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Abstract

Africa is experiencing high annual population growth in its major river basins. This growth has resulted in significant land use change and pollution pressure on the freshwater ecosystems. Among them, the Lake Victoria basin, with more than 42 million people, is a unique and vital resource that provides food and drinking water in East Africa. However, Lake Victoria (LV) experienced a progressive eutrophication and substantial changes in the fish community leading to recurrent proliferation of water hyacinth and cyanobacteria. Based on an extensive literature review, we show that cyanobacterial biomasses and microcystin concentrations are higher in the bays and gulfs (B&Gs) than in the open lake (OL), with *Microcystis* and *Dolichospermum* as the dominant genera. These differences between the B&Gs and the OL are due to differences in their hydrological conditions and in the origins, type and quantities of nutrients. Using data from the literature, in this paper we describe the multiple ways in which the human population growth in the LV watershed is connected to the increasing occurrence of cyanobacterial blooms in the OL and B&Gs. We also described the already documented consequences of cyanobacterial blooms on food resources and fishing and on direct water use and water supply of local populations, with their potential consequences on the human health. Finally, we discuss the actions that have been taken for the protection of LV. Although many projects have been implemented in the 15 past years in order to improve the management of waste waters or to reduce deforestation and erosion, the huge challenge of the reduction of cyanobacterial blooms in LV by the control of eutrophication seems far from being achieved.

Keywords: Cyanobacteria; Lake Victoria; Eutrophication; East Africa; Potential toxicity; Socioecological analysis; Consequences of cyanobacterial blooms

1. Introduction

Numerous studies have been conducted in the past 20 years with the goal of improving our knowledge of the causes and consequences of cyanobacterial blooms. Taranu et al. (2015) have shown that the increasing occurrence of cyanobacterial blooms is clearly associated with the increasing impact of human activities on freshwater ecosystems during the Anthropocene, and it is well established that the main cause of cyanobacterial blooms is the nutrient enrichment of phosphorus (P) and nitrogen (N) (O'Neil et al., 2012, Huisman et al., 2018). Recently, several papers also suggested that climate change might directly or indirectly promote cyanobacterial blooms (e.g., Moss et al., 2011; Paerl et al., 2016; Ho et al., 2019). Blooms are also well known to have multiple impacts on the ecological functioning of freshwater ecosystems (e.g., Paerl et al., 2016; Huisman et al., 2018, Escalas et al., 2019) and on the goods and services (G&S) they provide (e.g., Dodds et al., 2009). Finally, many papers deal with the production of harmful toxins by cyanobacteria and the sanitary risks associated with them (e.g., Briand et al., 2003; Merel et al., 2013; Meriluoto et al., 2017).

Among these previous studies, few papers have focused on developing countries, with the exception of a few countries such as Brazil and China (Merel et al., 2013). In particular, the issue of cyanobacterial blooms has been poorly investigated on the African continent, as illustrated recently by Svircev et al. (2019). When looking in this review at the distribution of cyanotoxins worldwide, it appears that data on cyanotoxins are available only for 14 of the 54 African countries and for 76 ecosystems on the continent. Among these ecosystems, Lake Victoria (LV) is the most studied, probably because it is the second largest lake in the world and provides goods and services (G&S) to millions of people (Downing et al., 2014; El-Noshokaty, 2017). Moreover, LV has experienced rapid water quality degradation that has led to eutrophication, which is considered a major threat to the ecological function of the lake (Hecky et al., 1994; Juma et al., 2014) as it results in the recurrent proliferations of aquatic weeds (e.g., water hyacinth) and cyanobacteria (Lung'ayia et al., 2000; Opande et al., 2004, Juma et al., 2014). The proliferation of water hyacinth has been more or less controlled since the end of the 1990s with biological, mechanical or physical strategies (Opande et al., 2004; Wanda et al., 2015), but cyanobacteria blooms persist in LV, particularly in the bays and gulfs (B&Gs) (Haande et al., 2011; Sitoki et al., 2012; Mbonde et al., 2015).

The LV basin has one of the highest population densities in Africa, with several large cities located along the banks of the large bays and gulfs (B&Gs) (e.g., Kampala in Uganda, Kisumu in Kenya, and Mwanza in Tanzania) (Figure 1). An understanding of the interplay of ecological and socioeconomic processes acting directly or indirectly on the lake is of primary interest. In this context, we address the state of knowledge on (i) the distribution of cyanobacterial blooms and cyanotoxins in LV; (ii) the social and environmental factors and processes potentially explaining the occurrence of cyanobacterial blooms, with a particular emphasis on changes that have occurred in its watershed during the last 50 years; (iii) the consequences of these blooms on the ecosystem G&S provided by the lake and (iv) the management practices implemented with the goal of reducing nutrient loads and consequently the cyanobacterial blooms.

Figure 1. The Lake Victoria catchment area with major land use occupation. Land use data obtained from the ESA Climate Change Initiative - Land Cover project 2017, accessed June 2019.

2. Study site: the Lake Victoria basin

The LV catchment area has a surface area of 184,200 km^2 and is shared between five countries (Burundi, Kenya, Rwanda, Tanzania and Uganda). As shown in Figure 1, the catchment is dominated by cropland and grassland, with major build-up areas (for example Kampala, Kisumu, Musoma and Mwanza) located on the shorelines of the B&Gs. LV is located 1,100 meters above sea level in East Africa and is the source of the White Nile. The lake is shared between the three countries of Kenya (6%), Tanzania (51%) and Uganda (43%). LV has a shoreline of 3,500 km with many B&Gs and a 68,000 km^2 surface area, making it the world's second largest freshwater lake and the largest lake in the intertropical area (Dobiesz et al., 2010). The maximum depth of the lake is 80 m, the average depth is 40 m, and the residence time of the water is 23 years. As shown by Talling (1966), Lake Victoria is monomictic, the overturn period occurring between May and August, while early thermal stratification occurs between September and December and persistent thermal stratification from January to April (Muggide et al. 2005).

Depending on the areas, the general climate of the Lake Victoria basin ranges from a modified equatorial type characterized by heavy rainfall throughout the year to a semiarid type characterized by intermittent drought periods. Overall, there are two rainfall periods (long rains, March-May, and short rains, October-December) with variations ranging from 870 -1,561 mm in Uganda and from 400-2,736 mm in Tanzania. (Kizza et al.,2009). Water temperature recorded at the surface of the lake range from 23°C to 29°C throughout the year (Muggide et al., 2005).

3. Historical and current status of cyanobacteria and cyanotoxins in Lake Victoria

3.1. Historical and current status of cyanobacterial blooms

Recent evolution of the LV phytoplankton community. As shown from paleolimnological data by Verschuren et al. (2002), the phytoplankton production in LV has increased since the 1930s. Though there is insufficient nutrient data for this time period, it appears that the phosphorus concentrations increased (from 1.1 to 2.9 µmoles L^{-1} between the 1960s and 1990s) and that eutrophication manifested towards the end of the 1980s (Hecky, 1993; Hecky et al., 2010). The increasing nutrient content led to an increase in the phytoplanktonic biomasses and shifts in the diatom community, from the dominance of *Aulacoseira* to the dominance of *Nitzschia* (Stager et al., 2009) and in the total phytoplankton community, from the dominance of green algae (Chlorophyta) and large diatoms (Bacillariophyta) to the dominance of cyanobacteria (Lehman and Branstrator, 1994; Ochumba and Kibaara, 1989; Kling et al. 2001; Verschuren et al., 2002; Hecky et al., 2010). This dominance of cyanobacteria in phytoplankton communities is now frequently found in the three countries bordering the lake (Kenya, Tanzania and Uganda), particularly in the numerous B&Gs (Figure 2).

Figure 2. Cyanobacteria blooms in Uganda, Murchison Bay (A); Kenya, Nyanza Gulf (B); Tanzania, Mwanza Gulf (C) (© Photos: J.F. Humbert, INRAE)

Differences in the phytoplankton biomasses and community compositions of the B&Gs and the OL. As noted by Talling (1987), the physicochemical conditions and microbial communities of the open lake (OL) are quite different from those of the B&Gs. In the B&Gs, phytoplankton biomasses are often >30 µg Chl-a L^{-1}, with cyanobacteria often comprising more than 60% of the total phytoplanktonic biomass and frequently comprising more than 80% (Table 1). The rest of the phytoplanktonic community is mainly composed of Chlorophyta, Cryptophyta, Dinophyta and Euglenophyta (e.g., Haande et al., 2011; Sitoki et al., 2012).

In the OL, the phytoplanktonic biomass is generally less than 20 µg Chl-a L^{-1}, and changes from a dominance of diatoms to a dominance of cyanobacteria are frequently found (Table 1). The works of Lung'ayia et al. (2000) and Sitoki et al. (2012) in the Nyanza Gulf and the OL in Kenya suggest that these changes could be partly driven by the alternation of dry and rainy seasons.

Irrespective of the season, cyanobacteria were dominant in the B&Gs, while diatoms were clearly dominant in the OL during the dry season and represented ≤ 50% of the phytoplanktonic biomass during the rainy season. In the latter case, cyanobacteria were the second most dominant group of phytoplankton. Interestingly, Mbonde et al. (2015) have shown in a comparative study performed in 16 closed and open bays that the degree of connectivity of these bays to the OL greatly impacts their phytoplankton communities. The average phytoplankton biovolumes were much higher in the closed bays than in the open bays, and the same finding was found when considering only the cyanobacterial biovolumes (Supplemental Fig. 1).

Table 1. Overview of the published phytoplankton biomass (either as biovolume, cells mL^{-1}, or chlorophyll-a estimates), the occurrence and abundance of cyanobacteria, the dominant species and the cyanotoxin microcystins in Lake Victoria. f.w.: fresh weight. w.w.: wet weight. MC: microcystins. Nd: not determined. NzG, Nyanza Gulf (Kenya), MB, Murchison Bay (Uganda); NG, Napoleon Gulf (Uganda); MG, Mwanza Gulf (Tanzania) (see the Supplemental Fig. 1 for the location of these sites) **Dolichospermum* genus name is used instead of *Anabaena.*

Main cyanobacterial genera found in Lake Victoria. A great diversity of cyanobacterial taxa, including both nitrogen fixing taxa such as *Dolichospermum*, *Cylindrospermopsis/Raphidiopsis* or *Anabaenopsis* and nonnitrogen fixing taxa such as *Microcystis*, *Planktolyngbya*, *Merismopedia*, *Cyanodictyon* or *Aphanocapsa,* is often found in B&Gs and the OL (Table 1). An underlying dominance of *Dolichospermum* spp. or *Microcystis* spp. cyanobacteria has been observed in the literature depending on the location, year and month of sampling considered. For example, Gikuma-Njuru et al. (2013a) observed a dominance of *Dolichospermum* and small cyanobacteria such as *Cyanodictyon* and *Aphanocapsa* between March 2005 and March 2006 in the Nyanza Gulf (Kenya), while Sitoki et al. (2012) found that *Microcystis* was clearly the most dominant cyanobacteria in the same area from July 2008 to September 2009. In Murchison Bay (Uganda), *Microcystis* dominance was noted by Poste et al. (2013), whereas the dominance of *Dolichospermum* was found in Murchison Bay and the Napoleon Gulf by Okello and Kurmayer (2011) and Okello et al. (2010a). Similar observations and alternations between a dominance of *Dolichospermum* and a very diversified cyanobacterial community were also observed by Haande et al. (2011), depending on the date and the sampling station within Murchison Bay. In Tanzania, Sekadende et al. (2005) found a dominance of diatoms and cyanobacteria belonging to the *Planktolyngbya* genus in the Mwanza Gulf between May and August 2002. Several years later, Mbonde et al. (2015) observed a dominance of *Dolichospermum* and *Microcystis* in the different B&Gs of Tanzania, including the Mwanza Gulf, between November and December 2009.

There is no clear explanation for these spatial and temporal variations in the dominant cyanobacterial genera, but it is known that variations in nutrient concentrations can influence the composition of cyanobacterial communities. For example, it has been proposed that high proportions of N-fixing cyanobacteria such as *Dolichospermum* sp. could be linked to a nitrogen limitation in the lake (Mugidde et al., 2003; Gikuma-Njuru and Hecky, 2005). In the same way, many studies have shown that *Microcystis* sp. is the most common bloom-forming species in freshwater ecosystems with high phosphorus concentrations (e.g., Poste et al., 2013).

3.2. Cyanotoxin production

Microcystis and *Dolichospermum* genera are well known as the main potential producers of cyanotoxins of the microcystins (MC) family, but *Dolichospermum* is also known to produce several families of cyanotoxins including anatoxin-a (ATX) (Bernard et al., 2017). To our knowledge, all studies in LV have focused on MC, and only one study performed in the

Nyanza Gulf (Kenya) focused on ATX (Kotut et al., 2006). Although *Dolichospermum* was dominant and *Microcystis* was marginal, ATX was undetectable in both environmental samples and in the isolated strains. During the same study period, the estimated MC concentration was approximately 1 µg eqMC-LR.L^{-1} (Krienitz et al., 2002; Kotut et al., 2006). Some of these cyanobacteria are also known to potentially produce other cyanotoxins such as the amino acid variant β-methyl-amino-L-alanine (BMAA) and saxitoxins, but these cyanotoxins have not been investigated in LV.

Numerous studies have dealt with the detection of MC in LV (Table 1). The first study reporting the presence of MC was that of Krienitz et al. (2002) and was performed in the Nyanza Gulf (Table 1). After this first study, MC occurrence was recorded in different parts of the lake, mainly in the B&Gs but also in the OL in some cases (Sekadende et al., 2005; Sitoki et al., 2012) (Table 1). Highly variable concentrations of MC were found in LV, from less than 1 µg.L^{-1} in Murchison Bay (Uganda) (Semyalo et al., 2010) up to 81 µg.L^{-1} and >2 mg. L^{-1} in Nyanza Gulf (Kenya) (Sitoki et al., 2012; Simiyu et al. 2018, respectively), the highest concentrations being found in scums or at the surface of the lake (Table 1). A positive correlation between the MC concentrations and *Microcystis* abundance was found by Okello et al. (2010a, b), Sitoki et al. (2012) and Mbonde et al. (2015). Finally, Okello et al. (2010b) observed during a one-year monitoring study (May 2007-April 2008) that the proportions of the *mcy*B+ genotypes (potentially producing MC) in *Microcystis* populations varied from 3.3% to 39.2% in Murchison Bay and from 12.9% to 59.3% in the Napoleon Gulf.

So far, 240 MC variants have been described in the world (Spoof and Catherine, 2017), but only a few studies have investigated the MC variant composition in the cyanobacterial blooms from LV (Table 1). Nevertheless, up to seven different variants have been identified by Okello and Kurmayer (2011) and up to 31 variants have been identified by Miles et al. (2013). However, the most common variants detected in the lake are MC-LR, MC-RR and MC-YR (e.g., Okello and Kurmayer, 2011, in Murchison Bay and the Napoleon Gulf; Sitoki et al., 2012, in the Nyanza Gulf; Mbonde et al., 2015, in the Mwanza Gulf). The proportions of all these MC variants were highly variable depending on the sampled area. For example, the average estimated proportions of the MC-LR variant in the Murchison Bay and the Napoleon Gulf (May 2007 - April 2008) were 12.4±2% and 0.5±0.3%, respectively, according to Okello and Kurmayer (2011) but reached 50±6% in the Nyanza Gulf (July 2008 - Sept 2009) (Sitoki et al., 2012). The small standard deviations associated with these proportions seem to express low temporal variations for a given area in LV. However, higher variations are sometimes reported in the literature, as shown for example by the large standard deviation found in the mean proportion (31±52%) of the MC-YR in the Nyanza Gulf (Sitoki et al. 2012).

4. Linking demographic changes with the increasing occurrence of cyanobacterial blooms

From the analysis of the data available in the literature on the causes of cyanobacterial blooms in LV, we built a flow diagram (Figure 3) describing the multiple ways in which the human population growth in the LV watershed is connected to the increasing occurrence of cyanobacterial blooms in the OL and B&Gs.

Figure 3. Links between the increase in the human population density around Lake Victoria and the occurrence of cyanobacteria blooms in the open lake and in the bays and gulfs.

OM: Organic matter; P: Phosphorus; N: Nitrogen

As summarized in Figure 3, the increase in the populations density in the LV basin, such as everywhere in the world, has resulted in increasing food, housing and product demands (FAO, 2016). All these demands have many consequences on land use in the watershed, including farming and fishing activities, as well as formal and informal urbanization and industrial and commercial activities. All these processes are described in section 4.1. Then, as developed in section 4.2, the changes occurring in anthropogenic activities and land use have led to increasing nutrient pollution in the OL and B&Gs through three main processes: the aerial deposition of phosphorus and nitrogen, the discharge of mineral and organic nutrients by rivers and a decrease in natural purification due to wetland degradation. Finally, section 4.3 shows why the B&Gs are more polluted than the OL and the processes leading to the decrease in water quality.

4.1. Determinism and consequences of human population growth in the LV watershed

Demographic data on the LV watershed. The African continent continues to experience a high annual population growth estimated at 2.6% per year in its major river basins (World Population Prospects, 2017). The population density in the LV basin almost doubled over the past 20 years from 27.2 million to ca. 42 million inhabitants (Bremer et al., 2013), which is considered the largest human population in the watersheds of the great lakes of the world (Dobiesz et al., 2010). This population increased by 2.4 – 3.2% annually (> 6% in some urban areas such as Kampala, Uganda; McDonald et al., 2014), a growth rate that is higher than that observed in the rest of the African continent (UNEP, 2006). The data from the Center for International Earth Science Information Network - CIESIN - Columbia University (2018) indicates that the population density in major cities has increased from a max of 100 persons per km^2 to over 23,000 persons per km^2 in the last two decades. A strong and similar exponential population increase has been observed since the 1960s in Kenya, Tanzania and

Uganda (Supplemental Figure 2). On the other hand, Burundi and Rwanda, which experienced civil war in the 1990s and do not have direct access to the lake, have seen much lower population growth.

Causes of this population growth in the LV watershed. A recent report of the International Institute for Sustainable Development (Dazé and Crawford, 2016) pointed out that migration in the Great Lakes Region in East Africa is due partly to both voluntary decisions to migrate and forced migration.

Concerning the voluntary migration, many people have migrated towards the lake basin to take advantage of the economic benefits linked to the fisheries in the basin (Awange and Obiero, 2006; Odada et al., 2009). As reported in Mkumbo & Marshall (2015), more than 1,200,000 people are directly or indirectly employed in fisheries, and income from fisheries supports approximately 4 million people. This makes LV the world’s largest host for inland freshwater fisheries (Simonit and Perrings, 2011).

On the other hand, forced migrations have resulted from armed conflicts and violence in Rwanda and Burundi (from 1993 to 2005) and in the Democratic Republic of Congo (from 1996 to 2002). Many of these migrants are located in rural areas (Dazé and Crawford, 2016).

Consequences of population growth on land use, urbanization and anthropogenic activities. As established in the diagnostic analysis performed by the Lake Victoria Environmental Management Project (LVEMP), more than 87% of the inhabitants living in the LV basin are from the rural populations in Burundi, Kenya, Rwanda and Tanzania (see also Figure 1), while in Uganda, 94% of the inhabitants living in the LV basin are urban (LVEMP, 2007). Meanwhile, as already observed in the developing world (Montgomery, 2008), the three countries with direct access to the lake and with livelihoods that rely on the lake have also experienced rapid urbanization that has led to the development of large cities located on the B&Gs, such as Kampala (>2 million inhabitants) on Murchison Bay (Uganda), Kisumu (approximately 1 million inhabitants) on the Nyanza Gulf (Kenya) and Mwanza (>400,000 inhabitants) on the Mwanza Gulf (Tanzania) (Supplemental Fig 3).

The main consequence of increasing population densities in rural areas is a change in land use, particularly to cropland (see Figure 1). The agricultural development involves ca. > 80% inhabitants’ that depend on small-scale mixed farming operations, thus, influencing the land use. As highlighted in the LVEMP report (LVEMP, 2007), agricultural development includes wetland destruction and/or degradation, livestock overgrazing, bush burning, land fragmentation, and deforestation. Deforestation (for settlement and agriculture development) is spreading at an alarming rate, e.g., in Uganda between 2000 and 2015, the deforestation rate was 3.3% annually, which is higher than that in other countries of the watershed (0.2% for Burundi, 0.3% for Kenya, 1.7% for Rwanda and 0.8% for Tanzania) (FAO, 2015). This deforestation rate has increased from 1990-2015 in Uganda (from 2.0% in 1990-2000 to 3.3% in 2000-2010, reaching 5.5% in 2010-2015). In typical developing countries, both rural and urban populations depend heavily on the forest environment and products, such as building materials, crafts, firewood, charcoal, food, flavoring, and traditional medicine, for their livelihood (UNEP, 2008; Mwavu & Witkowski, 2008).

The drivers of deforestation identified in the LV watershed can be classified into two broad categories (Waiswa et al., 2015). The direct human uses of forest resources (Geist & Lambin, 2002; Mwavu & Witkowski, 2008) include the unplanned spread of agricultural areas over forest areas, firewood and timber harvesting, clearing forestland for human settlement, sand mining and brickmaking. The indirect drivers concern the underlying sociopolitical factors impacting human practices, such as unclear land tenure and/or property rights, lack of forest monitoring and the noninvolvement of users in forest maintenance, conflicts of interest, political interference, and negative perceptions about planning policies (Place & Otsuka, 2000; Mwavu & Witkowski, 2008).

4.2. Relationships between land use changes and the eutrophication of LV

As shown in Figure 3, various processes associated with land occupation changes and activities have led to the eutrophication of the OL and B&Gs. Numerous studies have focused on identifying the different processes that lead to nitrogen and phosphorus pollution in LV, and four main processes have been identified. These processes include (i) the discharge of rivers from heavily polluted catchments (Verschuren et al., 2002; Musungu et al., 2014; Fuhrimann et al., 2015; Jovanelly et al., 2015); (ii) atmospheric deposition, in particular of phosphorus (P) (accounting for 55% of the total phosphorus input in LV) (Tamatamah et al., 2005); (iii) the biological fixation of atmospheric dinitrogen (N_2), which seems to greatly exceed the contributions of atmospheric N deposition and river N inputs (Mugidde et al., 2003); and to a lesser extent, (iv) nutrient recycling and release from the sediments (Gikuma-Njuru et al., 2010).

The two first nutrient pollution pathways for LV water are directly linked to human population growth and activities. First, changes in land use patterns have contributed to enhanced erosion. In Uganda and Tanzania, the presence of settlements on the LV shoreline zone were associated with high soil erosion estimates of between 17 and 87 ton. $ha^{-1}.yr^{-1}$ (Isabirye et al., 2010). The rate of soil loss in the LV basin also appears to depend on the land use system (tree plantation versus grassland) (Bamutaze et al., 2017). Other human-induced disturbances, such timber harvesting and soil compaction by cattle, also increase the risk of soil erosion (Karamage et al., 2017). Similarly, TP and TN atmospheric deposition mainly seem to result from burnt biomass, windblown dust and industrial and domestic activities (see the review of Cheruiyot and Muhandiki, 2014).

Second, due to the urban human population growth, increasing quantities of solid and liquid waste originate from (i) the human populations living in the large cities located near the B&Gs and (ii) industrial activities such as the activities of large manufacturers of steel construction materials, factories that produce batteries, soap, paint, metal, plastics, corrugated iron sheets, or pharmaceuticals, and breweries, tanneries, former copper smelters and abattoirs (Muwanga and Barifaijo, 2006). Moreover, as shown by Cockx et al. (2019) in Tanzania, the urbanization of the rural population results in changing food demands, which include increasing consumption of high-sugar foods and drinks. These changes in the demand for food have led for example to the installation of bottling factories in the three main cities located around the lake (Kampala, Mwanza and Kisumu). For Kampala (Uganda), only ca. 8% of all wastes (domestic and industrial) are collected and treated (Matagi, 2002), and the efficiency of the sewage treatment plants is poor, with up to ca. 89% frequency of noncompliance with the national standard for BOD_5 (LVEMP, 2005). In the same way, Oguttu et al. (2008) have shown that point source effluents due to increasing industrial activities in the Jinja area have contributed to the increasing nutrient loads in the Napoleon Gulf.

Finally, the progressive reduction and degradation of wetlands has played a major role in the degradation of water quality. This degradation is due to housing, industrialization, infrastructure development and agriculture (Kansiime & Nalubega, 1999; Fuhrimann et al., 2015). In the Kampala Metropolitan Area (Uganda), the proportion of severely degraded wetlands increased from 13% in 1993 to 46% by 1999 (Nyakaana et al., 2007). In particular, Nakivubo wetlands experienced a 62% loss in wetland vegetation between 2002 and 2014, mainly due to crop cultivation (Isunju, 2016), despite their high estimated economic value of between US$ 760,000-1,300,000 (Schuijt, 2002). Similar observations have been made for the Nyanza Gulf in Kenya by Juma et al. (2014). In Tanzania, Musamba et al. (2011), showed that an increase in the anthropogenic activities in the Musoma urban area was associated with the degradation of wetland coverage at the average rate of 6.5 ha yr^{-1} between 2001 and 2008. Knowing that wetlands are located at the mouths of the major rivers and in the inshore areas of the lake (Okeyo-Owuor et al., 2012) and that they play a major role in waste removal and water purification (Raburu et al., 2012), their degradation contributes to the decrease in water quality in the B&Gs.

The consequences of all these processes acting on the nutrient load in Lake Victoria is that high concentrations in soluble elements (SRP, NO_3 and NH_4) have been recorded in the twenty past years in the Lake Victoria (Supplemental Table 1). The average TN:TP ratios are almost double in B&Gs (14.5) than in OL (8.1) (Muggide et al., 2005). This suggests that there is a global N limitation in Lake Victoria, which is more pronounced in offshore area.

4.3. Why do the bays and gulfs of LV have more cyanobacteria blooms than the open lake?

Two main kinds of processes seem to be involved in the greater amount of eutrophication observed in the B&Gs compared to the OL.

First, several big towns are located on the banks of the B&Gs, such as Kampala on the Murchison Bay, Kisumu on the Nyanza Gulf and Mwanza on the Mwanza Gulf. As shown by Akurut et al. (2017) for the Murchison Bay (Uganda), the exponential deterioration of the water quality between 2001 and 2014 was largely due to increasing quantities of waste generated in Kampala City and discharged in the bay. Similar observations were made by Cornelissen et al. (2014) for the Mwanza Gulf (Tanzania). Several B&Gs also receive water from rivers carrying high nutrient loads resulting from agricultural farmland in the catchment. This contribution has been shown for example for the Nyanza Gulf (Kenya) by Gikuma-Njuru et al. (2013b). As already described in paragraph 3.2, the decrease in the natural depuration in the wetlands located in the B&Gs contributes to their hyper eutrophication.

Second, the hydrodynamic conditions experienced by the B&Gs favors cyanobacteria blooms. In the closed B&Gs (e.g., Murchison Bay, the Nyanza and Mwanza Gulfs) experiencing limited exchange with the OL, the water residence time is long, and the high nutrient load from their watersheds promote and sustain the development of cyanobacterial blooms. Moreover, the majority of the B&Gs are very shallow, as illustrated by the Nyanza Gulf, which has a mean depth of <10 m (<5 m in the eastern part of the gulf). Typically, at shallow depths, all water is mixed daily and there is thermal stratification during high insolation periods (Gikuma-Njuru, 2008). Consequently, the alternation of mixing and stratified periods can potentially promote the release of nutrients from the sediments, which can then sustain cyanobacteria growth (see for ex. Cao et al., 2016). In addition to the mixing and stratification that occurs at shallow water depths, the high turbidity occurring in these shallow and mixed B&Gs (Silsbe et al., 2006; Loiselle et al., 2008 & 2010) could promote the development of bloom-forming cyanobacteria such as *Microcystis* spp. or *Dolichospermum* spp., which are able to occupy the top of the water column where light is available for their growth, due to their gas vesicles (Gikuma-Njuru, 2008; Ssebiyonga et al., 2013).

4.4. Other processes involved in the increasing occurrence of cyanobacterial blooms in LV

Role of changes in the fish community. Nile perch and several tilapiine species (Nile tilapia: *Oreochromis niloticus* L.; *O. leucostictus*; *Tilapia zillii*) were introduced into the lake in the 1950s and became dominant (Ogutu-Ohwayo, 2004; Awange and Obiero, 2006). Consequently, Marshall (2018) discussed the possibility that the changes in the fish community composition during the 1960s could have aggravated the symptoms of eutrophication and the proliferations of cyanobacteria in the lake. Although Goldschmidt et al. (1993) emphasized the importance of endemic phytoplanktivorous and detritivorous haplochromine species in the littoral and sublittoral areas of LV before the 1980s, these species were victims of Nile perch predation, that led to a dramatic decrease in their biomasses (Marshall, 2018). Thus, in the context of eutrophication, Batjakas et al. (1997) suggested that the replacement of endemic phytoplanktivorous species by predatory Nile perch could have facilitated the proliferation of cyanobacterial blooms. Moreover, as suggested by Marshall (2018), cyanobacteria could have been favored by the decrease in the population of large phytoplankton grazers from the zooplanktonic community due to their consumption by juvenile Nile perch. The other main introduced fish species (Nile tilapia, *Oreochromis niloticus)* is well-known to ingest a diversity of prey items including phytoplankton (e.g. Bwanika et al. 2006). In LV, many authors have reported that the diet of *O. niloticus* often have large proportion of phytoplankton dominated by cyanobacterial species (Semyalo et al, 2011, Rumisha & Nehemia, 2013, Jihulya, 2014). Cyanobacteria has also been shown to contribute to the bulk of the diet of *O. niloticus* in other tropical aquatic ecosystems (Teferi et al. 2000, Turker et al. 2003, Lu et al. 2006, Torres et al. 2016, Zakaria et al. 2019). However, new data on the quantitative predation of cyanobacteria by *O. niloticus* are needed before concluding that this species may play a significant top-down role on the dynamics of cyanobacteria.

Since 2005, the stock of Nile perch in LV has rapidly decreased by approximately 50%, mainly due to overfishing (Matsuishi et al. 2006, Mkumbo et al. 2007; Mkumbo and Marshall, 2015) but also because of the degradation of the water quality (e.g. anoxia). During the same period, the biomasses of other species such as Nile tilapia, catfishes or *Protopterus* biomasses have increased because they are less susceptible to degraded water quality (Kolding et al., 2008). The recent decrease in Nile perch stocks also favored an increase in haplochromine prey species, although their biomass and diversity remains low compared to the pre Nile perch era (Marshall, 2018). It is difficult to predict the consequences for cyanobacterial blooms to all these changes occurring in fish communities of LV knowing that the grazing rates of both fish and zooplankton always have always been low in Lake Victoria, particularly since the 1980's (Witte et al., 2012).

In addition to the changes occurring in capture fisheries, the recent increases in cage culture farms in the B&Gs (Aura et al., 2018; Opiyo et al., 2018; Musinguzi et al., 2019) constitutes an additional threat for the lake. It is well known that aquaculture can contribute significantly to the nutrient enrichment of freshwater ecosystems (Zhang et al., 2006). In Napoleon Gulf (Uganda), Egessa et al. (2018) observed organic matter and nutrient enrichment in the sediment due to cage fish farming. In Shirati Bay (Tanzania), an increase in nutrient concentrations was observed after cage farming establishment (Kashindye et al. 2015), while in Kenya, Njiru et al, (2018) reported increasing eutrophication in shallow areas due to aquaculture waste feeds. These areas are only small portions of LV where caged fish farming has occurred, but farming has begun to spread among the various B&Gs of the lake. Thus, additional data are needed to study this issue and its related consequences on water quality.

Potential impact of climate change. The potential impact of climate change on eutrophication in LV and consequently on cyanobacterial blooms has been poorly investigated. Lehman et al. (1998) suggested that the eutrophication of LV may have been accelerated by climate change, particularly by increased water temperature and reduced vertical mixing, which are two processes that are known to influence the population dynamics of cyanobacteria.

Recently, Tariku and Gan (2018), modeled the impacts of climate change on the extreme precipitation indices and temperature of the River Nile Basin and indicated that the extreme precipitation indices are projected to increase in the second part of this century. Similarly, Thiery et al. (2016) projected that LV will be a hotspot for heavy thunderstorm events in a future with warmer climate scenarios. These changes might have dramatic consequences on LV because extreme rain events contribute to runoff and soil erosion, which enhance the eutrophication of aquatic ecosystems (e.g., Moss et al., 2011) and consequently the occurrence and intensity of cyanobacterial blooms (e.g., Michalak et al., 2013).

5. Consequences of cyanobacterial blooms on the different uses of the lake

5.1 Consequences on food resources and fishing

Fishing is an important food resource for approximately 1.5 million people living on the lake shores as well as for the 42 million inhabitants in the watershed of LV. In this context, cyanobacterial blooms have two main impacts on the fish communities: (i) the changes in the environmental conditions of the fish due to the blooms, with potential negative impacts on the abundance and diversity of the LV fish community, and (ii) the accumulation of cyanotoxins in the fish and the associated risks for the human populations consuming those fish.

It has been shown in numerous water bodies worldwide (e.g., Padmavathi & Veeraiah, 2009; Lehman et al., 2010) that severe cyanobacterial blooms impact fish populations, mainly through changes induced in environmental parameters such as dissolved oxygen concentrations. Indeed, severe anoxia is recorded at the bottom of deep lakes or throughout the water column in shallow lakes due to the high respiration activity of bacteria degrading organic matter produced by cyanobacteria. In LV, several studies have linked water quality degradation to eutrophication and the changes occurring in the fish communities. For instance, Kundu et al. (2017) reported significant differences in the fish community structure in the Nyanza Gulf, where severe cyanobacterial blooms are frequently observed, and just outside of the gulf where better water quality occurs. Furthermore, Kolding et al. (2008) examined the relationship between the deterioration of water quality and the decline of Nile perch in the lake. They hypothesized that the low oxygen concentrations at the bottom of the lake resulting from the degradation of phytoplanktonic organic matter may be the cause of the decline in Nile perch. However, this hypothesis is still in debate, as discussed by Mkumbo & Marshall (2015).

The second impact of cyanobacterial blooms on fish communities is associated with the potential accumulation of cyanotoxins in the fish and their subsequent potential consequences on human health. Based on laboratory and field studies in several countries, it is known that MC can accumulate in fish tissues (e.g., Jiang et al., 2012; Nchabeleng et al., 2014). In LV, three studies (Semyalo et al., 2010; Poste et al., 2011 and Simiyu et al., 2018) have shown the accumulation of MC in several fish species. The extent of MC accumulation displayed considerable variability (from 0.5 to 90 $\mu g.kg^{-1}$ wet weight) among the fish species. For the highest toxin concentrations, the estimated daily exposure to MC could exceed the tolerable daily intake (TDI) proposed by the WHO for chronic exposure from fish consumption (i.e., TDI of 0.04 µg MC-LR per kg body weight per day) (Ibelins and Chorus, 2007), especially for *Haplochromis* spp. and *Rastrineobola argentea* (Silver fish), which are consumed whole. With the growing cage aquaculture in the B&Gs of LV and the incidence of increasing nutrient loading from aquaculture, cultured fish could accumulate cyanotoxins, but no data are available. Consequently, all these data suggest that the consumption of fish from LV could significantly contribute to the chronic exposure of human populations to MCs.

5.2 Consequences of direct water use and water supply

As shown in Table 1, the MC concentrations in the LV water frequently exceed 1 $\mu g.L^{-1}$, which is the threshold proposed by the WHO (Chorus and Bartram, 1999) for drinking water, and sometimes exceed 10 $\mu g.L^{-1}$, which is the lowest threshold set by the sanitary authorities from the northern countries for recreational activities (Chorus et al., 2012). Consequently, as emphasized by Kotut et al. (2006), these MC concentrations in the B&Gs are now a real challenge for local water authorities. However, regular monitoring of the MC concentrations in the lake water and in the treated water produced by the plants located in the B&Gs is not regularly performed. Moreover, there is no information on the sanitary risks for people directly using lake water for domestic activities, including cooking and washing, or for recreational activities during bloom events.

In addition to the potential threat of cyanobacterial blooms to human populations through the consumption of raw or treated water or contaminated fish, these blooms have direct and indirect consequences on the price and quantity of drinking water produced by the treatment plants. In Uganda, Oyoo (2015) showed that cyanobacterial blooms impacted the price of the water in different ways. First, a clarification stage was added to the oldest water treatment plant (Gaba I) to improve the water quality. Second, the dosage of aluminum sulfate used in the plants increased three times from 1993 to 2008 due to the increasing prevalence of cyanobacterial blooms, and prechlorination was introduced to enhance coagulation and settling (Olokotum, 2017). Third, the cyanobacteria blooms in Murchison Bay have forced the water supply authorities and institutions to establish a new water treatment plant outside of the bay at Katosi (Damba channel), which will incur additional costs due to the construction of a long pipeline to carry the treated drinking water to the Kampala metropolitan area.

In addition to the increasing costs of water treatment due to cyanobacterial blooms, Oyoo (2015) reported the impacts of cyanobacterial blooms on the availability of water to local populations. The increased frequency of backwashing to avoid clogging of the sand filters during water treatment at Gaba I & II in Kampala decreases the runtime of the machinery, which consequently decreases the quantity of water produced by the plants for populations. The costs of production and the availability of treated water are very important in developing countries because when the price increases and/or the availability decreases, the local populations tend to use alternative water resources that are not safe for their health (Moe and Rheingans, 2006).

Finally, from all these data, Figure 4 shows the potential health impacts of cyanobacterial blooms for human populations living around LV. Concerning the health impacts of cyanotoxins, limited data demonstrates their real adverse effects on human populations. However, due to the high recorded MC concentrations and the potentially high exposure of humans to these toxins (in comparison to populations from developed countries), these impacts on human health should be seriously considered. This hypothesis is supported by the recent paper of Roegner et al. (2020) showing that the health of peri-urban fisher communities in the area of Kisumu is threatened by the consumption and use of lake water contaminated with MCs and other HAB components. Moreover, in addition to the disturbances caused by cyanobacteria during the production of drinking water, human populations can also consume nontreated water from the lake or poorly treated water with potential exposure to fecal pathogens associated with waterborne diseases.

Figure 4. Potential impacts of cyanobacterial blooms on human health in Lake Victoria

LW: Lake water; DW: Drinking water

6. Efforts to reduce eutrophication and the occurrence/intensity of cyanobacterial blooms

Knowing that it is well established that the eutrophication of freshwater ecosystems promotes cyanobacterial blooms, the reduction of external nutrient inputs in the lakes is the main sustainable strategy to reduce cyanobacterial blooms (e.g. Huisman et al., 2018). LV is a very complex socioecological ecosystem, and there is limited documented knowledge (and understanding) regarding the social and ecological dynamics and interactions involving LV. However, based on existing knowledge, we provide arguments for the eutrophication trajectory of LV and the necessity to carry out ambitious and sustainable management measures to address this major problem. The modeling approach developed by Downing et al. (2014) shows that controlling eutrophication is key to the protection and restoration of LV and its ecosystem functions and G&S. This finding is shared by many scientists as well as the local and international authorities in charge of the management of LV. Over the past 10 years, many actions have been taken to restore LV under the authorities of the East African Community (EAC), Lake Victoria Fisheries Organization (LVFO), Lake Victoria Environment Management Program (LVEMP), and Nile Basin Initiative (NBI) (Kayombo and Jorgensen, 2006).

We have attempted to differentiate the issues affecting the B&Gs and the OL resulting from population growth and human activity because (i) the B&Gs are more polluted than the OL and (ii) the main sources of pollutants affecting these areas are different. The pollution of the B&Gs is largely due to the discharge of (i) solid and liquid wastes/pollutants originating from big cities located on their banks and (ii) sediments and nutrients from the intensive agricultural farmland. Consequently, efficient wastewater collection and treatment of these domestic and industrial pollutants are critical in reducing the hyper eutrophication of the B&Gs. In Murchison Bay (Uganda), most of the influxing nutrients are carried by the Nakivubo channel (Fuhrimann et al., 2015), comprising mainly the rainwater and the domestic and industrial wastewater of Kampala (Matagi, 2002; Kayima et al., 2008). With this goal in mind, the Kampala Capital City Authority (KCCA) launched the Green Industry Campaign in 2016 with the goal of improving wastewater treatment (KCCA, 2018). Recently, the KCCA also piloted a new action plan to improve fecal sludge collection and transport from household pit latrines, which are common in Kampala suburbs (KCCA, 2017). Finally, the construction of a new wastewater treatment plant in Kampala (Bugolobi/Nakivubo sewage plant) should increase the sewage treatment capacities of the National Water and Sewerage

Corporation (NWSC), which oversees water sanitation in Uganda. Similar approaches have also been implemented for Kisumu located near the Nyanza Gulf in Kenya and for Mwanza located near the Mwanza Gulf in Tanzania in the framework of the Lake Victoria Water Sanitation Projects (LVWATSAN), which were first launched in 2004 but still continue to support actions for the improvement of solid and liquid waste management (https://unhabitat.org/the-lake-victoria-water-and-sanitation-project/).

All these actions are very important for the protection of the B&Gs of LV, but estimating their “real” impacts on the improvement of the water quality in the B&Gs remains difficult. Indeed, in urban areas, the wastewater collection networks are still limited, which results in the treatment of a small proportion of sewage, and with the predicted increased population growth rate (2 – 5% annually), sewerage production will increase.

In addition to improving wastewater collection and treatment, the protection and restoration of the numerous wetlands that are associated with the B&Gs is also important. As discussed before, many wetlands have been degraded due to the pressures linked to population growth. Consequently, several projects in the three riparian countries around LV focused on the rehabilitation of natural wetlands and the construction of artificial wetlands. These programs are aimed at securing and maintaining the hydrological and ecological integrity of wetlands (MWE, 2018). This initiative requires active involvement and participation of the local communities living in these areas, as shown in Kenya by Raburu et al. (2012) and in Uganda by Wacker et al. (2016).

Concerning the OL, it has been shown that in addition to river discharge, aerial depositions are the main source of nutrient inputs in the lake (e.g., Tamatamah et al., 2005; Kayombo & Jorgensen, 2006). Therefore, a reduction of these inputs would be associated with an integrated approach for the protection of the catchment area, including better soil cover management and improved land use patterns (Okungu & Opango, 2005; Vuai et al., 2013). To adequately protect the watershed, deforestation needs to be halted and forests need to be restored; this constitutes a much greater challenge due to the complexity of the drivers of this phenomenon (Masese et al., 2012; Waiswa et al., 2015). These authors also note the absolute need to involve local communities in all these processes.

In the framework of the Lake Victoria Environmental Management Project phases I and II (LVEMP I and II), several soil conservation and afforestation projects were implemented to limit soil erosion and the aerial deposition of nutrients in the lake. The impact of these projects on the water quality of the OL has not been estimated. However, considering the size of the watershed and the increasing population density, soil conservation projects will require considerable concerted efforts by the five countries before expecting “significant changes” in the water quality of the main lake.

In interaction with LVEMP projects, national management plans have also been implemented in the countries belonging to the LV watershed. In Kenya for example, a master plan for the conservation and sustainable management of water catchment areas was proposed in 2012 by the Ministry of Environment and Mineral Resources (MEMR, 2012). Sub catchment management plans have been implemented, for example for the Awach Kano, leading to reduced deforestation, water pollution, gully erosion, etc. (Nyanchaga and Openji, 2017). In Tanzania, similar catchment-based actions have been implemented for the protection of LV in the framework of Integrated Water Resources Management and Development (IWRMD) plans (Domasa, 2019).

7. Conclusion

Due to the demographic growth and the rising concentration of the population into urban areas in Africa (United Nation, 2018), we may fear that in the next decades, eutrophication of freshwater ecosystems and associated cyanobacterial blooms will continue to increase in LV and also in many other African lakes. Knowing that all these lakes provide numerous ecosystem G&S and are vital for the water and food supply, the high microcystin concentrations recorded in water and fishes of LV and the data of Roegner et al. (2020) suggest that cyanobacteria and their toxins constitute a serious health concern for local populations. The same is probably true in many countries of the intertropical area in Africa. Consequently, it is becoming urgent in Africa (i) to implement long term monitoring programs of cyanobacteria and cyanotoxins in lentic freshwater ecosystems, (ii) to define water policies and rules for cyanobacteria and cyanotoxins and to inform human populations about sanitary risks and (iii) to take actions for reducing the exposure of human populations to cyanotoxins knowing that among these actions, the provision of affordable and easily available treated-water is an urgent priority.

In a longer-term perspective, the battle against eutrophication will be one of the great challenge of African countries. As shown in this review, the three main axes in this battle will concern (i) the wastewater treatment and management in urban areas knowing that currently available treatment methods might not be used in Africa due for example, to the lack of appropriate structure (Wang et al., 2014), (ii) the promotion of a sustainable agriculture, such as conservation agriculture, allowing to provide foods to a growing population whilst minimizing environmental impacts (Giller et al., 2015) (iii) the protection and restoration of wetlands, which can play a very important role in nutrient retention and reduction, even for great lakes (Watson et al., 2016) .

As already experienced in developed countries, all these actions for reducing the exposure of human populations to cyanotoxins and the eutrophication will be very costly and consequently require international financial cooperation. There is also need for international collaborative research programs involving scientists and people from local institutions working in the water domain. Finally, the involvement and participation of the local communities will be also a key factor for their successful development.

Acknowledgement

This review paper has been prepared in the framework of the WaSAf program, which is funded by the French Facility for Global Environment (Fonds Français pour l'Environnement Mondial, FFEM).

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Supplemental Table 1. Dissolved nutrient and chlorophyll-a concentrations in the Lake Victoria

Supplemental Figure 1. Chlorophyll-a and microcystin concentrations in the main lake and in the bays and gulfs of the Lake Victoria

Supplemental Figure 2. Population size dynamics in the five countries of the watershed of Lake Victoria (data from the "World Population Prospects, The 2017 Revision", United Nations; https://population.un.org/wpp/Download/Standard/Population/)

Supplemental Figure 3. Geographical distribution of the human population densities in the Lake Victoria watershed.