

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

3

4 Mark Olokotum^{1,2}, Veronica Mitroi³, Marc Troussellier⁴, Ronald Semyalo⁵, Cécile Bernard⁶,
5 Bernard Montuelle⁷, William Okello², Catherine Quiblier^{6,8#}, Jean-François Humbert^{3#}

6

7 ¹Makerere University, Institute of Environment and Natural Resources, Kampala, Uganda

8 ²National Fisheries Resources Research Institute (NaFIRRI), Jinja, Uganda

9 ³INRAE-Institute of Ecology and Environmental Sciences of Paris (iEES), Sorbonne

10 University, Paris, France

11 ⁴UMR MARBEC, CNRS-University of Montpellier-IRD-IFREMER, Place Eugène Bataillon,

12 Montpellier, France

13 ⁵Department of Zoology, Entomology and Fisheries Sciences, Makerere University, Kampala,

14 Uganda

15 ⁶UMR 7245 Molécules de Communication et Adaptations des Microorganismes (MCAM),

16 CNRS-MNHN, Muséum National d'Histoire Naturelle, Paris, France

17 ⁷INRAE-UMR CARTELE, Thonon, France

18 ⁸University of Paris, France

19

20

21

22 # Corresponding authors

23

24

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,
36 type and quantities of nutrients. Using data from the literature, in this paper we describe the
37 multiple ways in which the human population growth in the LV watershed is connected to the
38 increasing occurrence of cyanobacterial blooms in the OL and B&Gs. We also described the
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.

46

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
52 knowledge of the causes and consequences of cyanobacterial blooms. Taranu et al. (2015)
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
58 promote cyanobacterial blooms (e.g., Moss et al., 2011; Paerl et al., 2016; Ho et al., 2019).
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
62 deal with the production of harmful toxins by cyanobacteria and the sanitary risks associated
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,
66 the issue of cyanobacterial blooms has been poorly investigated on the African continent, as
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,

76 Juma et al., 2014). The proliferation of water hyacinth has been more or less controlled since
77 the end of the 1990s with biological, mechanical or physical strategies (Opande et al., 2004;
78 Wanda et al., 2015), but cyanobacteria blooms persist in LV, particularly in the bays and gulfs
79 (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
92 **Figure 1.** The Lake Victoria catchment area with major land use occupation. Land use data
93 obtained from the ESA Climate Change Initiative - Land Cover project 2017, accessed June
94 2019.

95

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).

110 Depending on the areas, the general climate of the Lake Victoria basin ranges from a
111 modified equatorial type characterized by heavy rainfall throughout the year to a semiarid
112 type characterized by intermittent drought periods. Overall, there are two rainfall periods
113 (long rains, March-May, and short rains, October-December) with variations ranging from
114 870 -1,561 mm in Uganda and from 400-2,736 mm in Tanzania. (Kizza et al.,2009). Water
115 temperature recorded at the surface of the lake range from 23°C to 29°C throughout the year
116 (Muggide et al., 2005).

117

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

119 *3.1. Historical and current status of cyanobacterial blooms*

120 **Recent evolution of the LV phytoplankton community.** As shown from paleolimnological
121 data by Verschuren et al. (2002), the phytoplankton production in LV has increased since the
122 1930s. Though there is insufficient nutrient data for this time period, it appears that the
123 phosphorus concentrations increased (from 1.1 to 2.9 $\mu\text{moles L}^{-1}$ between the 1960s and
124 1990s) and that eutrophication manifested towards the end of the 1980s (Hecky, 1993; Hecky
125 et al., 2010). The increasing nutrient content led to an increase in the phytoplanktonic
126 biomasses and shifts in the diatom community, from the dominance of *Aulacoseira* to the

127 dominance of *Nitzschia* (Stager et al., 2009) and in the total phytoplankton community, from
128 the dominance of green algae (Chlorophyta) and large diatoms (Bacillariophyta) to the
129 dominance of cyanobacteria (Lehman and Branstrator, 1994; Ochumba and Kibaara, 1989;
130 Kling et al. 2001; Verschuren et al., 2002; Hecky et al., 2010). This dominance of
131 cyanobacteria in phytoplankton communities is now frequently found in the three countries
132 bordering the lake (Kenya, Tanzania and Uganda), particularly in the numerous B&Gs
133 (Figure 2).

134

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

137

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 $>30 \mu\text{g Chl-a L}^{-1}$, 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).

146 In the OL, the phytoplanktonic biomass is generally less than $20 \mu\text{g Chl-a L}^{-1}$, and
147 changes from a dominance of diatoms to a dominance of cyanobacteria are frequently found
148 (Table 1). The works of Lung'ayia et al. (2000) and Sitoki et al. (2012) in the Nyanza Gulf
149 and the OL in Kenya suggest that these changes could be partly driven by the alternation of
150 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).

160

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

168

169 **Main cyanobacterial genera found in Lake Victoria.** A great diversity of cyanobacterial
170 taxa, including both nitrogen fixing taxa such as *Dolichospermum*,
171 *Cylindrospermopsis/Raphidiopsis* or *Anabaenopsis* and nonnitrogen fixing taxa such as
172 *Microcystis*, *Planktolyngbya*, *Merismopedia*, *Cyanodictyon* or *Aphanocapsa*, is often found in
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
188 different B&Gs of Tanzania, including the Mwanza Gulf, between November and December
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).

198

199 3.2. Cyanotoxin production

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

204 Nyanza Gulf (Kenya) focused on ATX (Kotut et al., 2006). Although *Dolichospermum* was
205 dominant and *Microcystis* was marginal, ATX was undetectable in both environmental
206 samples and in the isolated strains. During the same study period, the estimated MC
207 concentration was approximately $1 \mu\text{g eqMC-LR.L}^{-1}$ (Krienitz et al., 2002; Kotut et al., 2006).
208 Some of these cyanobacteria are also known to potentially produce other cyanotoxins such as
209 the amino acid variant β -methyl-amino-L-alanine (BMAA) and saxitoxins, but these
210 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
216 less than $1 \mu\text{g.L}^{-1}$ in Murchison Bay (Uganda) (Semyalo et al., 2010) up to $81 \mu\text{g.L}^{-1}$ and >2
217 mg.L^{-1} in Nyanza Gulf (Kenya) (Sitoki et al., 2012; Simiyu et al. 2018, respectively), the
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.

224 So far, 240 MC variants have been described in the world (Spoof and Catherine,
225 2017), but only a few studies have investigated the MC variant composition in the
226 cyanobacterial blooms from LV (Table 1). Nevertheless, up to seven different variants have
227 been identified by Okello and Kurmayer (2011) and up to 31 variants have been identified by
228 Miles et al. (2013). However, the most common variants detected in the lake are MC-LR,

229 MC-RR and MC-YR (e.g., Okello and Kurmayer, 2011, in Murchison Bay and the Napoleon
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 $12.4\pm 2\%$ and $0.5\pm 0.3\%$, respectively,
234 according to Okello and Kurmayer (2011) but reached $50\pm 6\%$ 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 ($31\pm 52\%$) of the MC-YR in the Nyanza Gulf (Sitoki
239 et al. 2012).

240

241

242 **4. Linking demographic changes with the increasing occurrence of cyanobacterial** 243 **blooms**

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

248

249 **Figure 3.** Links between the increase in the human population density around Lake Victoria
250 and 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*

266 **Demographic data on the LV watershed.** The African continent continues to experience a
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)
275 indicates that the population density in major cities has increased from a max of 100 persons
276 per km² to over 23,000 persons per km² in the last two decades. A strong and similar
277 exponential population increase has been observed since the 1960s in Kenya, Tanzania and

278 Uganda (Supplemental Figure 2). On the other hand, Burundi and Rwanda, which
279 experienced civil war in the 1990s and do not have direct access to the lake, have seen much
280 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.

286 Concerning the voluntary migration, many people have migrated towards the lake
287 basin to take advantage of the economic benefits linked to the fisheries in the basin (Awange
288 and Obiero, 2006; Odada et al., 2009). As reported in Mkumbo & Marshall (2015), more than
289 1,200,000 people are directly or indirectly employed in fisheries, and income from fisheries
290 supports approximately 4 million people. This makes LV the world's largest host for inland
291 freshwater fisheries (Simonit and Perrings, 2011).

292 On the other hand, forced migrations have resulted from armed conflicts and violence
293 in Rwanda and Burundi (from 1993 to 2005) and in the Democratic Republic of Congo (from
294 1996 to 2002). Many of these migrants are located in rural areas (Dazé and Crawford, 2016).

295
296 **Consequences of population growth on land use, urbanization and anthropogenic**
297 **activities.** As established in the diagnostic analysis performed by the Lake Victoria
298 Environmental Management Project (LVEMP), more than 87% of the inhabitants living in the
299 LV basin are from the rural populations in Burundi, Kenya, Rwanda and Tanzania (see also
300 Figure 1), while in Uganda, 94% of the inhabitants living in the LV basin are urban (LVEMP,
301 2007). Meanwhile, as already observed in the developing world (Montgomery, 2008), the
302 three countries with direct access to the lake and with livelihoods that rely on the lake have

303 also experienced rapid urbanization that has led to the development of large cities located on
304 the B&Gs, such as Kampala (>2 million inhabitants) on Murchison Bay (Uganda), Kisumu
305 (approximately 1 million inhabitants) on the Nyanza Gulf (Kenya) and Mwanza (>400,000
306 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
316 deforestation rate has increased from 1990-2015 in Uganda (from 2.0% in 1990-2000 to 3.3%
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).

321 The drivers of deforestation identified in the LV watershed can be classified into two
322 broad categories (Waiswa et al., 2015). The direct human uses of forest resources (Geist &
323 Lambin, 2002; Mwavu & Witkowski, 2008) include the unplanned spread of agricultural
324 areas over forest areas, firewood and timber harvesting, clearing forestland for human
325 settlement, sand mining and brickmaking. The indirect drivers concern the underlying
326 sociopolitical factors impacting human practices, such as unclear land tenure and/or property
327 rights, lack of forest monitoring and the noninvolvement of users in forest maintenance,

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

330

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 $\text{ton. ha}^{-1}.\text{yr}^{-1}$
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 Cheruiyot 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; Fuhrmann 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

378 that an increase in the anthropogenic activities in the Musoma urban area was associated with
379 the degradation of wetland coverage at the average rate of 6.5 ha yr⁻¹ between 2001 and 2008.
380 Knowing that wetlands are located at the mouths of the major rivers and in the inshore areas
381 of the lake (Okeyo-Owuor et al., 2012) and that they play a major role in waste removal and
382 water purification (Raburu et al., 2012), their degradation contributes to the decrease in water
383 quality in the B&Gs.

384 The consequences of all these processes acting on the nutrient load in Lake Victoria is
385 that high concentrations in soluble elements (SRP, NO₃ and NH₄) have been recorded in the
386 twenty past years in the Lake Victoria (Supplemental Table 1). The average TN:TP ratios are
387 almost double in B&Gs (14.5) than in OL (8.1) (Muggide et al., 2005). This suggests that there is
388 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 eutrophication
392 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.
400 This contribution has been shown for example for the Nyanza Gulf (Kenya) by Gikuma-Njuru
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 (Ogotu-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**
441 **al. 2019). However, new data on the quantitative predation of cyanobacteria by *O. niloticus***
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

453 the grazing rates of both fish and zooplankton always have always been low in Lake Victoria,
454 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)
457 constitutes an additional threat for the lake. It is well known that aquaculture can contribute
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
466 quality.

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

478 events in a future with warmer climate scenarios. These changes might have dramatic
479 consequences on LV because extreme rain events contribute to runoff and soil erosion, which
480 enhance the eutrophication of aquatic ecosystems (e.g., Moss et al., 2011) and consequently
481 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*

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

503 lake resulting from the degradation of phytoplanktonic organic matter may be the cause of the
504 decline in Nile perch. However, this hypothesis is still in debate, as discussed by Mkumbo &
505 Marshall (2015).

506 The second impact of cyanobacterial blooms on fish communities is associated with
507 the potential accumulation of cyanotoxins in the fish and their subsequent potential
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
512 displayed considerable variability (from 0.5 to 90 $\mu\text{g}\cdot\text{kg}^{-1}$ wet weight) among the fish species.
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*

523 As shown in Table 1, the MC concentrations in the LV water frequently exceed 1 $\mu\text{g}\cdot\text{L}^{-1}$,
524 which is the threshold proposed by the WHO (Chorus and Bartram, 1999) for drinking water,
525 and sometimes exceed 10 $\mu\text{g}\cdot\text{L}^{-1}$, which is the lowest threshold set by the sanitary authorities
526 from the northern countries for recreational activities (Chorus et al., 2012). Consequently, as
527 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

553 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 cyanobacterial** 571 **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/>).

609 All these actions are very important for the protection of the B&Gs of LV, but
610 estimating their “real” impacts on the improvement of the water quality in the B&Gs remains
611 difficult. Indeed, in urban areas, the wastewater collection networks are still limited, which
612 results in the treatment of a small proportion of sewage, and with the predicted increased
613 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.

632 In the framework of the Lake Victoria Environmental Management Project phases I
633 and II (LVEMP I and II), several soil conservation and afforestation projects were
634 implemented to limit soil erosion and the aerial deposition of nutrients in the lake. The impact
635 of these projects on the water quality of the OL has not been estimated. However, considering
636 the size of the watershed and the increasing population density, soil conservation projects will
637 require considerable concerted efforts by the five countries before expecting “significant
638 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
669 as conservation agriculture, allowing to provide foods to a growing population whilst
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) .

673 As already experienced in developed countries, all these actions for reducing the
674 exposure of human populations to cyanotoxins and the eutrophication will be very costly and
675 consequently require international financial cooperation. There is also need for international
676 collaborative research programs involving scientists and people from local institutions

677 working in the water domain. Finally, the involvement and participation of the local
678 communities will be also a key factor for their successful development.

679

680

681

682

683

684 **Acknowledgement**

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

688

689

690

691

692 **References**

- 693 Akurut, M., Niwagaba, C.B., Willems, P., 2017. Long-term variations of water quality in the
694 Inner Murchison Bay, Lake Victoria. *Environ. Monit. Assess* 189(1), 22.
- 695 Aura, C. M., Musa, S., Yongo, E., Okechi, J. K., Njiru, J. M., Ogari, Z., Wanyama, R., Charo-
696 Karisa, H., Mbugua, H., Kidera, S., Ombwa V., Oucho, V., 2018. Integration of
697 mapping and socio-economic status of cage culture: Towards balancing lake-use and
698 culture fisheries in Lake Victoria, Kenya. *Aquacult. Res.* 49(1), 532-545.
- 699 Awange, J.L., Obiero, O., 2006. *Lake Victoria-Ecology, Resources, Environment.*
700 Heidelberg. Springer Berlin.
- 701 Bamutaze, Y., Wanyama, J., Diekrugger, B., Meadows, M., Opedes H., 2017. Dynamics of
702 surface runoff and soil loss from a toposequence under varied land use practices in
703 Rwizi catchment, Lake Victoria Basin. *J. Soil Water Cons.* 72, 480-492.
- 704 Batjakas, I.E., Edgar, R.K., Kaufman, L.S., 1997. Comparative feeding efficiency of
705 indigenous and introduced phytoplanktivores from Lake Victoria: Experimental
706 studies on *Oreochromis esculentus* and *Oreochromis niloticus*. *Hydrobiologia* 347, 75-
707 82.
- 708 Bernard, C., Ballot, A., Thomazeau, S., Maloufi, S., Furey, A., Mankiewicz-Boczek, J.,
709 Pawlik-Skowronska, B., Capelli, C., Salmaso, N., 2017. In book: *Handbook of*
710 *Cyanobacterial Monitoring and Cyanotoxin Analysis*, Edition: 1st, Chapter:
711 *Cyanobacteria associated with the production of cyanotoxins*, Publisher: Wiley,
712 Editors: Jussi Meriluoto, Lisa Spoo, Geoffrey Codd, pp. 501 – 525.
- 713 Bremer, J., Lopez-Carr, D., Zvoleff, A., Pricope, N., 2013. Using new methods and data to
714 assess and address population, fertility, and environment links in the Lake Victoria.
715 XXVII IUSSP International Population Conference.
716 https://iussp.org/sites/default/files/event_call_for_papers/IUSSP_paper_JBremner_et_al_0.pdf.
717
- 718 Briand, J.F., Jacquet, S., Bernard, C., Humbert, J.F., 2003. Health hazards for terrestrial
719 vertebrates from toxic cyanobacteria in surface water ecosystems. *Vet. Res.* 34, 361-
720 377.
- 721 Bwanika, G.N., Chapman, L.J., Kizito, Y., Balirwa, J., 2006. Cascading effects of introduced
722 Nile perch (*Lates niloticus*) on the foraging ecology of Nile tilapia (*Oreochromis*
723 *niloticus*). *Ecol. Freshw. Fish*, 15, 470-481.
- 724 Cao, X., Wang, Y., He, J., Luo, X., Zheng, Z., 2016. Phosphorus mobility among sediments,
725 water and cyanobacteria enhanced cyanobacteria blooms in eutrophic Lake Dianchi.
726 *Environmental Pollution* 219, 580-587.
- 727 Cheruiyot, C. Muhandiki, V., 2014. Review of estimation of pollution load to Lake Victoria.
728 *J. Environ. Earth Sci.* 4, 113-120.
- 729 Chorus, I., 2012. Current approaches to Cyanotoxin risk assessment, risk management and
730 regulations in different countries. Edited by Section II Drinking Water and Swimming
731 Pool Water Hygiene, Federal Environment Agency, Germany Eds, 151pp.
- 732 Chorus, I., Bartram, J., 1999. *Toxic cyanobacteria in water : A guide to their public health*
733 *consequences, monitoring and management.* E&FN Spon, London & New York.
- 734 Center for International Earth Science Information Network - CIESIN - Columbia University,
735 2018. *Gridded Population of the World, Version 4 (GPWv4): Population Density,*
736 *Revision 11.* Palisades, NY: NASA Socioeconomic Data and Applications Center
737 (SEDAC). Retrieved from: <https://doi.org/10.7927/H49C6VHW>. Thursday 13th June
738 2019.
- 739 Cockx, L., Colen, L., De Weerd, J., Gomez, Y., Paloma, S., 2019. Urbanization as a driver of
740 changing food demand in Africa: Evidence from rural-urban migration in Tanzania.

- 741 JCR Technical Reports, 51 p. (doi:10.2760/515064).
- 742 Cornelissen, I.J.M., Silsbe, G.M., Verreth, J.A.J., van Donk, E., Nagelkerke, L.A.J., 2014.
743 Dynamics and limitations of phytoplankton biomass along a gradient in Mwanza Gulf,
744 southern Lake Victoria (Tanzania). *Fresh. Biol.* 59, 127-141.
- 745 Dazé, A., Crawford, A., 2016. Human migration and ecosystems: Insights from the Great
746 Lakes Region of East and Central Africa. IISD Report, 20 p.
- 747 Dobiesz, N.E., Hecky, R.E., Johnson, T.B., Sarvala, J., Dettmers, J.M., Lehtiniemi, M.,
748 Rudstam, L.G., Madenjian, C.P., Witte, F., 2010. Metrics of ecosystem status for large
749 aquatic systems - A global comparison. *J. Great Lakes Res.* 36(1), 123-138.
- 750 Dodds, W.K., Bouska, W.W., Eitzmann, J.L., Pilger, T.J., Pitts, K.L., Riley, A.J., Schloesser,
751 J.T., Thornbrugh, D.J., 2009. Eutrophication of US freshwaters: Analysis of potential
752 economic damages. *Environ. Sci. Technol.* 43(1), 12-19.
- 753 Domasa, S., 2019. How can we best protect Lake Victoria's ecosystem? The Niles. Retrieved
754 from <https://www.theniles.org/en/articles/politics/20625/>
- 755 Downing, A.S., van Nes, E.H., Balirwa, J.S., Beuving, J., Bwathondi, P.O. J., Chapman,
756 L.J., Cornelissen, L., Cowx, I.G., Goudswaard, K.P.C., Kecky, R.E., Janse, J.H.,
757 Janssen, A.B.G., Kaufmann, L., Kische-Machumu, M.A., Kolding, J., Ligtvoet, W.,
758 Mbabazi, D., Merdard, M., Mkumbo, Malponi, E., Munyaho, A.T., Nagelkerke,
759 N.A.J., Ogutu-Ohwayo, R., Ojwang, W.O., Peter, H.K., Schindler, D.E., Seehausen,
760 O., Sharpe, D., Silsbe, G.M., Sitoki, L., Tumwebase, R., Tweddle, D., van de
761 Wolfshaar, K.E., van Dijk, H., van donk, E., van Rijssel, J.C., van Zwieten P.A.M.,
762 Wanink, J., Witte, F., Mooij, W.M., 2014. Coupled human and natural system
763 dynamics as key to the sustainability of Lake Victoria's ecosystem services. *Ecol. Soc.*
764 19(4), 31. doi.org/10.5751/ES-06965-190431.
- 765 Egessa, R., Pabire, G.W., Ocaya, H., 2018. Benthic macroinvertebrate community structure in
766 Napoleon Gulf, Lake Victoria: effects of cage aquaculture in eutrophic lake. *Environ.*
767 *Monitoring and Assessment*, 190(3), 112.
- 768 El-Noshokaty, D., 2017. Big Lakes, Big Problems. Is There Still Time to Secure the Water
769 Resources Lake Victoria Provides? International Reports of the Konrad-Adenauer-
770 Stiftung. 11p.
- 771 Escalas, A., Catherine, A., Maloufi, S., Cellamare, M., Hamlaoui, S., Yéprémian, C.,
772 Louvard, C., Troussellier, M., Bernard, C., 2019. Drivers and ecological consequences
773 of dominance in periurban phytoplankton communities using networks approaches.
774 *Wat. Res.* 163, 114893.
- 775 Food and Agricultural Research Organisation-FAO, 2015. The state of food insecurity in the
776 World. doi.org/http://www.fao.org/.
- 777 Food and Agricultural Research Organisation-FAO, 2016. Economic analysis of food supply
778 and demand in sub-Saharan Africa up to 2022 – special focus on fish and fishery
779 products, by Trond Bjørndal, Alena Lappo, Madan Dey, Audun Lem and Anna Child.
780 Fisheries and Aquaculture Circular No. 1101. Rome, Italy.
- 781 Fuhrmann, S., Stalder, M., Winkler, M.S., Niwagaba, C.B., Babu, M., Masaba, G.,
782 Kabatereine, N.B., Halage, A.A., Schneeberger, P.H.H., Utzinger, J., Cissé, G., 2015.
783 Microbial and chemical contamination of water, sediment and soil in the Nakivubo
784 wetland area in Kampala, Uganda. *Environ Monit. Assess.* 187:475. DOI
785 10.1007/s10661-015-4689-x
- 786 Geist, H., Lambin, E., 2002. Proximate causes and underlying driving forces of tropical
787 deforestation. *Biosci.* 52, 143-150.
- 788 Gikuma-Njuru, P., 2008. Physical and biogeochemical gradients and exchange processes in
789 Nyanza gulf and main Lake Victoria (East Africa). PhD Thesis, University of
790 Waterloo, Waterloo.

- 791 Gikuma-Njuru, P., Hecky, R.E., 2005. Nutrient concentrations in Nyanza Gulf, Lake Victoria,
792 Kenya: light limits algal demand and abundance. *Hydrobiologia* 534, 131-140.
- 793 Gikuma-Njuru, P., 2008. Physical and biogeochemical gradients and exchange processes in
794 Nyanza Gulf and main Lake Victoria (East Africa). PhD Thesis. University of
795 Waterloo, Ontario, Canada.
- 796 Gikuma-Njuru, P., Hecky, R.E., Guildford, S.J., 2010. Surficial sediment phosphorus
797 fractions along a biogeochemical gradient in Nyanza (Winam) Gulf, northeastern Lake
798 Victoria and their possible role in phosphorus recycling and internal loading.
799 *Biogeochem.* 97, 247-261.
- 800 Gikuma-Njuru, P., Guildford, S.J., Hecky, R.E., Kling, H.J., 2013a. Strong spatial
801 differentiation of N and P deficiency, primary productivity and community
802 composition between Nyanza Gulf and Lake Victoria (Kenya, East Africa) and the
803 implications for nutrient management. *Freshw. Biol.* 58(11), 2237-2252.
- 804 Gikuma-Njuru, P., Hecky, R.E., Guildford, S.J., Macintyre, S., 2013b. Spatial variability of
805 nutrient concentrations, fluxes, and ecosystem metabolism in Nyanza Gulf and
806 Rusinga Channel, Lake Uictoria (East Africa). *Limnol. Oceanogr.* 58(3), 774-789.
- 807 Giller, K.E., Andersson, J.A., Corbeels, M., Kirkegaard, J., Mortensen, D., Erenstein, O.,
808 Vanlauwe, B., 2015. Beyond conservation agriculture. *Front. Plant Sci.* 6, 870.
- 809 Goldschmidt, T., Witte, F., Wanink, J., 1993. Cascading Effects of the Introduced Nile Perch
810 on the Detritivorous/Phytoplanktivorous Species in the Sublittoral Areas of Lake
811 Victoria. *Conserv. Biol.* 7(3), 686-700.
- 812 Haande, S., Rohrlack, T., Semyalo, R. P., Brettum, P., Edvardsen, B., Lyche-Solheim, A.,
813 Sorensen, K., Larsson, P., 2011. Phytoplankton dynamics and cyanobacterial
814 dominance in Murchison Bay of Lake Victoria (Uganda) in relation to environmental
815 conditions. *Limnologica - Ecology and Management of Inland Waters* 41(1), 20-29.
- 816 Hecky, R.E., 1993. The eutrophication of Lake Victoria. *Verhandlungen Des Internationalen*
817 *Verein Limnol.* 25, 39-48.
- 818 Hecky, R.E., Bugenyi, F.W.B., Ochumba, P., Talling, J.F., 1994. Deoxygenation of the deep
819 water of Lake Victoria, East Africa. *Limnol. Oceanogr.* 39(6), 1476-1481.
- 820 Hecky, R.E., Muggide, R., Ramsal, P.S., Talbot, M.R., Kling, G.W., 2010. Multiple stressors
821 cause rapid ecosystem change in Lake Victoria. *Freshw. Biol.* 55(Suppl. 1), 19-42.
- 822 Ho, J.C., Michalak, A.M., Pahlevan, N., 2019. Widespread global increase in intense lake
823 phytoplankton blooms since the 1980s. *Nature* 574, 667
- 824 Huisman, J., Codd, G.A., Paerl, H.W., Ibelings, B.W., Verspagen, J.M.H., Visser, P.M., 2018.
825 Cyanobacterial blooms. *Nature Rev. Microbiol.* 16(8). DOI: 10.1038/s41579-018-
826 0040-1.
- 827 Ibelings, B.W., Chorus, I., 2007. Accumulation of cyanobacterial toxins in freshwater
828 “seafood” and its consequences for public health: A review. *Environ. Pollut.* 150,
829 177-192.
- 830 Isabirye, M., Kimaro, D., Semalulu, O., 2010. Sediment production from settlements and
831 farmlands within Lake Victoria shoreline zone in Uganda and Tanzania. *Tropicultura*
832 28, 89-95.
- 833 Isunju, J.B., 2016. Spatiotemporal analysis of encroachment on wetlands: hazards,
834 vulnerability and adaptations in kampala city, Uganda. PhD Dissertation. University of
835 Stellenbosch, South Africa.
- 836 Jiang, J., Shi, Y., Shan, Z., Yang, L., Wang, X., Shi, L., 2012. Bioaccumulation, oxydative
837 stress and HSP70 expression in *Cyprinus carpio* L. exposed to microcystin-LR under
838 laboratory conditions. *Comparative Biochemistry and Physiology Part C: Toxicol.*
839 *Pharmacol.* 155 (3), 483-490.
- 840 Jihulya, N.J. 2014. Diet and feeding ecology of Nile tilapia, *Oreochromis niloticus* and Nile

- 841 perch, *Lates niloticus* in protected and unprotected areas of Lake Victoria, Tanzania.
842 Int. J. Sci. Technol. Res. 3, 280–286.
- 843 Jovanelly, T. J., Johnson-Pynn, J., Okot-Okumu, J., Nyenje, R., Namaganda, E., 2015.
844 Pioneering water quality data on the Lake Victoria watershed: Effects on human
845 health. J. Wat. Health 13(3), 920-930.
- 846 Juma, D.W., Wang, H., Li F., 2014. Impacts of population growth and economic development
847 on water quality of a lake: case study of Lake Victoria Kenya water. Environ. Sci. Poll. Res.
848 21, 5737-5746
- 849 Kabenge, M., Wang, H., Li, F., 2016. Urban eutrophication and its spurring conditions in the
850 Murchison Bay of Lake Victoria. Environ. Sci. Pollut. Res. Int. 23, 234-241.
- 851 Kampala Capital City Authority-KCCA, 2017. Piloting a mobile sludge transfer tank in 5
852 parishes of Kampala. [https://www.kcca.go.ug/news/242/Piloting-a-mobile-sludge-
853 transfer-tank-in-5-parishes-of-Kampala#.XCTz5WIRWM8](https://www.kcca.go.ug/news/242/Piloting-a-mobile-sludge-transfer-tank-in-5-parishes-of-Kampala#.XCTz5WIRWM8)
- 854 Kampala Capital City Authority-KCCA, 2018. What is the Kampala Green Industry
855 Campaign. <https://www.kcca.go.ug/ptf-gic>
- 856 Kansiime, F., Nalubega, M., 1999. Wastewater Treatment by a Natural Wetland: The
857 Nakivubo Swamp, Uganda. IHE. <http://edepot.wur.nl/192727>.
- 858 Karamage, F., Zhang, C., Liu, T. Maganda, A., Isabwe, A., 2017. Soil erosion risk assessment
859 in Uganda. Forests 8, 52.
- 860 Kashindye, B. B., Nsinda, P., Kayanda, R., Ngupula, G. W., Mashafi, C. A., & Ezekiel, C. N.,
861 2015. Environmental impacts of cage culture in Lake Victoria: the case of Shirati Bay-
862 Sota, Tanzania. *SpringerPlus*, 4, 475-475. doi:10.1186/s40064-015-1241-y
- 863 Kayima, J., Kyakula, M., Komakech, W., Echimu, S.P., 2008. A study of the degree of
864 pollution in Nakivubo Channel, Kampala, Uganda. J. Environ. Sci. Appl. Manag.
865 12(2), 93-98.
- 866 Kayombo, S., Jorgensen, S.E., 2006. Lake Victoria: Experience and Lessons Learned Brief,
867 In: Lake Basin Management Initiative: Experience and Lessons Learned Briefs (on
868 CD). International Lake Environment Committee Foundation, Kusatsu, Japan, pp.
869 431-446.
- 870 Kizza, M., Rodhe, A., Xu, C.Y., Ntale, H.K., Halldin, S., 2009. Temporal rainfall variability
871 in the Lake Victoria Basin in East Africa during the twentieth century. Theor. Appl.
872 Climatol. 98, 119-135.
- 873 Kling, H.J., Mugidde, R., Hecky, R.E., 2001. Recent changes in the phytoplankton
874 community in response to eutrophication. In M. Munawar R.E. Hecky (Eds.), The
875 Great Lakes of the World (GLOW): Food-web, health and integrity (pp. 44-65).
876 Leiden, The Netherlands: Backhuys.
- 877 Kolding, J., van Zwieten, P., Mkumbo, O., Silsbe, G., Hecky, R.E., 2008. Are the Lake
878 Victoria fisheries threatened by exploitation or eutrophication? Towards an ecosystem
879 based approach to management. In R. Bianchi, & H. R. Skjoldal (Eds.), The
880 ecosystem approach to fisheries. (pp 309-354). Rome: CABI Publishing.
- 881 Kotut, K., Ballot, A., Krienitz, L., 2006. Toxic cyanobacteria and their toxins in standing
882 waters of Kenya: implications for water resource use. J. Wat. Health 4(Suppl. 2), 3-18.
- 883 Krienitz, L., Ballot, A., Wiegand, C., Kotut, K., Codd, G.A., Pflugmacher, S., 2002.
884 Cyanotoxin-producing bloom of *Anabaena flos-aquae*, *Anabaena discoidea* and
885 *Microcystis aeruginosa* (Cyanobacteria) in Nyanza Gulf of Lake Victoria, Kenya. J.
886 Appl. Bot. 76, 179-183.
- 887 Kundu, R., Aura, C.M., Nyamweya, C., Agembe, S., Sitoki, L., Lung'ayia, H., Ongore, C.,
888 Ogari, Z., Werimo, K., 2017. Changes in pollution indicators in Lake Victoria, Kenya
889 and their implications for lake and catchment management. Lakes Reserv. Res.
890 Manag. 22(3), 199-214.

- 891 Lake Victoria Environmental Management Project (LVEMP), 2005. Water quality and
892 ecosystem status. <http://hdl.handle.net/11671/718>
- 893 Lake Victoria Environmental Management Project (LVEMP), 2007. Preparation of National /
894 Regional Management Framework: Institutional Component for the Lake Victoria
895 Basin Final National Report. <http://repository.eac.int>.
- 896 Lehman, J.T., 1998. Role of climate in the modern condition of Lake Victoria. *Theor. Appl.*
897 *Climatol.* 61, 29-37.
- 898 Lehman, J.T., Branstrator, D.K., 1994. Nutrient dynamics and turnover rates of phosphate and
899 sulfate in Lake Victoria, East Africa. *Limnol. Oceanogr.* 39(2), 227-233.
- 900 Lehman, P.W., The, S.J., Boyer, G.L., Nobriga, M.L., Bass, E., Hogle, C., 2010. Initial
901 impacts of *Microcystis aeruginosa* blooms on the aquatic food web in the San
902 Francisco Estuary. *Hydrobiologia* 637, 229-248.
- 903 Loiselle, S.A., Azza, N., Cozar, A., Bracchini, L., Tognazzi, A., Dattilo, A., Rossi, C.,
904 2008. Variability in factors causing light attenuation in Lake Victoria. *Freshw. Biol.* 53
905 (3), 535-545.
- 906 Loiselle, S.A., Azza, N., Gichuki, J., Bracchini, L., Tognazzi, A., Dattilo, A.M., Rossi, C.,
907 2010. Spatial dynamics of chormophoric dissolved organic matter in nearshore waters
908 of Lake Victoria. *Aquat. Ecosyst. Health Manag.* 13, 1-11.
- 909 Lu, K., Jin, C., Dong, S., Gu, B., Bowen, S.H., 2006. Feeding and control of blue-green algal
910 blooms by tilapia (*Oreochromis niloticus*). *Hydrobiologia*, 568, 111-120.
- 911 Lung'aya, H.B.O., M'harzi, A., Tackx, M., Gichuki, J., Symoens, J.J., 2000. Phytoplankton
912 community structure and environment in the Kenyan waters of Lake Victoria. *Freshw.*
913 *Biol.* 43, 529-543.
- 914 Marshall, B.E., 2018. Guilty as charged: Nile perch was the cause of the haplochromine
915 decline in Lake Victoria. *Can. J. Fish. Aquat. Sci.* 75(9), 1542-1559.
- 916 Masese, F.O., Raburu, P.O., Mwasi, B.N., Etiégni, L., 2012. Effects of Deforestation on
917 Water Resources: Integrating Science and Community Perspectives in the Sondu-
918 Miriu River Basin, Kenya. *IntechOpen: New Advances and Contributions to Forestry*
919 *Research*, 3–18. doi.org/10.5772/2246.
- 920 Matagi, S.V., 2002. Some Issues of Environmental Concern in Kampala, the Capital City of
921 Uganda. *Environ. Monit. Assess.* 77, 121-138.
- 922 Matsuishi, T., Muhoozi, L., Mkumbo, O., Budeba, Y., Njiru, M., Asila, A., Othina, A., Cowx
923 I.G., 2006. Are the exploitation pressures on the Nile perch fisheries resources of Lake
924 Victoria a cause for concern? *Fish. Manag. Ecol.* 13(1), 53-71.
- 925 Mbonde, A.S., Sitoki, L., Kurmayer, R., 2015. Phytoplankton composition and microcystin
926 concentrations in open and closed bays of Lake Victoria, Tanzania. *Aquat. Ecosyst.*
927 *Health Manag.* 18(2), 212-220.
- 928 MEMR, 2012. Masterplan for the conservation and sustainable management of water
929 catchment areas in Kenya. Ministry of Environment and Mineral Resources
930 (https://www.preventionweb.net/files/34692_conservationmasterplanfinal.pdf).
- 931 Merel, S., Walker, D.B., Chicana, R., Synder, S.A., Baures, E., Thomas, O., 2013. State of
932 knowledge and concerns on cyanobacterial blooms and cyanotoxins. *Environ. Internat.*
933 59, 303-327.
- 934 Meriluoto, J., Blaha, L., Bojadzija, G., Bormans, M., Brient, L., Codd, G. A., Drobac, D.,
935 Faassen, E.J., Fastner, J., Hiskia, A., Ibelings, B.W., Kaloudis, T., Kokocinsky, M.,
936 Kurmayer, R., Pantelic, D., Quesada, A., Salmaso, N., Tokodi, N., Triants, T.M.,
937 Visser, P.M., Svirčev, Z., 2017. Toxic cyanobacteria and cyanotoxins in European
938 waters – recent progress achieved through the CYANOCOST Action and challenges
939 for further research. *Adv. Oceanogr. Limnol.* 8(1), 161-178.
- 940 Michalak, A. M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B.,

- 941 Chaffin, J.D., Cho, K., Confesor, R., Daqloglu, I., DePinto, J.V., Evans, M.A.,
 942 Fahnenstiel, G.L., He, L., Ho, J.C., Jenkins, L., Johengen, T.H., Kuo, K.C., LaPorte,
 943 E., Liu, X., McWilliams, M.R., Moore, M.M., Posselt, D.J., Richards, R.P., Scavia,
 944 D., Steiner, A.L., Verhamme, E., Wirght, D.M., Zagorski, M.A., 2013. Record-setting
 945 algal bloom in Lake Erie caused by agricultural and meteorological trends consistent
 946 with expected future conditions. *Proc. Nat. Acad. Sci. USA* 110(16), 6448-6452.
- 947 Miles, C.O., Sandvik, M., Nonga, H.E., Rundberget, T., Wilkins, A.L., Rise, F., Ballot, A.,
 948 2013. Identification of microcystins in a Lake Victoria cyanobacterial bloom using
 949 LC-MS with thiol derivatization. *Toxicon* 70, 21-31.
- 950 Ministry of Water and Environment-MWE, 2018. Wetlands Management Department.
 951 <https://www.mwe.go.ug/dept/wetlands-management-department>.
- 952 Mkumbo, O.C., Marshall, B.E., 2015. The Nile perch fishery of Lake Victoria: Current status
 953 and management challenges. *Fish. Manag. Ecol.* 22(1), 56-63.
- 954 Mkumbo, O.C., Nsinda, P., Ezekiel, C.N., Cowx, I.G., Aeron, M., 2007. Towards sustainable
 955 exploitation of Nile perch consequential to regulated fisheries in Lake Victoria. *Aquat.*
 956 *Ecosyst. Health Manag.* 10(4), 449-457.
- 957 Moe, C. L., Rheingans, R. D., 2006. Global challenges in water, sanitation and health. *J. Wat.*
 958 *Health* 4(Suppl. 1), 41-58.
- 959 Montgomery, M.R., 2008 The urban transformation of the developing world. *Science* 319,
 960 761-764.
- 961 Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., Havens, K.,
 962 Lacerot, G., Liu, Z., De Meester, L., Paerl, H., Scheffer, M., 2011. Allied attack:
 963 climate change and eutrophication. *Inland Wat.* 1(2), 101-105.
- 964 Muggide, R., Hecky, R.E., Hendzel, L.L., Taylor, W.D., 2003. Pelagic nitrogen fixation in
 965 Lake Victoria (East Africa). *Journal of Great Lakes Research* 29, 76-88.
- 966 Muggide, R., Hecky, R.E., Ndawula, L., 2005. Chapter Eight - Eutrophication of Lake
 967 Victoria, Uganda. In *Water Quality and Quantity Synthesis Final report, LVEMP*, pp.
 968 131-148.
- 969 Musamba, E.B., Ngaga, Y.M., Boon, E.K., Giliba, R.A., 2011. Impact of socio-economic
 970 activities around Lake Victoria: Land use and land use changes in Musoma
 971 municipality, Tanzania. *J. Hum. Ecol.* 35, 143-154.
- 972 Musungu, P.C., Lalah, J.O., Jondiko, I.O., Onger, D.M.K., 2014. The impact of nitrogenous
 973 and phosphorus nutrients from selected point sources in Kisumu City on River Kisat
 974 and Nyalenda Wigwa Stream before their discharge into Winam Gulf, Lake Victoria.
 975 *Environ. Earth Sci.* 71 (12), 5121-5127.
- 976 Muwanga, A., Barifaijo, E., 2006. Impact of industrial activities on heavy metal loading and
 977 their physico-chemical effects on wetlands of Lake Victoria basin (Uganda). *Afr. J.*
 978 *Sci. Tech.* 7, 51-63.
- 979 Musinguzi, L., Lugya, J., Rwezawula, P., Kanya, A., Nuwahereza, C., Halafo, J., Kamondo,
 980 S., Njaya, F., Aura, C., Shoko, A.P., Osinde, R., Natugonza, V., Ogutu-Ohwayo, R.,
 981 2019. The extent of cage aquaculture, adherence to best practices and reflections for
 982 sustainable aquaculture on African inland waters. *J. Great Lakes Res.* 45,1340-1347
- 983 Mwavu, E.N., Witkowski, E.T.F., 2008. Land-Use and Cover Changes (1998- 2002) around
 984 Budongo Forest Reserve, NW Uganda: Implicationz for Forest and Woodlands
 985 Sustainability. *Land Degrad. Dev.* 19, 606-622.
- 986 Nchabeleng, T., Cheng, P., Oberholster, P., Botha, A.-M., Smit, W., Luus-Powell, W., 2014.
 987 Microcystin-LR equivalent concentrations in fish tissue during a post bloom
 988 *Microcystis* exposure in Loskop Dam, South Africa. *Afr. J. Aquat. Sci.* 39, 459-466.

- 989 Ngupula, G.W, Mbonde, A.S.E, Ezekiel, C.N., 2011. Spatial and temporal patterns of
990 phytoplankton abundance and composition in three ecological zones in the Tanzanian
991 waters of Lake Victoria. *Afr. J. Aquat. Sci.* **36**,197-206.
- 992 Njiru, J. M., Aura, C. M., & Okechi, J. K., 2018. Cage fish culture in Lake Victoria: A boon
993 or a disaster in waiting? *Fisheries Management and Ecology*, *00*, 1-9.
994 doi:10.1111/fme.12283
- 995 Nyakaana, J.B., Sengendo, H., Lwasa, S., 2007. Population, urban development and the
996 environment in Uganda: the case of Kampala city and its environs. Faculty of Arts,
997 Makerere University, Kampala, Uganda.
- 998 Nyanchaga, E.N., Openji, S.O., 2017. Effectiveness of the implementation of the Sub-
999 Catchment Management Plan – A case study of Awach Kano water resources users
1000 association. *Int. J. Inn. Stu. Sci. Eng. Tech.* *3*, 9-15.
- 1001 O’Neil, J.M., Davis, T.W., Burford, M.A., Gobler, C.J., 2012. The rise of harmful
1002 cyanobacteria blooms: The potential roles of eutrophication and climate change.
1003 *Harmful Algae* *14*, 313-334.
- 1004 Ochumba, P.B.O., Kibaara, D.I., 1989. Observations on blue-green algal blooms in the open
1005 waters of Lake Victoria, Kenya. *Afr. J. Ecol.* *27*, 23-34.
- 1006 Odada, E.O., Ochola, W.O., Olago, D.O., 2009. Understanding future ecosystem changes in
1007 Lake Victoria basin using participatory local scenarios. *Afr. J. Ecol.* *47*(Suppl. 1), 147-
1008 153.
- 1009 Ogutu-Ohwayo, R., 2004. Management of the Nile perch, *Lates niloticus* fishery in Lake
1010 Victoria in light of the changes in its life history characteristics. *Afr. J. Ecol.* *42*, 306-
1011 314.
- 1012 Oguttu, H.W., Bugenyi, F.W.B., Leuenberger, H., Wolf, M., Bachofen, R., 2008. Pollution
1013 menacing Lake Victoria: Quantification of point sources around Jinja Town, Uganda.
1014 *Water S.A.* *34*, 89-98.
- 1015 Okello, W., Portmann, C., Erhard, M., Gademann, K., Kurmayer, R., 2010a. Occurrence of
1016 microcystin-producing cyanobacteria in Ugandan freshwater habitats. *Environ.*
1017 *Toxicol.* *25*(4), 367-380.
- 1018 Okello, W., Ostermaier, V., Portmann, C., Gademann, K., Kurmayer, R., 2010b. Spatial
1019 isolation favours the divergence in microcystin net production by *Microcystis* in
1020 Ugandan freshwater lakes. *Wat. Res.* *44*, 2803-2814
- 1021 Okello, W., Kurmayer, R., 2011. Seasonal development of cyanobacteria and microcystin
1022 production in Ugandan freshwater lakes. *Lakes Reserv. Res. Manag.* *16*, 123-135.
- 1023 Okeyo-Owuor, J.B, Raburu, P.O., Masese, F.O., Omari, S.N., 2012. Wetlands of Lake
1024 Victoria Basin, Kenya: distribution, current status and conservation challenges in
1025 Community Based Approach to the Management of Nyando Wetland. *Int. J. Novel*
1026 *Res. Hum. Soc. Sci.* *3*(5), 35-40.
- 1027 Okungu, J., Opango, P., 2005. Pollution loads into Lake Victoria from the Kenyan catchment.
1028 In: C.A. Mallya (Ed.), *Knowledge and Experiences gained from Managing the Lake*
1029 *Victoria Ecosystem* (pp. 90-108). Dar es Salaam. Regional Secretariat, Lake Victoria
1030 Environmental Management Project (LVEMP).
- 1031 Olokotum, M., 2017. The occurrence and elimination of cyanobacterial toxins in portable
1032 water in Uganda: A case study of Gaba III and Walukuba Waterworks. MSc Thesis.
1033 17192. University of Natural Resources and Life Sciences (BOKU), Vienna, Austria.
- 1034 Opande, G.O., Onyango, J.C., Wagai, S.O., 2004. Lake Victoria: The water hyacinth
1035 (*Eichhornia crassipes* [MART.] SOLMS), its socio-economic effects, control
1036 measures and resurgence in the Winam gulf. *Limnologica* *34*(1-2), 105-109.
- 1037 Opiyo, M.A., Marijani, E., Muendo, P., Odede, R., Leschene, W., Charo-Karisa, H., 2018.
1038 Review of aquaculture production and health management practices of farmed fish in

- 1039 Kenya. Int. J. Vet. Sci. Med. 6(2), 141-148.
- 1040 Oyoo, R., 2015. Deteriorating water quality in the Lake Victoria Inner Murchison Bay and its
1041 impact on the drinking water supply for Kampala, Uganda.
1042 http://wldb.ilec.or.jp/data/ilec/WLC13_Papers/others/3.pdf
- 1043 Padmavathi, P., Veeraiah, K., 2009. Studies on the influence of *Microcystis aeruginosa* on the
1044 ecology and fish production of carp culture ponds. J. Biotechnol 8(9), 1911-1918.
- 1045 Paerl, H.W., Gardner, W.S., Havens K.E., Joyner A.R., McCarthy M.J., Newell S.E., Qin, B.,
1046 Scott, J.T., 2016. Mitigating cyanobacterial harmful algal blooms in aquatic
1047 ecosystems impacted by climate change and anthropogenic nutrients. Harmful Algae
1048 54, 213-222.
- 1049 Place, F., Otsuka, K., 2002. Land tenure systems and their impacts on agricultural investments
1050 and productivity in Uganda. J. Dev. Studies 38(6), 105-128.
- 1051 Poste, A.E., Hecky, R.E., Guildford S.J., 2011. Evaluating Microcystin Exposure Risk
1052 through Fish Consumption. Env. Sci. Technol. 45, 5806-5811.
- 1053 Poste, A.E., Hecky, R.E., Guildford, S.J., 2013. Phosphorus enrichment and carbon depletion
1054 contribute to high *Microcystis* biomass and microcystin concentrations in Ugandan
1055 lakes. Limnol. Oceanogr. 58(3), 1075-1088.
- 1056 Raburu, P.O., Okeyo-Owuor, J.B., Kwena, F., 2012. Community Based Approach to the
1057 Management of Nyando Wetland, Lake Victoria Basin, Kenya. KDC - VIRED –
1058 UNDP. Nairobi, Kenya.
- 1059 Roegner, A., Sitoki, L., Weirich, C., Corman, J., Owage, D., Umami, M., Odada, E., Miruka,
1060 J., Ogari, Z., Smith, W., Rejmankova, E., Miller, T.R., 2020. Harmful algal blooms
1061 threaten the health of peri-urban fisher communities: A case study in Kisumu Bay,
1062 Lake Victoria, Kenya. Expos Health, Early access Feb 2020 ([https://doi-
1063 org.inee.bib.cnrs.fr/10.1007/s12403-019-00342-8](https://doi-org.inee.bib.cnrs.fr/10.1007/s12403-019-00342-8))
- 1064 Rumisha, C., Nehemia, A., 2013. Feeding selectivity of wild and pond-cultured Nile tilapia
1065 *Oreochromis niloticus* in the lake Victoria basin in Mara, Tanzania. Afr. J. Aquat. Sci.
1066 38, 55-60.
- 1067 Schuijt, K., 2002. Land and water use of wetlands in Africa: Economic values of African
1068 wetlands. doi.org/10.1016/j.molcel.2012.05.044.
- 1069 Sekadende, B.C., Lyimo, T.J., Kurmayer, R., 2005. Microcystin production by cyanobacteria
1070 in the Mwanza Gulf (Lake Victoria, Tanzania). Hydrobiologia 543(1), 299-304.
- 1071 Semyalo, R., Rohrlack, T., Naggawa, C., Nyakairu, G.W., 2010. Microcystin concentrations
1072 in Nile tilapia (*Oreochromis niloticus*) caught from murchison Bay, Lake Victoria and
1073 Lake Mburo: Uganda. Hydrobiologia 628, 235-244.
- 1074 Semyalo, R., Rohrlack, T., Kayiira, D., Kizito, Y.S., Byarujali, S., Nyakairu, G., Larsson, P.,
1075 2011. On the diet of Nile tilapia in two eutrophic tropical lakes containing toxin
1076 producing cyanobacteria. Limnologica 41, 30-36.
- 1077 Shayo, S.D., Lugomela, C., Machiwa, J.F., 2011. Influence of land use pattern on some
1078 limnological characteristics in the south-eastern part of Lake Victorian, Tanzania.
1079 Aquat. Ecosyst. Health Manag. 14, 246-251.
- 1080 Silsbe, G.M., Hecky, R.E., Guildford, S.J., 2006. Variability of chlorophyll *a* and
1081 photosynthetic parameters in a nutrient-saturated tropical great lake. Limnol.
1082 Oceanogr. 51(5), 2052-2063.
- 1083 Simiyu, B.M., Oduor, S.O., Rohrlack, T., Sitoki, L., Kurmayer, R., 2018. Microcystin content
1084 in phytoplankton and in small fish from eutrophic Nyanza Gulf, lake Victoria, Kenya.
1085 Toxins 10(7), 1-19.
- 1086 Simonit, S., Perrings, C., 2011. Sustainability and the value of the 'regulating' services:
1087 Wetlands and water quality in Lake Victoria. Ecol. Econom. 70(6), 1189-1199.
- 1088 Sitoki, L., Kurmayer, R., Rott, E., 2012. Spatial variation of phytoplankton composition,

- 1089 biovolume, and resulting microcystin concentrations in the Nyanza Gulf (Lake
1090 Victoria, Kenya). *Hydrobiologia* 691, 109-122.
- 1091 Spooof, L., Catherine, A., 2017. Appendix 3 – Tables of Microcystins and Nodularins.. In
1092 Handbook of Cyanobacterial Monitoring and Cyanotoxin Analysis. Meriluoto J.,
1093 Spooof L. and Codd G.A. Eds. Hohn Wiley & Sons, Ltd, 526-537.
- 1094 Ssebiyonga, N., Erga, S.R., Hamre, B., Stamnes, J.J., Frette, Ø., 2013. Light conditions and
1095 photosynthetic efficiency of phytoplankton in Murchison Bay, Lake Victoria, Uganda.
1096 *Limnologia* 43(3), 185-193.
- 1097 Stager, J.C., Hecky, R.E., Grzesik, D., Cumming, B.F., Kling, H., 2009. Diatom evidence for
1098 the timing and causes of eutrophication in Lake Victoria, East Africa. *Hydrobiologia*
1099 636, 463-478.
- 1100 Svircev, Z., Lalic, D., Bojadzija Savic, G., Tokodi, N., Drobac Backovic, D., Chen, L.,
1101 Meriluoto, J., Codd, G.A., 2019. Global geographical and historical overview of
1102 cyanotoxin distribution and cyanobacterial poisonings *Arch. Toxicol.* 93, 2429–2481.
- 1103 Talling, J.F., 1966. The annual cycle of stratification and phytoplankton growth in Lake
1104 Victoria. *Int. Revue ges. Hydrobiol.* 51, 545-621.
- 1105 Talling, J.F., 1987. The phytoplankton of Lake Victoria (East Africa). *Arch. Hydrobiol. Beih.*
1106 *Ergebn. Limnol.* 25, 229-256.
- 1107 Tamatamah, R.A., Hecky, R.E., Duthie, H.C., 2005. The atmospheric deposition of
1108 phosphorus in Lake Victoria (East Africa). *Biogeochem.* 73, 325-344.
- 1109 Taranu, Z.E., Gregory-Eaves, I., Leavitt, P.R., Bunting, L., Buchaca, T., Catalan J.,
1110 Domaison, I., Guilizzoni, P., Lami, A., McGowan, S., Moorhouse, H., Morabito, G.,
1111 Pick, F.R., Stevenson, M.A., Thompson, P.L., Vinebrooke, R.D., 2015. Acceleration
1112 of cyanobacterial dominance in north temperate-subarctic lakes during the
1113 Anthropocene. *Ecol. Lett.* 18(4), 375-384.
- 1114 Tariku, TB., Gan, T.Y., 2018. Regional climate change impact on extreme precipitation and
1115 temperature of the Nile river basin. *Clim. Dyna.* 51, 3487-3506.
- 1116 Teferi, Y., Admassu, D., Mengistou, S., 2000. The food and feeding habit of *Oreochromis*
1117 *niloticus* L. (Pisces: Cichlidae) in Lake Chamo, Ethiopia. *SINET: Ethiop. J. Sci.* 23(1),
1118 1-12.
- 1119 Thiery, W., Davin, E.L., Seneviratne, S.I., Bedka, K., Lhermitte, S., van Lipzig, N.P.M.,
1120 2016. Hazardous thunderstorm intensification over Lake Victoria. *Nature Comm.* 7,
1121 12786.
- 1122 Torres, G.S., Silva, L.H., Rangel, L.M., Attayde, J.L., Huszar, V. L., 2016. Cyanobacteria are
1123 controlled by omnivorous filter-feeding fish (Nile tilapia) in a tropical eutrophic
1124 reservoir. *Hydrobiologia*, 765, 115-129.
- 1125 Turker, H., Eversole, A. G., Brune, D. E., 2003. Filtration of green algae and cyanobacteria
1126 by Nile tilapia, *Oreochromis niloticus*, in the Partitioned Aquaculture System.
1127 *Aquaculture* 215, 93-101.
- 1128 United Nations Environment Program-UNEP, 2006. UNEP 2006 annual report.
1129 <https://www.unenvironment.org/resources/annual-report/unep-2006-annual-report>.
- 1130 United Nations Environment Program-UNEP, 2008. Africa: Atlas of our changing
1131 environment. Malta: Progress Press.
- 1132 United Nations, Department of Economic and Social Affairs, Population Division, 2019.
1133 World Urbanization Prospects 2018: Highlights (ST/ESA/SER.A/421).
- 1134 Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T.,
1135 Talbot, M.R., Hecky, R.E., 2002. History and timing of human impact on Lake
1136 Victoria, East Africa. *Proc. Biol. Sci. Royal Soc.* 269(1488), 289-294.
- 1137 Vuai, S.A.H., Ibembe, J.D., Mungai, N.W., 2013. Influence of land use activities on spatial
1138 and temporal variations of nutrient deposition in Mwanza region: Implication to the

- 1139 atmospheric loading to the Lake Victoria. *Atmosph. Clim. Sci.* 3, 224-234.
- 1140 Wacker, C., Okello, W., Gitau, M.K., Wolf, M., 2016. Participatory wetland management at
1141 the shoreline of Lake Victoria in Jinja, Uganda. Kampala: Fountain Publishers.
- 1142 Waiswa, D., Stezrn, M.J., Prisley, S.P., 2015. Drivers of deforestation in the Lake Victoria
1143 crescent, Uganda. *J. Sustain. Forest.* 34, 259-275.
- 1144 Wanda, F.M., Namukose, M., Matuha, M., 2015. Water hyacinth hotspots in the Uganda
1145 water of Lake Victoria in 1993-2012: implications for management. *Afr. J. Aqu. Sci.*
1146 40, 101-106.
- 1147 Wang, H., Wang, T., Zhang, B., Li, F., Toure, B., Omosa, I.B., Chiramba, T., Abdel-Monem,
1148 M., Pradhan, M., 2014. Water and wastewater treatment in Africa – Current practices
1149 and challenges. *Clean (Weinh)* 42, 1029-1035.
- 1150 Watson, S.B., Miller, C., Arhonditsis, G., Boyer, G.L., Carmichael, W., Charlton, M.N.,
1151 Confesor, R., Depew, D.C., Höök, T.O., Ludsins, S.A., Matisoff, G., McElmurry, S.P.,
1152 Murray, M.W., Richards, R.P., Rao, Y.R., Steffen, M.M., Wilhelm, S.W., 2016. The
1153 re-eutrophication of Lake Erie: Harmful algal blooms and hypoxia. *Harmful Algae* 56,
1154 44-66.
- 1155 Witte, F., Silsbe, G.M., Hecky, R.E., Goudswaard, P.C., Guildford, S.J., Kische-Machumu,
1156 M.A., Wanink, J.H., 2012. Did the loss of phytoplanktivorous fish contribute to algal
1157 blooms in the Mwanza Gulf of Lake Victoria? *Hydrobiologia* 679, 283-296.
- 1158 World Population Prospect, 2017. United Nations - DESA/Population Division.
1159 <https://population.un.org/wpp/>
- 1160 Zakaria, M., Zienab, A., Bakr, A., 2019. Assessment of phytoplankton species in gut and
1161 feces of cultured tilapia fish in Egyptian fishponds - Implications for feeding and
1162 bloom control. *Acta Limnol. Brasil.*, 31, e27.
- 1163 Zhang, S., Liu, J., Wei, S., Zhang, K., 2016. Impact of aquaculture on eutrophication in
1164 Changshou Reservoir. *Chin. J. Geochem.* 25(1), 90-96.
- 1165
- 1166
- 1167
- 1168
- 1169

1170 **Supplemental Table 1.** Dissolved nutrient and chlorophyll-a concentrations in the Lake
1171 Victoria

1172

1173 **Supplemental Figure 1.** Chlorophyll-a and microcystin concentrations in the main lake and
1174 in the bays and gulfs of the Lake Victoria

1175

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.

1182