

A review of the socioecological causes and consequences of cyanobacterial blooms in Lake Victoria

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▶ To cite this version:

Mark Olokotum, Veronica Mitroi, Marc Troussellier, Ronald Semyalo, Cecile Bernard, et al.. A review of the socioecological causes and consequences of cyanobacterial blooms in Lake Victoria. Harmful Algae, 2020, 96, pp.101829. 10.1016/j.hal.2020.101829. mnhn-02635416

HAL Id: mnhn-02635416 https://mnhn.hal.science/mnhn-02635416v1

Submitted on 24 Sep 2020

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1	A review of the socioecological causes and consequences of cyanobacterial
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25 Abstract

26 Africa is experiencing high annual population growth in its major river basins. This growth 27 has resulted in significant land use change and pollution pressure on the freshwater 28 ecosystems. Among them, the Lake Victoria basin, with more than 42 million people, is a 29 unique and vital resource that provides food and drinking water in East Africa. However, 30 Lake Victoria (LV) experienced a progressive eutrophication and substantial changes in the 31 fish community leading to recurrent proliferation of water hyacinth and cyanobacteria. Based 32 on an extensive literature review, we show that cyanobacterial biomasses and microcystin 33 concentrations are higher in the bays and gulfs (B&Gs) than in the open lake (OL), with 34 Microcystis and Dolichospermum as the dominant genera. These differences between the 35 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 36 37 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 38 39 already documented consequences of cyanobacterial blooms on food resources and fishing 40 and on direct water use and water supply of local populations, with their potential 41 consequences on the human health. Finally, we discuss the actions that have been taken for 42 the protection of LV. Although many projects have been implemented in the 15 past years in 43 order to improve the management of waste waters or to reduce deforestation and erosion, the 44 huge challenge of the reduction of cyanobacterial blooms in LV by the control of 45 eutrophication seems far from being achieved.

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

49

50 **1. Introduction**

51 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) 52 53 have shown that the increasing occurrence of cyanobacterial blooms is clearly associated with 54 the increasing impact of human activities on freshwater ecosystems during the Anthropocene, 55 and it is well established that the main cause of cyanobacterial blooms is the nutrient 56 enrichment of phosphorus (P) and nitrogen (N) (O'Neil et al., 2012, Huisman et al., 2018). 57 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). 58 59 Blooms are also well known to have multiple impacts on the ecological functioning of 60 freshwater ecosystems (e.g., Paerl et al., 2016; Huisman et al., 2018, Escalas et al., 2019) and 61 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 62 63 with them (e.g., Briand et al., 2003; Merel et al., 2013; Meriluoto et al., 2017).

64 Among these previous studies, few papers have focused on developing countries, with 65 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 66 67 illustrated recently by Svircev et al. (2019). When looking in this review at the distribution of 68 cyanotoxins worldwide, it appears that data on cyanotoxins are available only for 14 of the 54 69 African countries and for 76 ecosystems on the continent. Among these ecosystems, Lake 70 Victoria (LV) is the most studied, probably because it is the second largest lake in the world 71 and provides goods and services (G&S) to millions of people (Downing et al., 2014; El-72 Noshokaty, 2017). Moreover, LV has experienced rapid water quality degradation that has led 73 to eutrophication, which is considered a major threat to the ecological function of the lake 74 (Hecky et al., 1994; Juma et al., 2014) as it results in the recurrent proliferations of aquatic 75 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).

80 The LV basin has one of the highest population densities in Africa, with several large 81 cities located along the banks of the large bays and gulfs (B&Gs) (e.g., Kampala in Uganda, 82 Kisumu in Kenya, and Mwanza in Tanzania) (Figure 1). An understanding of the interplay of 83 ecological and socioeconomic processes acting directly or indirectly on the lake is of primary 84 interest. In this context, we address the state of knowledge on (i) the distribution of 85 cyanobacterial blooms and cyanotoxins in LV; (ii) the social and environmental factors and 86 processes potentially explaining the occurrence of cyanobacterial blooms, with a particular 87 emphasis on changes that have occurred in its watershed during the last 50 years; (iii) the 88 consequences of these blooms on the ecosystem G&S provided by the lake and (iv) the 89 management practices implemented with the goal of reducing nutrient loads and consequently 90 the cyanobacterial blooms.

91

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.

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96 2. Study site: the Lake Victoria basin

97 The LV catchment area has a surface area of 184,200 km² and is shared between five 98 countries (Burundi, Kenya, Rwanda, Tanzania and Uganda). As shown in Figure 1, the 99 catchment is dominated by cropland and grassland, with major build-up areas (for example 100 Kampala, Kisumu, Musoma and Mwanza) located on the shorelines of the B&Gs. LV is 101 located 1,100 meters above sea level in East Africa and is the source of the White Nile. The

102 lake is shared between the three countries of Kenya (6%), Tanzania (51%) and Uganda 103 (43%). LV has a shoreline of 3,500 km with many B&Gs and a 68,000 km² surface area, 104 making it the world's second largest freshwater lake and the largest lake in the intertropical 105 area (Dobiesz et al., 2010). The maximum depth of the lake is 80 m, the average depth is 40 106 m, and the residence time of the water is 23 years. As shown by Talling (1966), Lake Victoria 107 is monomictic, the overturn period occurring between May and August, while early thermal 108 stratification occurs between September and December and persistent thermal stratification 109 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).

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

119 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 μ moles 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).

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

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138 Differences in the phytoplankton biomasses and community compositions of the B&Gs 139 and the OL. As noted by Talling (1987), the physicochemical conditions and microbial 140 communities of the open lake (OL) are quite different from those of the B&Gs. In the B&Gs, 141 phytoplankton biomasses are often $>30 \ \mu g$ Chl-a L⁻¹, with cyanobacteria often comprising 142 more than 60% of the total phytoplanktonic biomass and frequently comprising more than 143 80% (Table 1). The rest of the phytoplanktonic community is mainly composed of 144 Chlorophyta, Cryptophyta, Dinophyta and Euglenophyta (e.g., Haande et al., 2011; Sitoki et 145 al., 2012).

In the OL, the phytoplanktonic biomass is generally less than 20 μ g 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.

151 Irrespective of the season, cyanobacteria were dominant in the B&Gs, while diatoms

152 were clearly dominant in the OL during the dry season and represented $\leq 50\%$ of the 153 phytoplanktonic biomass during the rainy season. In the latter case, cyanobacteria were the 154 second most dominant group of phytoplankton. Interestingly, Mbonde et al. (2015) have 155 shown in a comparative study performed in 16 closed and open bays that the degree of 156 connectivity of these bays to the OL greatly impacts their phytoplankton communities. The 157 average phytoplankton biovolumes were much higher in the closed bays than in the open 158 bays, and the same finding was found when considering only the cyanobacterial biovolumes 159 (Supplemental Fig. 1).

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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*.

168

169 Main cyanobacterial genera found in Lake Victoria. A great diversity of cyanobacterial 170 taxa, including both nitrogen fixing such Dolichospermum, taxa as 171 Cylindrospermopsis/Raphidiopsis or Anabaenopsis and nonnitrogen fixing taxa such as Microcystis, Planktolyngbya, Merismopedia, Cyanodictyon or Aphanocapsa, is often found in 172 173 B&Gs and the OL (Table 1). An underlying dominance of Dolichospermum spp. or 174 *Microcystis* spp. cyanobacteria has been observed in the literature depending on the location, 175 year and month of sampling considered. For example, Gikuma-Njuru et al. (2013a) observed 176 a dominance of Dolichospermum and small cyanobacteria such as Cyanodictyon and 177 Aphanocapsa between March 2005 and March 2006 in the Nyanza Gulf (Kenya), while Sitoki 178 et al. (2012) found that Microcystis was clearly the most dominant cyanobacteria in the same

179 area from July 2008 to September 2009. In Murchison Bay (Uganda), Microcystis dominance 180 was noted by Poste et al. (2013), whereas the dominance of *Dolichospermum* was found in 181 Murchison Bay and the Napoleon Gulf by Okello and Kurmayer (2011) and Okello et al. 182 (2010a). Similar observations and alternations between a dominance of Dolichospermum and 183 a very diversified cyanobacterial community were also observed by Haande et al. (2011), 184 depending on the date and the sampling station within Murchison Bay. In Tanzania, 185 Sekadende et al. (2005) found a dominance of diatoms and cyanobacteria belonging to the 186 *Planktolyngbya* genus in the Mwanza Gulf between May and August 2002. Several years 187 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 188 189 2009.

190 There is no clear explanation for these spatial and temporal variations in the dominant 191 cyanobacterial genera, but it is known that variations in nutrient concentrations can influence 192 the composition of cyanobacterial communities. For example, it has been proposed that high 193 proportions of N-fixing cyanobacteria such as Dolichospermum sp. could be linked to a 194 nitrogen limitation in the lake (Mugidde et al., 2003; Gikuma-Njuru and Hecky, 2005). In the 195 same way, many studies have shown that *Microcystis* sp. is the most common bloom-forming 196 species in freshwater ecosystems with high phosphorus concentrations (e.g., Poste et al., 197 2013).

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199 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 μ g 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.

211 Numerous studies have dealt with the detection of MC in LV (Table 1). The first study 212 reporting the presence of MC was that of Krienitz et al. (2002) and was performed in the 213 Nyanza Gulf (Table 1). After this first study, MC occurrence was recorded in different parts 214 of the lake, mainly in the B&Gs but also in the OL in some cases (Sekadende et al., 2005; 215 Sitoki et al., 2012) (Table 1). Highly variable concentrations of MC were found in LV, from less than 1 μ g.L⁻¹ in Murchison Bay (Uganda) (Semvalo et al., 2010) up to 81 μ g.L⁻¹ and >2 216 mg. L⁻¹ in Nyanza Gulf (Kenya) (Sitoki et al., 2012; Simiyu et al. 2018, respectively), the 217 218 highest concentrations being found in scums or at the surface of the lake (Table 1). A positive 219 correlation between the MC concentrations and *Microcystis* abundance was found by Okello 220 et al. (2010a, b), Sitoki et al. (2012) and Mbonde et al. (2015). Finally, Okello et al. (2010b) 221 observed during a one-year monitoring study (May 2007-April 2008) that the proportions of 222 the mcyB+ genotypes (potentially producing MC) in Microcystis populations varied from 223 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 229 230 Gulf; Sitoki et al., 2012, in the Nyanza Gulf; Mbonde et al., 2015, in the Mwanza Gulf). The 231 proportions of all these MC variants were highly variable depending on the sampled area. For 232 example, the average estimated proportions of the MC-LR variant in the Murchison Bay and 233 the Napoleon Gulf (May 2007 - April 2008) were $12.4\pm2\%$ and $0.5\pm0.3\%$, respectively, 234 according to Okello and Kurmayer (2011) but reached 50±6% in the Nyanza Gulf (July 2008 235 - Sept 2009) (Sitoki et al., 2012). The small standard deviations associated with these 236 proportions seem to express low temporal variations for a given area in LV. However, higher 237 variations are sometimes reported in the literature, as shown for example by the large standard 238 deviation found in the mean proportion (31±52%) of the MC-YR in the Nyanza Gulf (Sitoki 239 et al. 2012).

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241

4. Linking demographic changes with the increasing occurrence of cyanobacterialblooms

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.

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

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

252

253 As summarized in Figure 3, the increase in the populations density in the LV basin, 254 such as everywhere in the world, has resulted in increasing food, housing and product 255 demands (FAO, 2016). All these demands have many consequences on land use in the 256 watershed, including farming and fishing activities, as well as formal and informal 257 urbanization and industrial and commercial activities. All these processes are described in 258 section 4.1. Then, as developed in section 4.2, the changes occurring in anthropogenic 259 activities and land use have led to increasing nutrient pollution in the OL and B&Gs through 260 three main processes: the aerial deposition of phosphorus and nitrogen, the discharge of 261 mineral and organic nutrients by rivers and a decrease in natural purification due to wetland 262 degradation. Finally, section 4.3 shows why the B&Gs are more polluted than the OL and the 263 processes leading to the decrease in water quality.

264

265 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 266 267 high annual population growth estimated at 2.6% per year in its major river basins (World 268 Population Prospects, 2017). The population density in the LV basin almost doubled over the 269 past 20 years from 27.2 million to ca. 42 million inhabitants (Bremer et al., 2013), which is 270 considered the largest human population in the watersheds of the great lakes of the world 271 (Dobiesz et al., 2010). This population increased by 2.4 - 3.2% annually (> 6% in some urban 272 areas such as Kampala, Uganda; McDonald et al., 2014), a growth rate that is higher than that 273 observed in the rest of the African continent (UNEP, 2006). The data from the Center for 274 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 275 276 per km² to over 23,000 persons per km² in the last two decades. A strong and similar exponential population increase has been observed since the 1960s in Kenva, Tanzania and 277

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.

281

282 Causes of this population growth in the LV watershed. A recent report of the International 283 Institute for Sustainable Development (Dazé and Crawford, 2016) pointed out that migration 284 in the Great Lakes Region in East Africa is due partly to both voluntary decisions to migrate 285 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).

307 The main consequence of increasing population densities in rural areas is a change in 308 land use, particularly to cropland (see Figure 1). The agricultural development involves ca. >309 80% inhabitants' that depend on small-scale mixed farming operations, thus, influencing the 310 land use. As highlighted in the LVEMP report (LVEMP, 2007), agricultural development 311 includes wetland destruction and/or degradation, livestock overgrazing, bush burning, land 312 fragmentation, and deforestation. Deforestation (for settlement and agriculture development) 313 is spreading at an alarming rate, e.g., in Uganda between 2000 and 2015, the deforestation 314 rate was 3.3% annually, which is higher than that in other countries of the watershed (0.2% 315 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% 316 317 in 2000-2010, reaching 5.5% in 2010-2015). In typical developing countries, both rural and 318 urban populations depend heavily on the forest environment and products, such as building 319 materials, crafts, firewood, charcoal, food, flavoring, and traditional medicine, for their 320 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,

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328 conflicts of interest, political interference, and negative perceptions about planning policies
329 (Place & Otsuka, 2000; Mwavu & Witkowski, 2008).

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331 4.2. Relationships between land use changes and the eutrophication of LV

332 As shown in Figure 3, various processes associated with land occupation changes and 333 activities have led to the eutrophication of the OL and B&Gs. Numerous studies have focused 334 on identifying the different processes that lead to nitrogen and phosphorus pollution in LV, 335 and four main processes have been identified. These processes include (i) the discharge of 336 rivers from heavily polluted catchments (Verschuren et al., 2002; Musungu et al., 2014; 337 Fuhrimann et al., 2015; Jovanelly et al., 2015); (ii) atmospheric deposition, in particular of 338 phosphorus (P) (accounting for 55% of the total phosphorus input in LV) (Tamatamah et al., 339 2005); (iii) the biological fixation of atmospheric dinitrogen (N_2) , which seems to greatly 340 exceed the contributions of atmospheric N deposition and river N inputs (Mugidde et al., 341 2003); and to a lesser extent, (iv) nutrient recycling and release from the sediments (Gikuma-342 Njuru et al., 2010).

343 The two first nutrient pollution pathways for LV water are directly linked to human 344 population growth and activities. First, changes in land use patterns have contributed to 345 enhanced erosion. In Uganda and Tanzania, the presence of settlements on the LV shoreline 346 zone were associated with high soil erosion estimates of between 17 and 87 ton. ha⁻¹.yr⁻¹ 347 (Isabirye et al., 2010). The rate of soil loss in the LV basin also appears to depend on the land 348 use system (tree plantation versus grassland) (Bamutaze et al., 2017). Other human-induced 349 disturbances, such timber harvesting and soil compaction by cattle, also increase the risk of 350 soil erosion (Karamage et al., 2017). Similarly, TP and TN atmospheric deposition mainly 351 seem to result from burnt biomass, windblown dust and industrial and domestic activities (see 352 the review of Cheruivot and Muhandiki, 2014).

353 Second, due to the urban human population growth, increasing quantities of solid and 354 liquid waste originate from (i) the human populations living in the large cities located near the 355 B&Gs and (ii) industrial activities such as the activities of large manufacturers of steel 356 construction materials, factories that produce batteries, soap, paint, metal, plastics, corrugated 357 iron sheets, or pharmaceuticals, and breweries, tanneries, former copper smelters and abattoirs 358 (Muwanga and Barifaijo, 2006). Moreover, as shown by Cockx et al. (2019) in Tanzania, the 359 urbanization of the rural population results in changing food demands, which include 360 increasing consumption of high-sugar foods and drinks. These changes in the demand for 361 food have led for example to the installation of bottling factories in the three main cities 362 located around the lake (Kampala, Mwanza and Kisumu). For Kampala (Uganda), only ca. 363 8% of all wastes (domestic and industrial) are collected and treated (Matagi, 2002), and the 364 efficiency of the sewage treatment plants is poor, with up to ca. 89% frequency of 365 noncompliance with the national standard for BOD₅ (LVEMP, 2005). In the same way, 366 Oguttu et al. (2008) have shown that point source effluents due to increasing industrial 367 activities in the Jinja area have contributed to the increasing nutrient loads in the Napoleon 368 Gulf.

369 Finally, the progressive reduction and degradation of wetlands has played a major role 370 in the degradation of water quality. This degradation is due to housing, industrialization, 371 infrastructure development and agriculture (Kansiime & Nalubega, 1999; Fuhrimann et al., 372 2015). In the Kampala Metropolitan Area (Uganda), the proportion of severely degraded 373 wetlands increased from 13% in 1993 to 46% by 1999 (Nyakaana et al., 2007). In particular, 374 Nakivubo wetlands experienced a 62% loss in wetland vegetation between 2002 and 2014, 375 mainly due to crop cultivation (Isunju, 2016), despite their high estimated economic value of 376 between US\$ 760,000-1,300,000 (Schuijt, 2002). Similar observations have been made for the 377 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, NO₃ and NH₄) 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.

389

390 4.3. Why do the bays and gulfs of LV have more cyanobacteria blooms than the open lake?

391 Two main kinds of processes seem to be involved in the greater amount of eutrophication392 observed in the B&Gs compared to the OL.

393 First, several big towns are located on the banks of the B&Gs, such as Kampala on the 394 Murchison Bay, Kisumu on the Nyanza Gulf and Mwanza on the Mwanza Gulf. As shown by 395 Akurut et al. (2017) for the Murchison Bay (Uganda), the exponential deterioration of the 396 water quality between 2001 and 2014 was largely due to increasing quantities of waste 397 generated in Kampala City and discharged in the bay. Similar observations were made by 398 Cornelissen et al. (2014) for the Mwanza Gulf (Tanzania). Several B&Gs also receive water 399 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-Niuru 400 401 et al. (2013b). As already described in paragraph 3.2, the decrease in the natural depuration in 402 the wetlands located in the B&Gs contributes to their hyper eutrophication.

403 Second, the hydrodynamic conditions experienced by the B&Gs favors cyanobacteria 404 blooms. In the closed B&Gs (e.g., Murchison Bay, the Nyanza and Mwanza Gulfs) 405 experiencing limited exchange with the OL, the water residence time is long, and the high 406 nutrient load from their watersheds promote and sustain the development of cyanobacterial 407 blooms. Moreover, the majority of the B&Gs are very shallow, as illustrated by the Nyanza 408 Gulf, which has a mean depth of <10 m (<5 m in the eastern part of the gulf). Typically, at 409 shallow depths, all water is mixed daily and there is thermal stratification during high 410 insolation periods (Gikuma-Njuru, 2008). Consequently, the alternation of mixing and 411 stratified periods can potentially promote the release of nutrients from the sediments, which 412 can then sustain cyanobacteria growth (see for ex. Cao et al., 2016). In addition to the mixing 413 and stratification that occurs at shallow water depths, the high turbidity occurring in these 414 shallow and mixed B&Gs (Silsbe et al., 2006; Loiselle et al., 2008 & 2010) could promote the 415 development of bloom-forming cyanobacteria such as Microcystis spp. or Dolichospermum 416 spp., which are able to occupy the top of the water column where light is available for their 417 growth, due to their gas vesicles (Gikuma-Njuru, 2008; Ssebiyonga et al., 2013).

418

419 4.4. Other processes involved in the increasing occurrence of cyanobacterial blooms in LV

420 Role of changes in the fish community. Nile perch and several tilapiine species (Nile tilapia: 421 Oreochromis niloticus L.; O. leucostictus; Tilapia zillii) were introduced into the lake in the 422 1950s and became dominant (Ogutu-Ohwayo, 2004; Awange and Obiero, 2006). 423 Consequently, Marshall (2018) discussed the possibility that the changes in the fish 424 community composition during the 1960s could have aggravated the symptoms of 425 eutrophication and the proliferations of cyanobacteria in the lake. Although Goldschmidt et al. 426 (1993) emphasized the importance of endemic phytoplanktivorous and detritivorous 427 haplochromine species in the littoral and sublittoral areas of LV before the 1980s, these 428 species were victims of Nile perch predation, that led to a dramatic decrease in their 429 biomasses (Marshall, 2018). Thus, in the context of eutrophication, Batjakas et al. (1997) 430 suggested that the replacement of endemic phytoplanktivorous species by predatory Nile 431 perch could have facilitated the proliferation of cyanobacterial blooms. Moreover, as 432 suggested by Marshall (2018), cyanobacteria could have been favored by the decrease in the 433 population of large phytoplankton grazers from the zooplanktonic community due to their 434 consumption by juvenile Nile perch. The other main introduced fish species (Nile tilapia, 435 Oreochromis niloticus) is well-known to ingest a diversity of prey items including 436 phytoplankton (e.g. Bwanika et al. 2006). In LV, many authors have reported that the diet of 437 O. niloticus often have large proportion of phytoplankton dominated by cyanobacterial 438 species (Semyalo et al, 2011, Rumisha & Nehemia, 2013, Jihulya, 2014). Cyanobacteria has 439 also been shown to contribute to the bulk of the diet of O. niloticus in other tropical aquatic 440 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 441 442 are needed before concluding that this species may play a significant top-down role on the 443 dynamics of cyanobacteria.

444 Since 2005, the stock of Nile perch in LV has rapidly decreased by approximately 445 50%, mainly due to overfishing (Matsuishi et al. 2006, Mkumbo et al. 2007; Mkumbo and 446 Marshall, 2015) but also because of the degradation of the water quality (e.g. anoxia). During 447 the same period, the biomasses of other species such as Nile tilapia, catfishes or *Protopterus* 448 biomasses have increased because they are less susceptible to degraded water quality 449 (Kolding et al., 2008). The recent decrease in Nile perch stocks also favored an increase in 450 haplochromine prey species, although their biomass and diversity remains low compared to 451 the pre Nile perch era (Marshall, 2018). It is difficult to predict the consequences for 452 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).

455 In addition to the changes occurring in capture fisheries, the recent increases in cage 456 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 457 458 significantly to the nutrient enrichment of freshwater ecosystems (Zhang et al., 2006). In 459 Napoleon Gulf (Uganda), Egessa et al. (2018) observed organic matter and nutrient 460 enrichment in the sediment due to cage fish farming. In Shirati Bay (Tanzania), an increase in 461 nutrient concentrations was observed after cage farming establishment (Kashindye et al. 462 2015), while in Kenya, Njiru et al. (2018) reported increasing eutrophication in shallow areas 463 due to aquaculture waste feeds. These areas are only small portions of LV where caged fish 464 farming has occurred, but farming has begun to spread among the various B&Gs of the lake. 465 Thus, additional data are needed to study this issue and its related consequences on water quality. 466

467

468 Potential impact of climate change. The potential impact of climate change on 469 eutrophication in LV and consequently on cyanobacterial blooms has been poorly 470 investigated. Lehman et al. (1998) suggested that the eutrophication of LV may have been 471 accelerated by climate change, particularly by increased water temperature and reduced 472 vertical mixing, which are two processes that are known to influence the population dynamics 473 of cyanobacteria.

474 Recently, Tariku and Gan (2018), modeled the impacts of climate change on the
475 extreme precipitation indices and temperature of the River Nile Basin and indicated that the
476 extreme precipitation indices are projected to increase in the second part of this century.
477 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).

482

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

484 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.

491 It has been shown in numerous water bodies worldwide (e.g., Padmavathi & Veeraiah, 492 2009; Lehman et al., 2010) that severe cyanobacterial blooms impact fish populations, mainly 493 through changes induced in environmental parameters such as dissolved oxygen 494 concentrations. Indeed, severe anoxia is recorded at the bottom of deep lakes or throughout 495 the water column in shallow lakes due to the high respiration activity of bacteria degrading 496 organic matter produced by cyanobacteria. In LV, several studies have linked water quality 497 degradation to eutrophication and the changes occurring in the fish communities. For 498 instance, Kundu et al. (2017) reported significant differences in the fish community structure 499 in the Nyanza Gulf, where severe cyanobacterial blooms are frequently observed, and just 500 outside of the gulf where better water quality occurs. Furthermore, Kolding et al. (2008) 501 examined the relationship between the deterioration of water quality and the decline of Nile 502 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).

506 The second impact of cyanobacterial blooms on fish communities is associated with the potential accumulation of cyanotoxins in the fish and their subsequent potential 507 508 consequences on human health. Based on laboratory and field studies in several countries, it is 509 known that MC can accumulate in fish tissues (e.g., Jiang et al., 2012; Nchabeleng et al., 510 2014). In LV, three studies (Semyalo et al., 2010; Poste et al., 2011 and Simiyu et al., 2018) 511 have shown the accumulation of MC in several fish species. The extent of MC accumulation displayed considerable variability (from 0.5 to 90 µg.kg⁻¹ wet weight) among the fish species. 512 513 For the highest toxin concentrations, the estimated daily exposure to MC could exceed the 514 tolerable daily intake (TDI) proposed by the WHO for chronic exposure from fish 515 consumption (i.e., TDI of 0.04 µg MC-LR per kg body weight per day) (Ibelins and Chorus, 516 2007), especially for Haplochromis spp. and Rastrineobola argentea (Silver fish), which are 517 consumed whole. With the growing cage aquaculture in the B&Gs of LV and the incidence of 518 increasing nutrient loading from aquaculture, cultured fish could accumulate cyanotoxins, but 519 no data are available. Consequently, all these data suggest that the consumption of fish from 520 LV could significantly contribute to the chronic exposure of human populations to MCs.

521

522 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 μ g.L⁻¹, which is the threshold proposed by the WHO (Chorus and Bartram, 1999) for drinking water, and sometimes exceed 10 μ 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 528 challenge for local water authorities. However, regular monitoring of the MC concentrations 529 in the lake water and in the treated water produced by the plants located in the B&Gs is not 530 regularly performed. Moreover, there is no information on the sanitary risks for people 531 directly using lake water for domestic activities, including cooking and washing, or for 532 recreational activities during bloom events.

533 In addition to the potential threat of cyanobacterial blooms to human populations 534 through the consumption of raw or treated water or contaminated fish, these blooms have 535 direct and indirect consequences on the price and quantity of drinking water produced by the 536 treatment plants. In Uganda, Oyoo (2015) showed that cyanobacterial blooms impacted the 537 price of the water in different ways. First, a clarification stage was added to the oldest water 538 treatment plant (Gaba I) to improve the water quality. Second, the dosage of aluminum sulfate 539 used in the plants increased three times from 1993 to 2008 due to the increasing prevalence of 540 cyanobacterial blooms, and prechlorination was introduced to enhance coagulation and 541 settling (Olokotum, 2017). Third, the cyanobacteria blooms in Murchison Bay have forced the 542 water supply authorities and institutions to establish a new water treatment plant outside of 543 the bay at Katosi (Damba channel), which will incur additional costs due to the construction 544 of a long pipeline to carry the treated drinking water to the Kampala metropolitan area.

545 In addition to the increasing costs of water treatment due to cyanobacterial blooms, 546 Oyoo (2015) reported the impacts of cyanobacterial blooms on the availability of water to 547 local populations. The increased frequency of backwashing to avoid clogging of the sand 548 filters during water treatment at Gaba I & II in Kampala decreases the runtime of the 549 machinery, which consequently decreases the quantity of water produced by the plants for 550 populations. The costs of production and the availability of treated water are very important in 551 developing countries because when the price increases and/or the availability decreases, the 552 local populations tend to use alternative water resources that are not safe for their health (Moe and Rheingans, 2006).

554 Finally, from all these data, Figure 4 shows the potential health impacts of 555 cyanobacterial blooms for human populations living around LV. Concerning the health 556 impacts of cyanotoxins, limited data demonstrates their real adverse effects on human 557 populations. However, due to the high recorded MC concentrations and the potentially high 558 exposure of humans to these toxins (in comparison to populations from developed countries), 559 these impacts on human health should be seriously considered. This hypothesis is supported 560 by the recent paper of Roegner et al. (2020) showing that the health of peri-urban fisher 561 communities in the area of Kisumu is threatened by the consumption and use of lake water 562 contaminated with MCs and other HAB components. Moreover, in addition to the 563 disturbances caused by cyanobacteria during the production of drinking water, human 564 populations can also consume nontreated water from the lake or poorly treated water with 565 potential exposure to fecal pathogens associated with waterborne diseases.

566

567 Figure 4. Potential impacts of cyanobacterial blooms on human health in Lake Victoria
568 LW: Lake water; DW: Drinking water

569

570 6. Efforts to reduce eutrophication and the occurrence/intensity of cyanobacterial571 blooms

572 Knowing that it is well established that the eutrophication of freshwater ecosystems promotes 573 cyanobacterial blooms, the reduction of external nutrient inputs in the lakes is the main 574 sustainable strategy to reduce cyanobacterial blooms (e.g. Huisman et al., 2018). LV is a very 575 complex socioecological ecosystem, and there is limited documented knowledge (and 576 understanding) regarding the social and ecological dynamics and interactions involving LV. 577 However, based on existing knowledge, we provide arguments for the eutrophication 578 trajectory of LV and the necessity to carry out ambitious and sustainable management 579 measures to address this major problem. The modeling approach developed by Downing et al. 580 (2014) shows that controlling eutrophication is key to the protection and restoration of LV 581 and its ecosystem functions and G&S. This finding is shared by many scientists as well as the 582 local and international authorities in charge of the management of LV. Over the past 10 years, 583 many actions have been taken to restore LV under the authorities of the East African 584 Community (EAC), Lake Victoria Fisheries Organization (LVFO), Lake Victoria 585 Environment Management Program (LVEMP), and Nile Basin Initiative (NBI) (Kayombo 586 and Jorgensen, 2006).

587 We have attempted to differentiate the issues affecting the B&Gs and the OL resulting 588 from population growth and human activity because (i) the B&Gs are more polluted than the 589 OL and (ii) the main sources of pollutants affecting these areas are different. The pollution of 590 the B&Gs is largely due to the discharge of (i) solid and liquid wastes/pollutants originating 591 from big cities located on their banks and (ii) sediments and nutrients from the intensive 592 agricultural farmland. Consequently, efficient wastewater collection and treatment of these 593 domestic and industrial pollutants are critical in reducing the hyper eutrophication of the 594 B&Gs. In Murchison Bay (Uganda), most of the influxing nutrients are carried by the 595 Nakivubo channel (Fuhrimann et al., 2015), comprising mainly the rainwater and the 596 domestic and industrial wastewater of Kampala (Matagi, 2002; Kayima et al., 2008). With 597 this goal in mind, the Kampala Capital City Authority (KCCA) launched the Green Industry 598 Campaign in 2016 with the goal of improving wastewater treatment (KCCA, 2018). Recently, 599 the KCCA also piloted a new action plan to improve fecal sludge collection and transport 600 from household pit latrines, which are common in Kampala suburbs (KCCA, 2017). Finally, 601 the construction of a new wastewater treatment plant in Kampala (Bugolobi/Nakivubo sewage 602 plant) should increase the sewage treatment capacities of the National Water and Sewerage 603 Corporation (NWSC), which oversees water sanitation in Uganda. Similar approaches have 604 also been implemented for Kisumu located near the Nyanza Gulf in Kenya and for Mwanza 605 located near the Mwanza Gulf in Tanzania in the framework of the Lake Victoria Water 606 Sanitation Projects (LVWATSAN), which were first launched in 2004 but still continue to 607 support actions for the improvement of solid and liquid waste management 608 (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.

614 In addition to improving wastewater collection and treatment, the protection and 615 restoration of the numerous wetlands that are associated with the B&Gs is also important. As 616 discussed before, many wetlands have been degraded due to the pressures linked to 617 population growth. Consequently, several projects in the three riparian countries around LV 618 focused on the rehabilitation of natural wetlands and the construction of artificial wetlands. 619 These programs are aimed at securing and maintaining the hydrological and ecological 620 integrity of wetlands (MWE, 2018). This initiative requires active involvement and 621 participation of the local communities living in these areas, as shown in Kenya by Raburu et 622 al. (2012) and in Uganda by Wacker et al. (2016).

623 Concerning the OL, it has been shown that in addition to river discharge, aerial 624 depositions are the main source of nutrient inputs in the lake (e.g., Tamatamah et al., 2005; 625 Kayombo & Jorgensen, 2006). Therefore, a reduction of these inputs would be associated 626 with an integrated approach for the protection of the catchment area, including better soil 627 cover management and improved land use patterns (Okungu & Opango, 2005; Vuai et al., 628 2013). To adequately protect the watershed, deforestation needs to be halted and forests need 629 to be restored; this constitutes a much greater challenge due to the complexity of the drivers 630 of this phenomenon (Masese et al., 2012; Waiswa et al., 2015). These authors also note the 631 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.

639 In interaction with LVEMP projects, national management plans have also been 640 implemented in the countries belonging to the LV watershed. In Kenya for example, a master 641 plan for the conservation and sustainable management of water catchment areas was proposed 642 in 2012 by the Ministry of Environment and Mineral Resources (MEMR, 2012). Sub 643 catchment management plans have been implemented, for example for the Awach Kano, 644 leading to reduced deforestation, water pollution, gully erosion, etc. (Nyanchaga and Openji, 645 2017). In Tanzania, similar catchment-based actions have been implemented for the 646 protection of LV in the framework of Integrated Water Resources Management and 647 Development (IWRMD) plans (Domasa, 2019).

648

649 **7. Conclusion**

650 Due to the demographic growth and the rising concentration of the population into urban 651 areas in Africa (United Nation, 2018), we may fear that in the next decades, eutrophication of 652 freshwater ecosystems and associated cyanobacterial blooms will continue to increase in LV 653 and also in many other African lakes. Knowing that all these lakes provide numerous 654 ecosystem G&S and are vital for the water and food supply, the high microcystin 655 concentrations recorded in water and fishes of LV and the data of Roegner et al. (2020) 656 suggest that cyanobacteria and their toxins constitute a serious health concern for local 657 populations. The same is probably true in many countries of the intertropical area in Africa. 658 Consequently, it is becoming urgent in Africa (i) to implement long term monitoring 659 programs of cyanobacteria and cyanotoxins in lentic freshwater ecosystems, (ii) to define 660 water policies and rules for cyanobacteria and cyanotoxins and to inform human populations 661 about sanitary risks and (iii) to take actions for reducing the exposure of human populations to 662 cyanotoxins knowing that among these actions, the provision of affordable and easily 663 available treated-water is an urgent priority.

664 In a longer-term perspective, the battle against eutrophication will be one of the great 665 challenge of African countries. As shown in this review, the three main axes in this battle will 666 concern (i) the wastewater treatment and management in urban areas knowing that currently 667 available treatment methods might not be used in Africa due for example, to the lack of 668 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 669 670 minimizing environmental impacts (Giller et al., 2015) (iii) the protection and restoration of 671 wetlands, which can play a very important role in nutrient retention and reduction, even for 672 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 localcommunities will be also a key factor for their successful development.

684 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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1170	Supplemental Table 1. Dissolved nutrient and chlorophyll-a concentrations in the Lake
1171	Victoria
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1173	Supplemental Figure 1. Chlorophyll-a and microcystin concentrations in the main lake and
1174	in the bays and gulfs of the Lake Victoria
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1176	Supplemental Figure 2. Population size dynamics in the five countries of the watershed of
1177	Lake Victoria (data from the "World Population Prospects, The 2017 Revision", United
1178	Nations; https://population.un.org/wpp/Download/Standard/Population/)
1179	
1180	Supplemental Figure 3. Geographical distribution of the human population densities in the
1181	Lake Victoria watershed.
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