth parasites of genera *Eustrongylide*, *Amplicaecum*, *Procamallanus*, *Paracamallanus*, *Capillarias*, *Monobothrioides*, *Polyoncobothrium*, *Proteocephalus*, *Clinostomum*, *Posthodiplostomum*, and *Zoognoides*, were recorded on the African catfish. The change in the host coincided with both increase in temperature and decrease in lake water levels (Natugonza et al., 2016), and a shift in fish abundance from Nile tilapia to the more environmentally resilient North African catfish that can survive in the adjacent wetlands (Natugonza et al., 2015). Most of these helminth parasites are zoonotic and pose a health threat to the riparian fish consumers, which is yet to be documented and necessary measures taken. Notwithstanding the lack of sufficient data to allow accurate and site-specific predictions of the impacts of global climate change on parasite and disease outbreaks, the observed thermal effects on parasites, fishes, and water quality suggest that continued climate warming will increase the virulence and the transmission of some parasites and decrease it for others (Pojmanska et al., 1980; Ficke et al., 2007; Karvonen et al., 2010). The implications of this are global in nature and will involve both wild and cultured fish species.

Invasive aquatic weeds

In Africa, the aquatic weed that has had most devastating ecological and economic impact is the water hyacinth (*Eichhornia crassipes*). The water hyacinth was first seen in Lake Victoria in the late 1980s, and by mid-1990s, the plant had covered about c. 18,000 ha (Albright et al., 2004). However, the water hyacinth that was introduced into the Lake Victoria catchment as an ornamental pond plant in the 20th century only exploded after 1980s, a period where both climate warming and eutrophication became manifest (Williams et al., 2005; Hecky et al., 2010). The weed mats later collapsed in the late 1990s after the introduction of a weevil, and the plant is now no more than a localized nuisance, although it is feared that continued nutrient loading (especially phosphorus), as well as increased land use and land cover change could lead to resurgence of this weed (Williams et al., 2005) especially in river mouths.

However, there is still disagreement on the main cause of the collapse of the weed. All researchers agree that climate perturbation and biological control led to collapse of the weed but disagree on what played a dominant role. Some suggest that the collapse of water hyacinth was mainly due to the 1997/1998 El Niño, when increased cloud cover reduced light intensity and the growth rate of photosynthesizing

plant, and that heavy storms physically destroyed the plants by dislodging their mats and enhanced their natural mortality (Williams et al., 2005, 2007). These views were opposed on grounds that the dislodging of weed mats by the El Niño in 1997/1998 helped distribute the weed over the entire lake, increasing the chances of contact with herbivorous weevil (*Neochetina* sp.) (Wilson et al., 2007). Considering the timing of water hyacinth explosion and sudden collapse of the weed, climate perturbation seems to have played a critical role, both in the proliferation and collapse, although the weevils weakened and enhanced collapse of the weed. Resurgence of the weed under a warming climate, therefore, cannot be ruled out, especially if the allochthonous input of nutrients from the heavily degraded catchment is not checked.

Human responses to changing lake ecosystems

Livelihoods

The impacts of climate variability and change on fisheries have affected the livelihoods of fishers and riparian communities. Extreme climatic events, besides endangering human life and destroying assets, such as fishing boats, fishing gear, and landing sites, have reduced income from fishing. Examples of such events are available from some African systems where extreme events have occurred. On Lake Chad, droughts have led to reduction in potable water and fish catches, increased cases of diarrhea, cholera, typhoid, and malnutrition in the Chad basin (Fortnam and Oguntola, 2004). Drying up of Lake Chilwa in 1996 led to loss of income of fishing communities worth at least US\$1,000,000 per year (Lunduka, 2013). Fishers from Lake Wamala reported low income from fishing during the floods, linked to the corresponding increase in fish catches, high fish supply, and reduced demand (Musunguzi et al., 2015). Conversely, low fish supply resulting from reduced catches during prolonged droughts on Lake Wamala lead to high demand for fish, increase in prices, which enables fishers to obtain high income. Such short-term benefits, however, can be counterproductive as the high profits are likely to promote excessive fishing effort in order to catch more fish than the lake can sustain. The exact economic implications of such climate events, however, remain unquantified.

Adaptation and mitigation strategies

Climate variability and change have forced fishers to adapt in order to sustain their livelihoods. In some cases, fishers have changed fishing gears and methods, migrated to less heavily exploited fisheries, or diversified out of fisheries to crops, livestock, and other income generating activities (Allison and Ellis, 2001; Badjeck et al., 2010; Musunguzi et al., 2015). Diversified fisher livelihoods better adapt to change, and therefore, fishers with diversified farming livelihood have better wellbeing than those without (Allison et al., 2007). For instance, the wealthiest fishers on Lake Chilwa were those who earned additional income by diversifying to farming (Phipps, 1973). On Lake Chad, fishers grow crops like sweet pepper on rich soils exposed by reduced water levels, and return to fishing when the lake-level rise (Sarch and Birkett, 2000; Luxereau et al., 2012). On Lake Chilwa, fishermen shift to swamps, streams, and lagoons, while others migrate to other lakes, such as Malombe, Malawi, and Chiuta, in response to reduced fish catches (Lunduka, 2013). These fishers develop other survival strategies such as gathering wild fruits and plants, hunting wild animals and birds, and cultivating rice, cotton, cassava, and vegetables in the riparian zones. On Lake Wamala, the annual income of fishers with diversified livelihoods (including crops and livestock) is about US\$3400 compared to US\$1400 for fishers who do fishing alone (Musunguzi et al., 2015).

Unguided diversification, both in and out of fisheries, has however been observed to lead to unsustainable practices that may adversely affect lake ecosystems. This has been observed on Lakes Wamala, Chad,

and Chilwa (Luxereau et al., 2012; Lunduka, 2013; Musinguzi et al., 2015). On these lakes, when fish yields decline during prolonged drought, some fishers adapt by increasing the time they spend on fishing, while others change fishing grounds, target species, landing sites, and types and number of fishing gear. Such practices can be counterproductive because they lead to overfishing and limit the long-term benefits from adaptation (Smit and Wandel, 2006; Cinner et al., 2011), and require regulation. Agriculture related strategies, such as grazing along the lake shores and cultivating on the edge of lake, contribute to degradation of water quality (from fertilizers and agrochemicals), critical habitats for aquatic invertebrates, and fish and, ultimately, a reduction in fish production (Junk et al., 2000; McGrath et al., 2007; Allison et al., 2007).

Although mitigation of effects of climate change by fishers may be inconsequential on the global scale, a shift from smoking fish using wood to other low cost and environmentally innocuous preservation methods, such as sun drying and salting, as well as planting trees and preserving the riparian wetlands can help in modulation of local climate change. These, also, can reduce the cumulative impacts from other stressors such as sedimentation. Limited effort, however, has been registered by African fishers or managers to mitigate the effects from climate change, at least on a local basis. The application of land-based mitigation measures, including mulching and planting trees, on shores of Lake Wamala is still trivial and would need to be scaled up to have a local impact (Musinguzi et al., 2015).

Adaptation and mitigation efforts are frequently constrained by the rapid population growth, which is highest in riparian areas of the African Great Lakes (Bootsma and Hecky, 2003), fewer opportunities for other work, lack of access to new and improved crop varieties, poor social services, and potentially more extreme weather conditions. Such is the case at Lakes Chilwa and Wamala, where adaptation is

limited by a lack of credit facilities, awareness, land availability, appropriate planting materials, inadequate law enforcement, lack of affordable irrigation facilities, and a high dependence on fishing (Njaya et al., 2011; Musinguzi et al., 2015).

Policy interventions

All over the world, optimally managed fisheries with abundant stocks are better able to adapt to climate variability and change compared to ones that are less efficiently managed (Cheung et al., 2008; Sumaila et al., 2011). Fisheries management institutions in Africa need to control and regulate human driven stressors, such as illegal gears and fishing effort, nutrient loading, land use change, pollution, and species introductions, which exacerbate the impacts of climate variability and change on fisheries. Auspiciously, there are existing international, regional, and national policies specific to climate variability and change, as well as other issues or sectors, such as fisheries, agriculture, and biodiversity that can be applied to enhance the resilience of fisheries resources. Some of these policies include those that aim at promoting efficient use of water, afforestation and reforestation, sustainable land use and agricultural practices, and protecting wetlands, river banks, and lake shores. Where these policies are not available, they should be developed and the development of new policies should incorporate climate information and management plans for climate resilient fishes and other aquatic organisms that persist, or adjust their life history characteristics in response to climatic conditions. As provided for the Lake Chad basin (FAO, 2012), for instance, the policies developed or implemented should focus on strengthening the resilience of fisheries resources to climate variability and change; increasing capacity of fishing communities to adapt through schemes that provide credit, technologies, and awareness to climate change; promoting positive

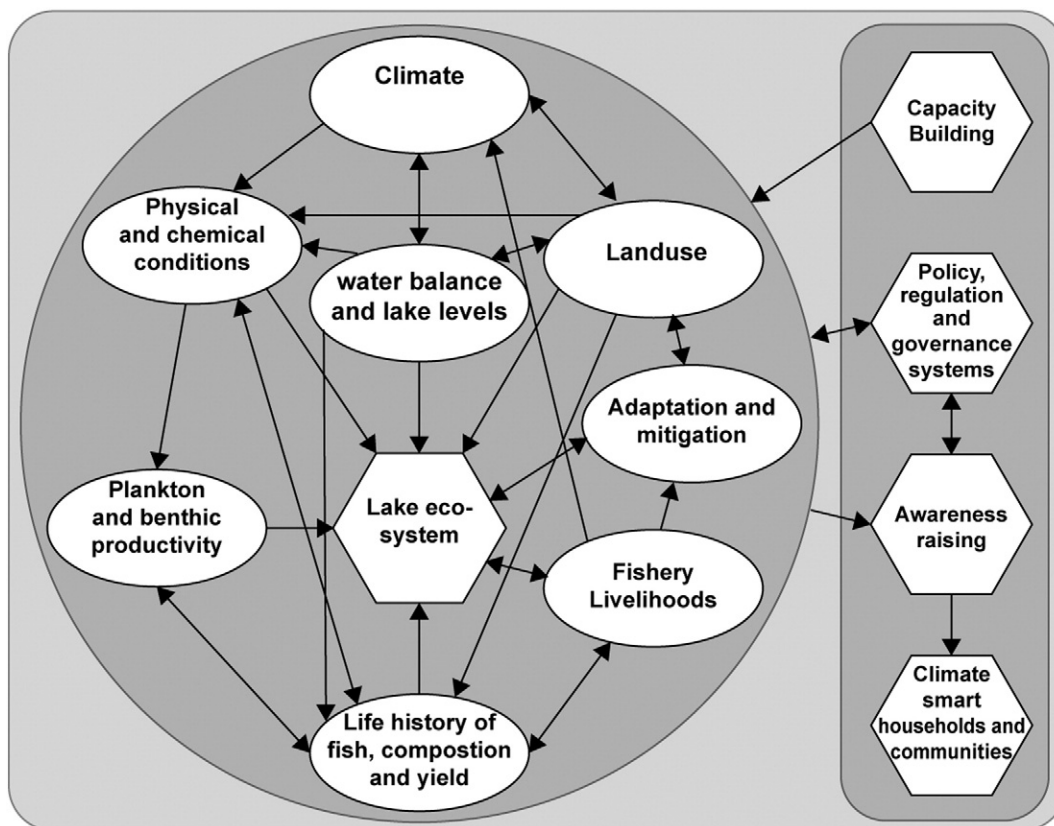


Fig. 4. A flow chart showing aspects of climate-smart development in fisheries. The chart describes complex linkages that require scientific data to untangle the role of cause–effect relationship between climate change and fisheries from other confounding factors. Knowledge from these scientific studies could be integrated into fisheries policy and management decisions for resilient households and communities.

adaptation strategies and discourage the negative ones; address constraints to adaptation and challenges that accompany adaptation efforts; and create linkages and improve capacity of institutions to address climate variability and change challenges.

Conclusions

Climate variability and change pose a threat to fisheries despite limited appreciation and knowledge on how this is influencing fishery productivity processes, fish yield, and livelihoods of fishery-dependent communities in inland aquatic systems in Africa. At present, knowledge on how climate is changing and how it is expected to change in future, and how this might impact tropical inland aquatic productivity, fisheries, and livelihood is still fragmented. This information is needed to guide policy for adaptation and mitigation to build resilience especially of poor fishery-dependent communities who have limited capacity to adapt. Nevertheless, this analysis has shown that climate warming is warming all major inland lakes in Africa, and environmental changes induced by warming have the potential to threaten fisheries, and livelihoods of fishery-dependent communities.

The responses to climate change vary among aquatic systems depending on location, morphometric characteristics (especially surface area and depth), and magnitude of changes in climate variables. For the African Great Lakes, the responses also depend on the rate of warming in the Indian Ocean, while those in the Lake Chad region on sea surface temperature anomalies over the Atlantic Ocean. The future variability in these oceans, associated with anthropogenic climate change, will affect the future climate system of African inland lakes. Lake depth, surface area, and magnitude of change in climate variables, especially temperature and wind speed, affect the sensitivity of lakes to climate variability and change because they determine the extent of stability and mixing in lakes, and thus can promote or limit changes in lake mixing and exchange of nutrients. Continued warming will therefore force lakes to shift between states, e.g., from less extensive anoxic conditions to more extensive anoxic conditions or from less eutrophic to more eutrophic conditions, with consequences on productivity processes and fish yield. Such changes have implications for fishery-dependent livelihoods through shifts in distribution and loss of important food fish species, decline in production of preferred target species, and reduced diversity of rural livelihoods and displacement of fishing communities.

Given that the majority of the African lakes are warming with no possibility of reversing the trends in the next few decades, fishers should be prepared to adapt to the influence of climate variability and change. Fisheries research and management institutions will therefore need to generate the knowledge required and to take actions to guide adaptation (Fig. 4). At community level, the capacity to address climate variability and change will depend on socioeconomic conditions, institutional, and policy frameworks. A wide number of livelihood diversification mechanisms are possible, including diversification inside and outside of fisheries, depending on the costs and returns. However, some adaptation strategies, such as cultivation and grazing in the riparian wetlands during drought periods are unsustainable and may negatively impact the lake ecosystem. This review has provided insight on how the increasing variability and change in climate is affecting fisheries productivity processes of different inland aquatic systems in Africa. More information is required to advance this knowledge and identify climate-smart fisheries and adaptation strategies to guide the development of policies that integrate climate information in management of fisheries to building resilience in affected communities.

Acknowledgments

Research on climate variability and change at NaFIRRI was initiated with support from the Rockefeller Foundation to whom we are very grateful. This review has been done as part of the Hydroclimate for

Lake Victoria (HyVIC) project, which is a regional project of the Global Energy and Water Cycles Exchange (GEWEX) Hydro-climatology Panel (GHP). We are grateful to Prof. Robert Hecky and Prof. Brian Marshall for commenting on the original draft of this manuscript.

References

- Albright, T.P., Moorhouse, T.G., McNabb, T.J., 2004. The rise and fall of water hyacinth in Lake Victoria and the Kagera river basin, 1989–2001. *J. Aquat. Plant Manag.* 42, 73–84.
- Allison, E.H., Perry, A.L., Badjeck, M.C., Adger, W.N., Brown, K., Conway, D., Halls, A.S., Pilling, G.M., Reynolds, J.D., Andrew, Neil L., Dulvy, N.K., 2009. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish Fish.* 10, 173–196.
- Allison, E.H., Andrews, N.L., Oliver, J., 2007. Enhancing the resilience of inland fisheries and aquaculture systems to climate change. *SAT J.* (4), 1 (e-journal: <http://www.icrisat.org/Journal/SpecialProject/sp15.pdf> accessed October 2011).
- Allison, E.H., Ellis, F., 2001. The livelihoods approach and management of small-scale fisheries. *Mar. Policy* 25, 377–388.
- Awange, J.L., Ogalo, L., Bae, K., Were, P., Omondi, P., Omute, P., Omullo, M., 2008. Falling Lake Victoria water levels: is climate a contributing factor? *Clim. Chang.* 89, 281–297.
- Badjeck, M.C., Allison, E.H., Halls, A.S., Dulvy, N.K., 2010. Impacts of climate variability and change on fishery-based livelihoods. *Mar. Policy* 34, 375–383.
- Bootsma, H.A., Hecky, R.E., 2003. A comparative introduction to the biology and limnology of the African Great Lakes. *J. Great Lakes Res.* 29, 3–18.
- Butcher, J.B., Nover, D., Johnson, T.E., Clark, C.M., 2015. Sensitivity of lake thermal and mixing dynamics to climate change. *Clim. Chang.* 129, 295–305.
- Cheung, W.W.L., Close, C., Lam, V.W.Y., Watson, R., Pauly, D., 2008. Application of macroecological theory to predict effects of climate change on global fisheries potential. *Mar. Ecol. Prog. Ser.* 365, 187–197.
- Cinner, J.E., Folke, C., Dawc, T., Hicks, C.C., 2011. Responding to change: using scenarios to understand how socioeconomic factors may influence amplifying or dampening exploitation feedbacks among Tanzanian fishers. *Glob. Environ. Chang.* 21, 7–12.
- Cochrane, K., De Young, C., Soto, D., Bahri, T., 2009. Climate change implications for fisheries and aquaculture: overview of current scientific knowledge. *FAO Fisheries and Aquaculture Technical Paper No.530*. FAO, Rome.
- Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci.* 106, 12788–12793.
- de Graaf, G., Garibaldi, L., 2014. The value of African fisheries. *FAO Fisheries and Aquaculture Circular*. No. 1093 FAO, Rome, p. 76.
- Dembski, S., Masson, G., Monnier, D., Wagner, P., Phan, J.C., 2006. Consequences of elevated temperatures on life history traits of an introduced fish, pumpkinseed *Lepomis gibbosus*. *J. Fish Biol.* 69, 331–346.
- Donelson, J.M., Munday, P.L., McCormick, M.I., Pankhurst, N.W., Pankhurst, P.M., 2010. Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. *Mar. Ecol. Prog. Ser.* 401, 233–243.
- FAO, 2012. Climate change implications for fishing communities in the Lake Chad basin. What have we learnt and what can we do better? *FAO/Lake Chad Basin Commission Workshop 18–20 November 2011, N'Djamena, Chad*. FAO Fisheries and Aquaculture proceedings 25, Rome.
- FAO, 2003. Management, co-management or no management? Major dilemmas in southern African freshwater fisheries. *FAO Fisheries technical paper No. 426/1*, FAO, Rome.
- FAO, 2009. The State of World Fisheries and Aquaculture (SOFIA, 2008). *FAO Fisheries and Aquaculture Department*. Food and Agriculture Organization of the UN, Rome.
- FAO, 2010. The State of Food Insecurity in the World. Addressing food insecurity in protracted areas. *FAO, Rome*, p. 62.
- Ficke, A.D., Myrick, C.A., Hansen, L.J., 2007. Potential impacts of global climate change on freshwater fisheries. *Rev. Fish Biol. Fish.* 17, 581–613.
- Foli, E., Makungwa, S., 2011. Enhancing Adaptation of Forests and People in Africa Development of Pilot Cases for Selected Forest Ecosystems in Ghana and Malawi. *Forestry Research Network of Sub-Saharan Africa (FORNESSA: Thematic Group on Climate Change)*, Vienna, p. 68.
- Fortnam, M.P., Oguntola, J.A., 2004. Lake Chad Basin, GIWA Regional Assessment 43. *University of Kalmar, Kalmar, Sweden*.
- Funk, C., Rowland, J., Eilerts, G., Adoum, A., White, L., 2012. A Climate Trend Analysis of Chad. *U.S. Geological Survey Fact Sheet 2012–3070*, p. 4.
- Gikuma-Njuru, P., Hecky, R.E., 2005. Nutrient concentrations in Nyanza Gulf, Lake Victoria, Kenya: light limits algal demand and abundance. *Hydrobiologia* 534, 131–140.
- Greenwood, P.H., 1986. The natural history of African lungfishes. *J. Morphol.* 1, 163–179.
- Guildford, S.J., Bootsma, H.A., Taylor, W.D., Hecky, R.E., 2007. High variability of phytoplankton photosynthesis in response to environmental forcing in oligotrophic Lake Malawi/Nyasa. *J. Great Lakes Res.* 33, 170–185.
- Hecky, R.E., 1993. Eutrophication of Lake Victoria. *Verh. Int. Ver. Theor. Angew. Limnol.* 25, 39–48.
- Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., Kling, G.W., 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. *Freshw. Biol.* 55, 19–42.
- Hickley, P., Muchiri, M., Boar, R., Britton, R., Adams, C., Gichuru, N., Harper, D., 2004. Habitat degradation and subsequent fishery collapse in Lakes Naivasha and Baringo, Kenya. *Ecohydrol. Hydrobiol.* 4, 503–517.
- Hulme, M., Doherty, R., Ngara, T., New, M., Lister, D., 2010. Africa climate change: 1900–2010. *Clim. Res.* 17, 145–168.
- IPCC, 2014. *Climate Change: The Physical science basis*. IPCC, p. WG1.

- Jamu, D., Banda, M., Njaya, F., Hecky, R.E., 2011. Challenges to sustainable management of the lakes of Malawi. *J. Great Lakes Res.* 37, 3–14.
- Jeppesen, E., Meerhoff, M., Holmgren, K., Gonza'lez-Bergonzoni, I., Teixeira-deMello, F., Declerck, S.A.J., De Meester, L., Søndergaard, M., Lauridsen, T.L., Bjerring, R., Conde-Porcuna, J.M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H.J., Liu, Z., Balayla, D., Lazzaro, X., 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia* 646, 73–90.
- Junk, W.J., Ohly, J.J., Piedade, M.T., Soares, M.G.M., 2000. Actual use and options for the sustainable management of the Central Amazonian floodplain: discussion and conclusions. In: Junk, W.J., Ohly, J.J., Piedade, M.T.F., Soares, M.G.M. (Eds.), *The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management*. Backhuys Publishers, Leiden, pp. 533–580.
- Karvonen, A., Rintamäki, P., Jokela, J., Valtonen, E.T., 2010. Increasing water temperature and disease risks in aquatic systems: climate change increases the risk of some, but not all, diseases. *Int. J. Parasitol.* 40, 1483–1488.
- Katsev, S., Aaberg, A.A., Crowe, S.A., Hecky, E.R., 2014. Recent warming of Lake Kivu. *PLoS One* 9 (10), e109084. <http://dx.doi.org/10.1371/journal.pone.0109084>.
- Kolding, J., Medard, M., Mkumbo, O., van Zwieten, P., 2014. Status, trends and management of the Lake Victoria Fisheries. In: Welcomme, R., Valbo-Jorgensen, J., Halls, A. (Eds.), *Inland Fisheries Evolution: Case Studies from Four Continents*. Food and Agriculture Organisation of the United Nations, Rome, Italy, pp. 49–62.
- Kolding, J., Van Zwieten, P., Mkumbo, O., Silsbe, G., Hecky, R., 2008. Are the Lake Victoria fisheries threatened by exploitation or eutrophication? Towards an ecosystem-based approach to management. In: Bianchi, G., Skjoldal, H.R. (Eds.), *The Ecosystem Approach to Fisheries*. CAB International, London, pp. 309–350.
- Kraemer, B.M., Anneville, O., Chandra, S., Dix, M., Kuusisto, E., Livingstone, D.M., Rimmer, A., Schladow, S.G., Silow, E., Sitoki, L.M., Tamatamah, R., Vadeboncoeur, Y., McIntyre, P.B., 2015a. Morphometry and average temperature affect lake stratification responses to climate change. *Geophys. Res. Lett.* 42, 4981–4988.
- Kraemer, B.M., Hook, S., Huttul, T., Kotilainen, P., O'Reilly, C.M., Peltonen, A., Pilsnier, P.-D., Sarvala, J., Tamatamah, R., Vadeboncoeur, Y., Wehrli, B., McIntyre, P.B., 2015b. Century-long warming trends in the upper water column of Lake Tanganyika. *PLoS One* 10 (7), e0132490.
- Kumambala, P.G., Ervine, A., 2010. Water balance model of Lake Malawi and its sensitivity to climate change. *Open Hydrol. J.* 4, 152–162.
- Kumbuyo, C.P., Yasuda, H., Kitamura, Y., Shimizu, K., 2014. Fluctuation of rainfall time series in Malawi: an analysis of selected areas. *Geofizika* <http://dx.doi.org/10.15233/gfz.2014.31.1>.
- Landsberg, J.H., 2002. The effects of harmful algal blooms on aquatic organisms. *Rev. Fish. Sci.* 10, 113–390.
- Lehman, J.T., 1998. *Environmental Change and Response in East African Lakes*. Kluwer Academic Publishers, The Netherlands.
- Lehman, J.T., Mbahinzireki, G., Ndawula, L.M., 1994. *Caridina nilotica* In Lake Victoria: abundance, distribution and vertical migration. *Hydrobiologia* 317, 177–182.
- Lévêque, C., 1995. Role and consequences of fish diversity in functioning of African freshwater ecosystems: a review. *Aquat. Living Resour.* 8, 59–78.
- Loiselle, S., Co'zar, A., Adgo, E., Ballatore, T., Chavula, G., Descy, J.P., Harper, D.M., Kansime, F., Kimirei, I., Langenberg, V., Ma, R., Sarmiento, H., Odada, E., 2014. Decadal trends and common dynamics of the bio-optical and thermal characteristics of the African Great Lakes. *PLoS One* 9 (4), e93656.
- Lorke, A., Tietze, K., Halbwachs, M., Wuest, A.C., 2004. Response of Lake Kivu stratification to lava inflow and climate warming. *Limnol. Oceanogr.* 49, 778–783.
- Lunduka, R.W., 2013. Multiple stakeholders' economic analysis of climate change adaptation. A Case Study of Lake Chikwi Catchment, Malawi. International Institute for Environment and Development, London.
- Luxereau, A., Genthon, P., Karimou, J.M.A., 2012. Fluctuations in the size of Lake Chad: consequences on the livelihoods of the riverine peoples in Eastern Niger. *Reg. Environ. Chang.* 12, 507–521.
- MAAIF, 2012. Operationalisation of the Non-ATAAS Component of the Development Strategy and Investment Plan (DSIP), Situation Analysis Report, Fish Production, Ministry of Agriculture Animal Industry and Fisheries (MAAIF), Entebbe, Uganda. p. 90.
- MacDonald, W.W., 1953. Lake-flies. *Uganda J.* 17, 124–134.
- McIntyre, S., 2012. Climate variability, mixing dynamics, and ecological consequences in the African Great lakes. In: Goldman, C.R., Kamagai, M., Robarts, R.D. (Eds.), *Climatic Change and Global Warming of Inland Waters: Impacts and Mitigations for Ecosystems and Societies*. Wiley & Sons Ltd, pp. 311–336.
- McIntyre, S., Romero, J.R., Silbe, G.M., Emery, B.M., 2014. Stratification and horizontal exchange in Lake Victoria, East Africa. *Limnol. Oceanogr.* 59, 1805–1838.
- Macnab, V., Barber, I., 2012. Some (worms) like it hot: fish parasites grow faster in warmer water, and alter host thermal preferences. *Glob. Chang. Biol.* 18, 1540–1548.
- Magadza, C.H.D., 2011. Indications of the effects of climate change on the pelagic fishery of Lake Kariba, Zambia–Zimbabwe. *Lakes Reserv. Res. Manag.* 16, 15–22.
- Mahere, T.S., Mtsambiwab, M.Z., Chifambaa, P.C., Nhwatiwaa, T., 2014. Climate change impact on the limnology of Lake Kariba, Zambia–Zimbabwe. *Afr. J. Aquat. Sci.* 39, 215–221.
- Marcogliese, D.J., 2008. The impact of climate change on the parasites and infectious diseases of aquatic animals. *Rev. Sci. Tech. Off. Int. Epizoot.* 27, 467–484.
- Marshall, B.E., 2012. Does climate change really explain changes in the fisheries productivity of Lake Kariba (Zambia–Zimbabwe)? *Trans. R. Soc. S. Afr.* 67, 45–51.
- Marshall, B.E., 2013. Climate change does not explain historical changes in the pelagic ecosystem of Lake Kariba (Zambia–Zimbabwe). *Lakes Reserv. Res. Manag.* 17, 265–274.
- Marshall, B.E., Ezekiel, C.N., Gichuki, J., Mkumbo, O.C., Sitoki, L., Wanda, F., 2013. Has climate change disrupted stratification patterns in Lake Victoria, East Africa? *Afr. J. Aquat. Sci.* 38, 249–253.
- Mbungu, W., 2015. *Climate Change Vulnerability Assessment in the Lake Rukwa Basin*. Lake Rukwa Basin Water Board, Mbeya, Tanzania.
- McInnes, K.L., Erwin, T.A., Bathols, J.M., 2011. Global climate model projected changes in 10 m wind speed and direction due to anthropogenic climate change. *Atmos. Sci. Lett.* 12, 325–333.
- McGrath, D.G., Almeida, O.T., Merry, F.D., 2007. The influence of community management agreements on household economic strategies: cattle grazing and fishing agreements on the lower Amazon floodplain. *IJC* 1, 67–87.
- Mekonnen, M.M., Hoekstra, A.Y., Becht, R., 2012. Mitigating the water footprint of export cut flowers from the Lake Naivasha Basin, Kenya. *Water Resour. Manag.* 26, 3725–3742.
- Moyle, P.B., Purkey, D.R., Mosepele, K., Merron, G., Mosepele, B., 2009. Fish, floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. *Bioscience* 59, 53–64.
- Mugidde, R., 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). *Verh. Int. Ver. Limnol.* 25, 846–849.
- Mugidde, R., 2001. *Nutrient Status and Planktonic Nitrogen Fixation in Lake Victoria, Africa* Unpublished PhD thesis, University of Waterloo, Ontario, Canada.
- Musinguzi, L., Efitre, J., Odongkara, O.K., Ogutu-Ohwayo, R., Muyodi, F.J., Natugonza, V., Olokotum, M., Namboowa, S., Naigaga, S., 2015. Fishers' perceptions of climate change, impacts on their livelihoods and adaptation strategies in environmental change hot spots: A case of Lake Wamala, Uganda. *Environ. Dev. Sustain.* <http://dx.doi.org/10.1007/s10668-015-9690-6>.
- NaFIRRI, 2014. Vulnerability, impacts and adaptations of inland riparian and aquatic ecosystems and fisheries to climate variability and change: a case study of lakes Wamala and Kawi (Uganda). Final Technical Progress Report. Available at http://www.firi.go.ug/climate_change/climate_progress_reports.php (Accessed August 15, 2015).
- Natugonza, V., Ogutu-Ohwayo, R., Efitre, J., Muyodi, F.J., Mbabazi, D., Olokotum, M., Musinguzi, L., Namboowa, S., Naigaga, S., 2015. The responses of Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) in Lake Wamala (Uganda) to changing climatic conditions. *Lakes Reserv. Res. Manag.* 20, 101–119.
- Natugonza, V., Ogutu-Ohwayo, R., Musinguzi, L., Olokotum, M., Naigaga, S., Kitabona, J., 2016. Implications of climate warming for hydrology and water balance of small shallow lakes: a case of Wamala and Kawi, Uganda. *Aquat. Ecosyst. Health Manag.* <http://dx.doi.org/10.1080/14634988.2016.1142167>.
- Ndebele-Murisa, M.R., Mashonjowa, E., Hill, T., 2011. The implications of a changing climate on the Kapenta fish stocks of Lake Kariba, Zimbabwe. *Trans. R. Soc. S. Afr.* 66, 105–119.
- Ndebele-Murisa, M.R., Musil, C.F., Raitt, L.M., 2012. Phytoplankton biomass and primary production dynamics in Lake Kariba. *Lakes Reserv. Res. Manag.* 17, 275–289.
- Ngongondo, C.S., Xu, C.Y., Gottschalk, L., Alemaw, B., 2011. Evaluation of spatial and temporal characteristics of rainfall in Malawi: a case of data scarce region. *Theor. Appl. Climatol.* 106, 79–93.
- Nicholson, S.E., 1999. Historical and modern fluctuations of Lakes Tanganyika and Rukwa and their relationship to rainfall variability. *Clim. Chang.* 41, 53–71.
- Njaya, F., Snyder, K.A., Jamu, D., Wilson, J., Howard-Williams, C., Allison, E.H., Neil, L., Andrew, N.L., 2011. The natural history and fisheries ecology of Lake Chilwa, southern Malawi. *J. Great Lakes Res.* 37, 15–25.
- NOAA, 2013. National Climatic Data Center, State of the Climate: Global Analysis for Annual 2013. <http://www.ncdc.noaa.gov/sotc/global/2013/13> (Accessed, 22 Jan. 2014).
- Nsubuga, F.N.W., Namutebi, E.N., Nsubuga-Ssenfuma, M., 2014. Water resources of Uganda: An assessment and review. *J. Water Resour. Prot.* 6, 1297–1315.
- O' Reilly, C.M., Alin, S.R., Pilsnier, P.D., Cohen, A.S., McKee, B.A., 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature* 424, 766–768.
- Ogutu-Ohwayo, R., 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. *Environ. Biol. Fish.* 27, 81–96.
- Paerl, H.W., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environ. Microbiol. Rep.* 1, 27–37.
- Patterson, G., Kachinjika, O., 1995. Limnology and Phytoplankton Ecology. In: Menz, A. (Ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Natural Resource Institute, pp. 1–67.
- Phipps, P., 1973. The 'Big' fishermen of Lake Chilwa. A preliminary study in entrepreneurship in rural Malawi. In: Page, M.E. (Ed.), *Land and Labour in Rural Malawi*. Rural Africana 21, pp. 39–48.
- Pojmanska, T., Grabda-Kazubska, B., Kazubska, S.L., Machalska, J., Niewiadomska, K., 1980. Parasite fauna of five fish species from the Konin lakes complex, artificially heated with thermal effluents, and from Goplo Lake. *Acta Parasitol. Pol.* 27, 319–357.
- Portner, H.O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F.J., Serendero, I., Sirabella, P., Thorkildsen, S., Zakhartsev, M., 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Cont. Shelf Res.* 21, 1975–1997.
- Poste, A.E., Hecky, R.E., Guildford, S.J., 2011. Evaluating microcystin exposure risk through fish consumption. *Environ. Sci. Technol.* 45, 5806–58011.
- PRB (Population reference Bureau), 2014. Population Data Sheet. PRB, New York (Available at the website <http://www.prb.org> Accessed January 10, 2016).
- Reichler, T., 2009. Changes in the atmospheric circulation as indicator of climate change. In: Trevor, M.L. (Ed.), *Climate Change: Observed Impacts on Planet Earth*, pp. 145–164. The Netherlands.
- Reynolds, C.S., 2005. *Ecology of Phytoplankton*. Cambridge University Press, Cambridge.
- Sarch, M.T., Birkett, C., 2000. Fishing and farming at Lake Chad: responses to lake-level fluctuations. *Geogr. J.* 166, 156–172.

- Sarvala, J., Langenberg, V.T., Salonen, K., Chitambweba, D., Coulter, G.W., Hutula, T., Kanyaru, R., Kotilainen, P., Mukasa, L., Mulimbwa, N., Molsa, H., 2006. Fish catches in Lake Tanganyika mainly reflect changes in fishery practices, not climate. *Proc. Int. Soc. Limnol.* 29, 1182–1188.
- Saulnier-Talbot, É., Gregory-Eaves, I., Simpson, K.G., Efitre, J., Nowlan, T.E., Taranu, Z.E., Chapman, L.J., 2014. Small changes in climate can profoundly alter the dynamics and ecosystem services of tropical crater lakes. *PLoS One* 9, e86561.
- Scheren, P.A.G.M., Zanting, H.A., Lemmens, A.M.C., 2000. Estimation of water pollution sources in Lake Victoria, East Africa: application and elaboration of the rapid assessment methodology. *J. Environ. Manag.* 58, 235–248.
- Schisler, G.J., Walker, P.G., Chittum, L.A., Bergersen, E.P., 1999. Gill ectoparasites of juvenile rainbow trout and brown trout in the upper Colorado River. *J. Aquat. Anim. Health* 11, 170–174.
- Seitzinger, S.P., 1988. Denitrification in freshwater and marine ecosystems: ecological and geochemical significance. *Limnol. Oceanogr.* 35, 702–724.
- Sekiranda, S.B.K., Okot-Okumu, J., Bugenyi, F.W.B., Ndawula, L.M., Gandhi, P., 2004. Variations in composition of macro-benthic invertebrates as an indication of water quality status in three bays in Lake Victoria. *UJAS* 9, 396–411.
- Seto, C.K., Guneralp, B., Hutyrá, R.L., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *PNAS* 109, 16083–16088.
- Sharma, S., Gray, D.K., Read, J.S., et al., 74 authors, 2015. A global database of lake surface temperatures collected by in situ and satellite methods from 1985 to 2009. *Sci. Data* 2, 150008. <http://dx.doi.org/10.1038/sdata.2015.8>.
- Silsbe, G., Hecky, R., Guildford, S., Mugidde, R., 2006. Variability of chlorophyll a and photosynthetic parameters in a nutrient-saturated tropical great lake. *Limnol. Oceanogr.* 51, 2052–2063.
- Sitoki, L., Gichuki, J., Ezekiel, C., Wanda, F., Mkuambo, O.C., Marshall, B.E., 2010. The environment of Lake Victoria (East Africa): current status and historical changes. *Int. Rev. Hydrobiol.* 95, 209–223.
- Smit, B., Wandel, J., 2006. Adaptation, adaptive capacity and vulnerability. *Glob. Environ. Chang.* 16, 282–292.
- Stager, J.C., Hecky, R.E., Grzesik, D., Cumming, B.F., Kling, H., 2009. Diatom evidence for the timing and causes of eutrophication in Lake Victoria, East Africa. *Hydrobiologia* 636, 463–478.
- Sumaila, U.R., Cheung, W.W.L., Lam, V.W.Y., Pauly, D., Herrick, S., 2011. Climate change impacts on the biophysics and economics of world fisheries. *Nat. Clim. Chang.* 1, 449–456.
- Swenson, S., Wahr, J., 2009. Monitoring the water balance of Lake Victoria, East Africa, from space. *J. Hydrol.* 370, 163–176.
- Talling, J.F., Lemoalle, J., 1998. *Ecological Dynamics of Tropical Inland Waters*. Cambridge University Press, p. 441.
- Talling, J.F., 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Int. Rev. Hydrobiol.* 51, 545–621.
- Tamatamah, R.L., Duthie, H.C., Hecky, R.E., 2005. The importance of atmospheric deposition to the phosphorus loading of Lake Victoria (East Africa). *Biogeochemistry* 73, 325–344.
- Tierney, J.E., Mayes, M.T., Mayer, N., Johnson, C., Swarzenki, P.W., Cohen, A.S., Russell, J.M., 2010. Late twentieth century warming in Lake Tanganyika unprecedented since AD 500. *Nat. Geosci.* 3, 422–425.
- Traoré, M., Thompson, B., Thomas, G., 2012. *Sustainable Nutrition Security: Restoring the Bridge between Agriculture and Health*. Food and Agriculture Organization of the United Nations, Rome.
- Tseng, W., Chen, C., 2008. Valuing the potential economic impact of climate change on the Taiwan trout. *Ecol. Econ.* 65, 282–291.
- USAID, 2013. *Uganda Climate Change Vulnerability Assessment Report*. USAID, Washington, DC.
- Van der Waal, B.C.W., 1998. Survival strategies of sharptooth catfish *Clarias gariepinus* in desiccating pans in the northern Kruger National Park. *Koedoe* 41, 131–138.
- Van Dolah, F.M., 2000. Marine algal toxins: origins, health effects, and their increased occurrence. *Environ. Health Perspect.* 108, 133–141.
- Verburg, P., Hecky, R.E., 2009. The physics of warming Lake Tanganyika by climate change. *Limnol. Oceanogr.* 54, 2418–2430.
- Verburg, P., Hecky, R.E., Kling, H., 2003. Ecological consequences of warming in Lake Tanganyika. *Science* 301, 505–507.
- Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., Hecky, R.E., 2002. The chronology of human impacts on Lake Victoria, East Africa. *Proc. R. Soc. Lond. B* 269, 289–294.
- Vollmer, M.K., Bootsma, H.A., Hecky, R.E., Patterson, G., Halfman, J.D., Edmond, J.M., Eccles, D.H., Weiss, R.F., 2005. Deep-water warming trend in Lake Malawi, East Africa. *Limnol. Oceanogr.* 50, 727–732.
- Wanink, J.H., Katunzi, E.F.B., Goudswaard, P.C., Witte, F., van Densen, W.L.T., 2002. The shift to smaller zooplankton in Lake Victoria cannot be attributed to the 'sardine' *Rastrineobola argentea* (cyprinidae). *Aquat. Living Resour.* 15, 37–43.
- Williams, E.D., Duthie, H.C., Hecky, E.R., 2005. Water hyacinth in Lake Victoria: why did it vanish so quickly and will it return? *Aquat. Bot.* 81, 300–314.
- Williams, E.D., Hecky, E.R., Duthie, H.C., 2007. Water hyacinth decline across Lake Victoria—was it caused by climatic perturbation or biological control? A reply. *Aquat. Bot.* 87, 94–96.
- Wilson, J.R.U., Ajuonu, O., Center, T.D., Hill, M.P., Julien, M.H., Katagira, F.F., Neuwander, P., Njoka, S.W., Ogwang, J., Reeder, R.H., T., Van, 2007. The decline of water hyacinth on Lake Victoria was due to biological control by *Neochetina* spp. *Aquat. Bot.* 87, 90–93.
- WWF (Worldwide Fund for Nature), 2006. *Climate Change Impacts on East Africa*. Glang, Switzerland (11 pp.).
- Yildiz, S., Altındag, A., Ergonul, M.B., 2007. Seasonal fluctuations in the zooplankton composition of a eutrophic lake: Lake Marmara (Manisha, Turkey). *Turk. J. Zool.* 31, 26–121.
- Zilefac, A.S., 2010. *Analysis of Climate Variability and Anthropogenic Impacts on the Water Balance of Lake Chad Drainage Basin* MSc thesis Lund University, Lund, Sweden, p. 51.