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REVIEW ARTICLE

State of knowledge of aquatic ecosystem and fisheries of the Lake Edward System, East Africa

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Abstract

Poor and unreliable knowledge of the status of freshwater fisheries limits their inclusion in governance processes, thereby impeding effective management measures. This threatens the livelihoods of people, particularly in developing countries. Improved knowledge is required to draw the attention of policymakers and stimulate effective management measures to accelerate the sustainability of the freshwater fisheries. In line with this requirement, this paper provides the state of knowledge of the aquatic ecosystem and fisheries of the Lake Edward system, East Africa, focusing on lakes Edward, George and the Kazinga channel. The state of knowledge was accomplished by reviewing existing data and information on aspects of primary productivity and water quality, invertebrates, fish fauna, fish life history and ecology, and fisheries. The waterbodies have been monitored since the 1930s, albeit sporadically, providing data on all the above aspects but with substantial temporal gaps. Adequate and updated data and information exist on the water quality status of the water bodies, extant aquatic taxa (including fishes) and fish catches but with uncertainties in the latter. Data and information gaps exist on the abundance of biotic communities, fish life history, quantitative trophic ecology and fisheries management reference points. The aggregated data and information can directly support decisions for fisheries management. We recommend regular monitoring to fill the data and information gaps, more comprehensive stock assessments and the development of aquatic ecosystem models.

KEYWORDS
Democratic Republic of the Congo, fisheries management, freshwater, inland fisheries, Lake George, small-scale fisheries, stock assessment, Uganda

1 | INTRODUCTION

Inland fisheries require effective management approaches to achieve the targets of the sustainable development goals (SDGs). Such approaches are urgent in Africa because inland fisheries are intrinsically linked to food security and income. Inland fisheries on the continent employ ∼ca. 5 million people and contribute 0.33% to the continent's GDP, with a gross added value of ∼US$6.3 billion (de Graaf & Garibaldi, 2014). The need for effective management of inland fisheries in Africa is consistent with global, regional and national development strategies. Although the SDGs do not directly cover inland fisheries (Cooke et al., 2016), some targets in most SDGs, such as 14 (life below water), 2 (zero hunger), 15 (life on land) and 12 (responsible consumption and production), are applicable. For instance, SDG 14 has targets to end pollution, eutrophication and overfishing, which are all relevant to inland fisheries (United Nations, 2017). In Africa, relevant strategies include the African Union's 2063 agenda, the Africa blue economy strategy and the Pan-African fisheries and aquaculture policy framework and reform strategy (AUC, 2015; NEPAD & AU-IBAR, 2016). Numerous other applicable strategies exist at the national level to operationalize their global and regional equivalents. All these strategies aspire to use water resources sustainably for food security and wealth creation.

Achieving the stipulated targets in all the development strategies requires tools to set priorities, allocate resources, stimulate action and measure progress (SDSN, 2015). For inland fisheries, priority requirements are improved knowledge and effective management measures (Cooke et al., 2016; FAO & MSU, 2016). Knowledge is particularly an integral part for achieving the targets because it is the basis not only for inland fisheries to feature in governance processes, but also for effective management measures (Cooke et al., 2016).

Unlike most marine resources, the knowledge of aspects of inland fisheries, such as trophic interactions, the status of fish stocks and the magnitude and impact of threats, is scanty. Ultimately, inland fisheries are often forgotten in critical governance processes, and when management occurs, it is based on unreliable information (Cooke et al., 2016). This state hinders effective management and undermines progress on the SDGs and associated policies.

Given that knowledge is vital for the sustainability of inland fisheries, we conducted a literature review to aggregate available data and information to establish the state of knowledge of the aquatic ecosystem and fisheries, and identify knowledge gaps in the Lake Edward system focusing on lakes Edward, George and the Kazinga channel. Located in East Africa, these waterbodies are among the most productive freshwater systems (Beadle, 1981). Fisheries on these water bodies are vital to the riparian rural communities (Bassa et al., 2014; Lubala et al., 2018). The state of knowledge is useful for guiding decisions for fisheries management and development. The data and information aggregated could support aquatic ecosystem modelling and comprehensive fish stock assessments, strongly improving our understanding of the aquatic ecosystem and fisheries, thus stimulating more effective management measures.

2 | METHODS

2.1 | Lakes Edward and George

The Lake Edward system is a watershed encompassing lakes Edward and George as the main waterbodies, numerous crater lakes, rivers and streams (Figure 1). The two lakes are connected by the 40 km long Kazinga Channel. The system (~29,000 km^2) is transboundary: Lake George (250 km^2) and the Kazinga Channel are entirely situated within Uganda, whereas Lake Edward (2325 km^2) is shared between Uganda (29%) and the Democratic Republic of the Congo (DRC) (71%). The whole of Lake Edward and the Kazinga Channel and a larger part of Lake George are surrounded by protected areas (Queen Elizabeth National Park in Uganda and Virunga National Park in the DRC). The Lake Edward system drains into Lake Albert through the Semliki River. However, the exchange of fish species between the system and Lake Albert is effectively limited by the Semliki rapids on the river (Greenwood, 1976a).

The Lake Edward system is important for freshwater biodiversity and fisheries. The system is the fourth largest among the African great lakes in terms of fish species richness (Snoeks, 2000). Lakes Edward, George and the Kazinga channel, which do not depend on fish stocking, support about 23,000 fishers in the two riparian countries. In Uganda, the waterbodies are the fourth most important producers of fish after lakes Victoria, Kyoga and Albert. In the DRC, Lake Edward is a major contributor to inland fish production, with its annual catches placing it among the top 5 major fish-producing inland water bodies in the country (Breuil & Grima, 2014). Other key features of the system and the waterbodies within the system were described in detail by Decru et al. (2020) and Stoyneva-Gärtner et al. (2020), Rumes et al. (2011).

2.2 | Approach and scope

This review was based on literature to aggregate data and information on biophysical aquatic ecosystem indicators, invertebrate communities, fish fauna, fish life history and ecology, and fisheries. The review was conducted to guide fishery development and management. Aspects of the biophysical aquatic ecosystem included physical and chemical indicators of water quality and primary production. Aspects of fish life history and ecology focused mainly on length–weight relationships, reproductive biology, growth parameters and trophic ecology. For fisheries, the focus was on catches, species composition in the catches, fishing effort and fisheries management reference points.

A literature search was conducted for published papers in the web of science (https://login.webofknowledge.com), AquaDocs (https://aquadocs.org) and the published resources of the Food Agricultural Organization of the United Nations (FAO) (http://www.fao.org/fishery/publications/en). These were searched using terms including Lake Edward, Lake George, Lake George AND Lake Edward and the Lake Edward system. However, these terms would be refined if necessary to narrow the search, for instance, to one of the aspects covered in this review. All relevant literature was retained. Relevance was based on whether the resources retrieved covered the aspects of interest, that is biophysical aquatic ecosystem indicators, invertebrate communities, fish fauna, fish life history and ecology, and fisheries. AquaDocs is a global repository of published and unpublished research, contributed by members of the International Association of Aquatic and Marine Science Libraries and Information Centres (IAMSLIC) and the International Oceanographic Data and Information Exchange (IODE). It is a source of literature from, for example research project reports and annual reports of fisheries departments, which do not exist in

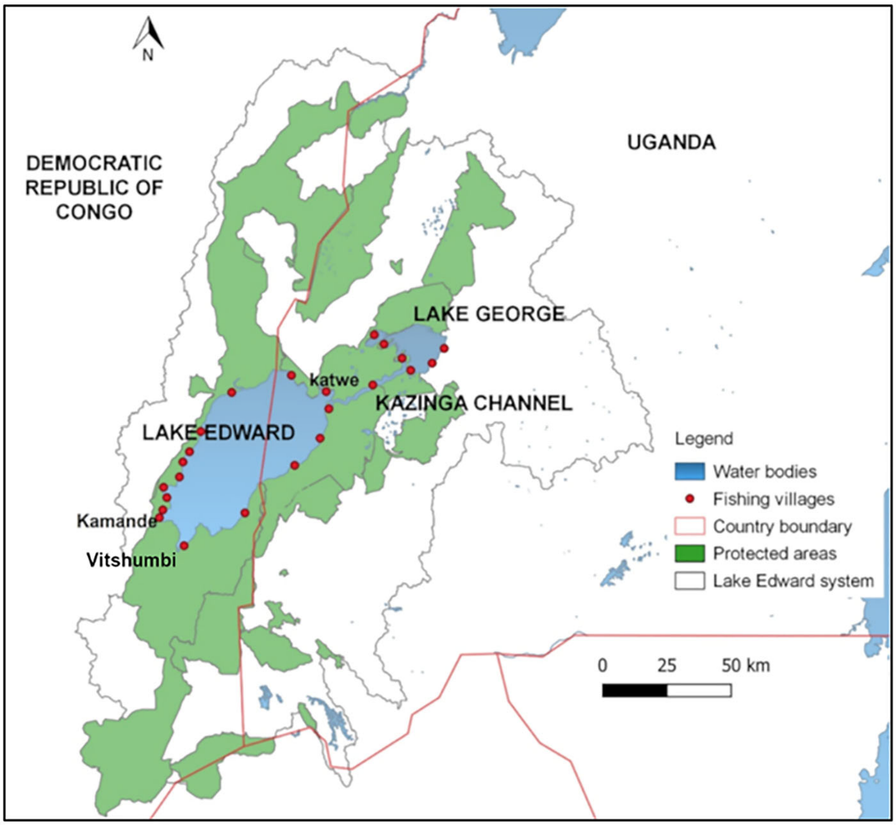

FIGURE 1 Lake Edward system indicating the location of lakes Edward, George and the interconnecting Kazinga channel, fishing villages and protected areas. Shapefiles of protected areas were obtained from UNEP-WCMC and IUCN (2021) and those of waterbodies from Lehner and Grill (2013).

academic journals. AquaDocs provided access to reports from the past Game and Fisheries Department in Uganda and the National Fisheries Resources Research Institute (NaFIRRI), Uganda, which conducts research on water bodies in the system. The publications retained for review (Musinguzi, 2023) were 95 including 47 peer reviewed publications equivalent to 49.5% of the total (43 journal papers and 4 books or book chapters), and 48 publications of grey literature (50.5%). Most of the publications of grey literature (64.6%) were from AquaDocs, followed by 29.2% from other internet sources, and 6.3% from the FAO.

From the NaFIRRI, we also obtained data from catch assessment surveys (CAS), and other fishery-dependent and fishery-independent surveys that are conducted to examine the status of fish stocks. The data from CAS was analysed to determine annual catches, fishing effort and species composition in the catch. The data was available from 2000 to 2019, but with gaps within years for lakes Edward (2006–2008, 2011–2013, 2017, 2019), George (2000–2001, 2011–2013, 2017, 2019) and the Kazinga Channel (2000, 2011–2013, 2017, 2019). Details on the design of the CAS are available in Bassa et al. (2014). We used weight for each species or species group in catches to generate daily catch rates for vessel gear combinations (kg/boat/day). The average number of fishing days in a week, available from the CAS, was used to determine the number of fishing days in a year to estimate annual catch rates from the daily catch rates. The number of boats obtained from frame surveys (surveys that provide data on fishers, fishing gear and boats, and landing site facilities) was used to raise the annual catch rates to annual catches.

3 | RESULTS

3.1 | Primary production and water quality as indicators of aquatic ecosystem productivity and health

Physical and chemical water quality indicators are indicators of aquatic ecosystem productivity and health (Carlson & Simpson, 1996). Table 1 presents values for available water quality indicators from past studies on lakes Edward, George and the Kazinga Channel.

The earliest studies on water quality occurred in 1921 and 1931 (Worthington, 1932). Although most of the indicators used at the time are not in use anymore (Binding et al., 2007; Carlson & Simpson, 1996), qualitative observations and measurements of Secchi depth (water transparency) provide insights into how productive the water bodies were at the time. Water in Lake George and the Kazinga Channel was depicted as green due to the presence of more phytoplankton than that of Lake Edward. The water transparency was 0.4 m in Lake George, and the Kazinga Channel, 1.4 m in Katwe bay (Lake Edward) and 2.2–2.8 m in offshore sites of Lake Edward (Figure 1) (Worthington, 1932).

TABLE 1 Physical and chemical parameters of lakes Edward, George and the Kazinga Channel with: conductivity (σ), temperature (T), Secchi depth (SD), total dissolved solids (TDS), dissolved oxygen (DO), chlorophyll *a* (chl-*a*), total phosphorus (TP), nitrate (NO_3^-) and soluble reactive phosphorus (SRP).

Water body	σ (μS/cm)	T (°C)	SD (cm)	TDS (mg/L)	DO (mg/L)	Chl *a* (μg/L)	TP (μg/L)	NO_3^- (μg/L)	SRP (μg/L)	Year of sampling	Reference
Lake Edward/parts of Lake Edward											
	–	–	180–280	–	–	–	–	–	–	–	Worthington (1932)
	–	18.7–30.4	190.0–300.0	–	6.0–9.0	–	–	–	–	1952/1953	Verbeke (1957)
Katwe bay			250–350							1952/53	Verbeke (1957)
	–	–	–	–		–	–	99.2	95.1	1954	Talling (1963)
	–	–	–	–		–	127.0	105.4	57.0	1961	Talling and Talling (1965)
	830	24–26	130	700–800	5.0–7.5	–	–	–	240.0 ± 40.0	1976/77	Bugenyi (1979, 1982)
	–	27.5	–	–	6.2	–	–	>6.2	57.0	1995	Lehman et al. (1998)
	–	26.6 ± 0.5	105 ± 27	–		21.3 ± 22.8	58.9 ± 9.2	–	10.6 ± 5.2	2008/2009	Poste et al. (2013)
	920.5–939.4	25.5–26.9	–	–	7.6	8.2	34.2–52.8	34.6	16.4	2008	NaFIRRI (2008)
	718.3 ± 4.2	27.55 ± 0.19	108.56 ± 10.7	361.12 ± 1.47	5.16 ± 0.36	-	-	-	-	2011/2012	Mbalassa et al. (2014)
	685.85 ± 150.7	23.76 ± 1.71	130	–	4.63 ± 0.55	–	–	–	–	2013	Bagalwa et al. (2014)
Lake Edward, excluding Katwe bay	862 (819–884)	26.1 (25.5–27.8)	150 (68–232)	-	6.1 (0.8–9.9)	6.8 ± 2.7–10.7 ± 5.6	-	99.2 (0–539.4)	123.5 (0–379.9)	2016/2018	Stoyneva-Gärtner et al. (2020)
Pelagic (10–85 m)	–	–	107–232	–	–	8.0 ± 3.9	61.9 ± 27.9	86.8 ± 99.2	–	–	Stoyneva-Gärtner et al. (2020)

(Continues)

TABLE 1 (Continued)

Water body	σ (μS/cm)	T (°C)	SD (cm)	TDS (mg/L)	DO (mg/L)	Chl *a* (μg/L)	TP (μg/L)	NO_3^- (μg/L)	SRP (μg/L)	Year of sampling	Reference
Littoral sites (0–6.1 m)	–	–	68–149	–	–	8.4 ± 3.7	–	–	–	–	Stoyneva-Gärtner et al. (2020)
	692 (589–791)	26.5 (25.7–28.8)	45 (17–69)	–	9.1 (8.1–11.6)	50.4 ± 31.8	–	31.0 (0.0–74.2)	41.0 (12.1–145.9)	2016/2018	Stoyneva-Gärtner et al. (2020)
Lake George											
	–	–	40	–	–	–	–	–	–	–	Worthington (1932)
		–	–	–	–	–	412.0	–	<57.0	1961	Talling and Talling (1965)
	227.5 ± 18.9*	–	–	–	–	–	–	n.d	171.0–398.9	1967/68	Viner (1969)
	200	25–35	–	–		–	–	–	–	1967/68	Dunn et al. (1969)
	230	23–30	20	160–200	4.0–8.0	–	–	–	520.0 ± 130	1976/77	Bugenyi (1979, 1982)
	–	–	–	–	–	–	–	–	123.5	1995	Lehman et al. (1998)
	–	–	–	–	7 ± 3.8	–	–	–	–	2001/2003	Owor et al. (2007)
	–	26.4 ± 1.0	37 ± 8	–	–	138.0 ± 39.1	186.5 ± 26.2	–	9.9 ± 4.9	2008/2009	Poste et al. (2013)
	250 (237–276)	25.7 (24.5–29.5)	28 (24–32)	–	9.0 (5.0–22.5)	190.7 ± 114.3	–	155.0 (55.8–303.8)	63.2 (5.8–162.2)	2016/2018	Stoyneva-Gärtner et al. (2020)
Kazinga channel											
			40	–	–	–	–	–	–	–	Worthington (1932)

(Continues)

TABLE 1 (Continued)

Water body	σ (μS/cm)	T (°C)	SD (cm)	TDS (mg/L)	DO (mg/L)	Chl *a* (μg/L)	TP (μg/L)	NO_3^- (μg/L)	SRP (μg/L)	Year of sampling	Reference
	500	24–27	-	180–300	6.5–7.0		-	-	400.0 ± 80.0	1976/77	Bugenyi (1979, 1982)
	241	-	-	-	7.4	61.5	159.8	46.5	13.2	2008	NaFIRRI (2008)
	-	25.5 ± 2.1	50 ± 25	-	-	66.3 ± 46.2	129.1 ± 54.7	-	10.3 ± 6.1	2008/2009	Poste et al. (2013)
	266 (202–726)	26.4 (25.2–28.6)	30 (19–44)	-	8.4 (5.9–15.4)	128.9 ± 114.3	-	62.0 (0.0–223.2)	64.0 (12.1–135.7)	2016/2018	Stoyneva-Gärtner et al. (2020)

Note: *Value was aggregated from values for wet and dry seasons in 1967 and 1968. Values in μmol/L for TP, SRP and NO_3^- were converted to μg/L using unit conversions of the International Council for the Exploration of the Sea (ICES) (https://www.ices.dk/data/tools/Pages/Unit-conversions.aspx).

Abbreviation: n.d, non-detectable.

Using data collected in 1952 and 1953 in Lake Edward, Verbeke (1957) reported water transparency as 1.9–3 m in offshore sites, 0.5 m in Vitshumbi Bay, 0.25–0.35 m in Kamande and Katwe bays (see location of these sites in Figure 1) and 0.25–0.5 m in the deltas of rivers. Comparing these values to the trophic categories, where values >4 m denote oligotrophic, 2–4 m mesotrophic, 0.5–1.99 m eutrophic and <0.5 m hypertrophic states (Carlson, 2007; Forsberg & Ryding, 1980), suggests that Lake George, Kazinga Channel and most bays and river mouths in Lake Edward were hypertrophic.

Stoyneva-Gärtner et al. (2020) conducted a comprehensive study of water quality and primary production in these water bodies, offering the most recent observations. Values of lake-wide water transparency from Stoyneva-Gärtner et al. (2020), excluding Katwe bay, indicated that Lake Edward is eutrophic, with an average water transparency of 1.5 m. However, the range was 0.68–2.32 m, suggesting that some areas are mesotrophic. On the other hand, the mean water transparency in Katwe bay was 0.45 m, indicating that the bay was hypertrophic and as productive as Lake George (0.28 m) and the Kazinga Channel (0.30 m), in agreement with past studies (Table 1). The hypertrophic state of Katwe bay may be attributed to the influence of the Kazinga Channel (Verbeke, 1957; Worthington, 1932). Measurements of chlorophyll *a* (chl-*a*) also demonstrated high productivity in Katwe bay, Lake George and the Kazinga Channel, with recent values indicating increased productivity compared to historical values (Table 1). Based on the values of chl-*a*, the Kazinga Channel and Lake George are hypertrophic, whereas Katwe bay is eutrophic with some hypertrophic parts. The rest of Lake Edward is mainly mesotrophic, but with eutrophic littoral zones.

Bugenyi (1982) attributed the higher productivity in Lake George and the Kazinga Channel to a higher concentration of phosphates compared to Lake Edward. Phosphorous concentration in these waterbodies is vital for primary production because they are limited in Nitrogen (Ganf & Viner, 1973; Stoyneva-Gärtner et al., 2020). In the past, Lake George and the Kazinga Channel appeared to have more soluble reactive phosphorous (SRP) than Lake Edward (Bugenyi, 1982; Lehman et al., 1998; Table 1). This trend has changed with SRP concentration being highest in Lake Edward compared to Lake George and the Kazinga Channel, where the concentration is reduced by demand by the higher biomass of phytoplankton (Stoyneva-Gärtner et al., 2020).

Primary production in the waterbodies supports a rich phytoplankton community. Stoyneva-Gärtner et al. (2020) identified 248 taxa of the phytoplankton community belonging to Cyanoprokaryota, Euglenophyta, Pyrrhophyta, Cryptophyta, Ochrophyta, Tribophyceae, Chrysophyceae, Synurophyceae, Bacillariophyceae, Chlorophyta and Streptophyta. Confirming the trophic status described above, measurements of absolute primary production showed that Lake George and the Kazinga Channel have higher phytoplankton biomass than Lake Edward. Burgis et al. (1973) estimated the mean phytoplankton biomass of Lake George as 46.8 gm^{-2}. Ganf and Viner (1973) estimated a mean of 30 g C m^{-2} and a range of 20–40 g C m^{-2} for the same lake. The phytoplankton biomass of the Kazinga Channel was probably similar. In contrast, primary production in Lake Edward was lower, ranging from 1.5 to 12 g C m^{-2} (Lehman et al., 1998). Unlike the data in Lehman

(1998) that was collected within only 1 month, the data in Burgis et al. (1973) and Ganf and Viner (1973) was obtained over a period of 1 year, and thus spans seasons.

Cyanobacteria (Cyanoprokaryota) are the most dominant group of phytoplankton (Stoyneva-Gärtner et al., 2020). In Lake Edward, this group is responsible for approximately 90% of the primary production (measured as chl-*a* concentration) in Katwe bay and approximately 60% in the rest of the lake. Ochrophyta is the second most dominant group responsible for 24.7%–27.7% of the primary production in the lake excluding Katwe bay, where the group contributes 7.7%. In Lake George and the Kazinga Channel, nearly all primary production is by Cyanobacteria, comprising 98.6% and 96.1%, respectively. The dominance of Cyanobacteria corresponds with earlier studies. In the late 1960s, Cyanobacteria were responsible for 80% of the mean phytoplankton biomass of Lake George biomass (Burgis et al., 1973). These water bodies are limited in nitrogen (Ganf & Viner, 1973). Cyanobacteria are dominant because of their ability to fix atmospheric nitrogen, tolerance to low dissolved oxygen, their higher efficiency in light absorption and nutrient assimilation, and their tendency to limit the availability of light to other phytoplankton (Burgus et al., 1973; Ganf & Viner, 1973; Stoyneva-Gärtner et al., 2020).

Water quality and primary production are relatively stable in Lakes Edward and George, and the Kazinga Channel (Ganf & Viner, 1973). However, some temporal and spatial differences may occur. Stoyneva-Gärtner et al. (2020) demonstrated differences in water quality and primary production among littoral sites, pelagic sites and within Katwe bay in Lake Edward. Dissolved nutrients (SRP and Dissolved Inorganic Nitrogen [DIN]) and chl-*a* exhibited significant differences between rainy and dry seasons. Unlike Lake George and the Kazinga Channel, which are shallow, thermal stratification in Lake Edward is eminent and affects water quality. Worthington (1932) showed that temperature in Lake Edward was uniform within 10 m, dropping slightly and remaining uniform between 10 and 40 m, and then dropping by 1°C beyond 60 m. This stratification had substantial effects on other water quality conditions and biotic communities. For instance, below 50–60 m, water was anoxic. No zooplankton was found below 60 m, where only *Chaoborus* larvae (macroinvertebrates) were found. A few fish were found to enter the hypolimnion. Stoyneva-Gärtner et al. (2020) found uniform water quality within 15–20 m throughout the year and expansion of the mixed layer to 55 m during the dry season, suggesting that stratification in the lake has weakened since the 1920s.

3.2 | Aquatic invertebrates

3.2.1 | Macroinvertebrates

For Lake George, information on macroinvertebrates was mainly available from the International Biological Programme for the period 1966 and 1971 (Green, 2009; Greenwood, 1976b). The lake has a benthic macroinvertebrate community composed of Gastropoda, Bivalvia, *Chaoborus* spp., Oligochaeta, Chironomidae, Hydracarina, Ostracoda, Ephemeroptera, Nematoda and Trichoptera (Burgis et al., 1973; Darlington, 1977; Greenwood, 1976a). In the open waters of the lake, *Chaoborus* spp., Chironomidae (*Chironomus* spp. and *Procladius* sp.), Oligochaeta and Ostracoda are the main groups (Burgis et al., 1973). These groups are species-poor due to the unstable, soft and deoxygenated mud in the lake (Burgis et al., 1973). The abundance and species richness of groups of macroinvertebrates, apart from Ostracoda, increase from the middle of the lake, where mud is dominant, towards the inshore habitats that have firmer, less disturbed and more diverse benthic habitats with sand, clay and gravel substrates (Burgis et al., 1973; Darlington, 1977; Greenwood, 1976b). Some taxa like Gastropoda, Bivalvia, Ephemeroptera, Nematoda, Oligochaeta and Trichoptera, and some taxa of Chironomidae, such as *Chironomus imicola and Tanytarsus* sp., are infrequent in the open lake (Burgis et al., 1973; Darlington, 1977).

Burgis et al. (1973) reported the total absolute biomass of macroinvertebrates as 0.519 gm^{-2} based on mid-lake samples. *Chaoborus* spp. comprised 41.2% of the total biomass (0.214 gm^{-2}). Darlington (1977) also estimated the total biomass of macroinvertebrates in the open lake, agreeing with Burgis et al. (1973) on the dominance of *Chaoborus* spp. However, the estimate of *Chaoborus* spp. by the former was higher at 0.348 gm^{-2}, comprising 35.7% of the biomass. Other taxa were recorded by Darlington (1977) as follows: Oligochaeta (0.186 gm^{-2}), *C. imicola* (0.178 gm^{-2}), *Procladius brevipetiolatus* (0.171 gm^{-2}) and Ostracoda (0.92 gm^{-2}). The dominance of the inshore habitats was by oligochaeta, with a total biomass of 0.533 gm^{-2}, equivalent to 41.6% of the total biomass of macroinvertebrates (Darlington, 1977).

In Lake Edward, the community of macroinvertebrates was examined comprehensively in studies undertaken between 1930 and 1960. Synthesized in Green (2009), the studies grouped the macroinvertebrates in the lake into Turbellaria, Ostracoda, Decapoda, Hemiptera, Trichoptera, Coleoptera, Diptera, Mollusca, Oligochaeta, Nematoda, Hirudinea, Acarina, Collembola, Ephemeroptera, and Odonata. Coleoptera (69 species), Hemiptera (30 species), Ostracoda (20 species) and Trichoptera (15 species) were the most species-rich groups.

A single sampling event conducted in January 2008 as part of Environmental Impact Assessments for oil exploration projects provided the most recent information on macroinvertebrates of the lake (NaFIRRI, 2008). Macroinvertebrates were recorded in seven broad groups: Gastropoda, Bivalvia, Diptera, Ephemeroptera, Odonata, Trichoptera and Oligochaeta, differing from past observations due to the absence of some groups like *Caridina* spp. and Ostracoda. Ostracoda are everywhere in the lake and can be observed in the stomachs of some fish species (Vranken, Steenberge, Kayenbergh et al., 2020). This group was probably missed in these samples because its individuals are smaller than the size spectrum of groups that are considered macroinvertebrates in these samples. Gastropoda, Diptera, and Oligochaeta were the most widely distributed, with at least one representative taxon in all six sampled sites for the first two groups, and five sites for Oligochaeta. Gastropoda and Diptera were the most taxa-rich groups with four and seven representative taxa, respectively. Other groups were each represented by one taxon. Ephemeroptera, Odonata, and Trichoptera were each recorded in only one of the six sampled sites, suggesting limited distribution and abundance in the lake. Taxa richness did not differ remarkably among sites, and between offshore and nearshore regions. Density (individuals per square meter) suggested that Diptera, comprising *Chaoborus* spp. and Chironomidae, was the most dominant group.

3.2.2 | Zooplankton

Zooplankton in Lakes Edward and George have been studied from the perspective of three major groups: Copepoda, Rotifera and Cladocera. Dunn et al. (1969) reported Copepoda as the most abundant in Lake George (72% relative abundance), followed by Rotifera (25%) and Cladocera (3%). Burgis et al. (1973) observed that, generally, the abundance of zooplankton peaked during the wet season and was higher in open water than in inshore habitats, except for Rotifera, whose abundance was higher in the inshore parts of the lake. The lower abundance of zooplankton in inshore habitats was attributed to intense grazing by fish, whose biomass is higher in the inshore habitats (Gwahaba, 1975). The absolute biomass of zooplankton in the lake was estimated as 0.488 g m^{-2}, with copepods comprising more than 80% of the biomass (Burgis et al., 1973).

In Lake Edward, copepods also dominate the zooplankton community, comprising 40%–60% of the density (number of individuals per square meter) at sites of varying depths (8.5–29.5 m). Unlike Lake George, Cladocera follows in abundance, comprising 6%–36% of the density. Rotifera is the least abundant with 0.2%–2% of the density (Green, 2009). These observations are corroborated by observations from the most recent study, which indicated that Cladocera and Copepoda exhibited a lake-wide distribution, whereas Rotifera were rare (NaFIRRI, 2008). Copepoda comprised 76%–97% of the abundance at inshore and offshore sites, followed by Cladocera (1%–17%) and Rotifera (1%–12%). However, Rotifera was the most diverse group with 11 taxa (nine species and two genera), followed by Cladocera with six (five species and one genus) and Copepoda with one genus, one species in addition to nauplius larvae and copepodites. Estimates of total zooplankton biomass for Lake Edward are available from Lehman et al. (1998), as 0.66, 2.21, and 1.28 g C m^{-2} at sites at 4, 18 and 25 m from the shoreline, respectively.

3.3 | Fish species

3.3.1 | Species extant in Lakes Edward and George

Knowledge of fish species in an ecosystem is important for effective fisheries management. Lakes Edward and George are rich in fish species, including a large assemblage in the genus: *Haplochromis*. The list of the species in the water bodies was based on recent reviews and descriptions of fish species in the Lake Edward system (Table 2). Decru et al. (2020) reviewed literature, FishBase and museum collections, listing 34 fish species in 21 genera (excluding *Haplochromis*) and 10 families in the system. A recent review of *Enteromius* re-identified specimens of *Enteromius perince* and *Enteromius stigmatopygus* as *Enteromius cf. mimus* and *Enteromius alberti*, respectively (Maetens et al., 2020). Based on these studies, lakes Edward and George have 19 non-*Haplochromis* species in 8 families and 15 genera occurring in the lakes. Although the lakes share most of these fish species, *Laciris pelagica* (endemic to the open water of Lake Edward), *Labeo forskalii* and *Heterobranchus longifilis* are not known to be in Lake George. *H. longifilis* has not been reported in Lake Edward since 1956 (Hulot, 1956). For this reason, the presence of the species in the lake can be classified as possibly extant.

More than 60 species of *Haplochromis* spp. are estimated to occur in lakes Edward, George and the Kazinga Channel (Greenwood, 1991; Snoeks, 2000; Vranken et al., 2019). However, only 40 are described (Table 2), presenting a substantial knowledge gap in the ichthyofauna of the system. However, efforts are underway to describe more species (Vranken, Steenberge, Kayenbergh et al., 2020, Vranken, Steenberge, Snoeks, 2020, Vranken, Steenberge, Balagizi et al., 2020, Vranken 2022).

3.3.2 | Habitat use, distribution, and relative abundance of the fish species in Lakes Edward and George

Notes on habitats and the distribution of the fish species in the two lakes are presented in Table 2. Worthington (1932) and Poll and Damas (1935) provided the earliest insights into the habitat use, distribution and abundance of the fish species. Fish species, including *Clarias liocephalus*, *Mormyrus kannume*, and those belonging to Cyprinidae, other than *Labeobarbus altianalis*, were depicted as being less abundant or rare. Only a few individuals were recorded for these species at the time. Apart from *L. forskalii*, these species predominantly use inshore areas, vegetated fringes and river mouths as habitats. *L. forskalii* was restricted to rocky deep open waters in Lake Edward, such as those close to the western shores in the DRC. Other species recorded at the time (*L. altianalis*, *Bagrus docmak*, *Oreochromis niloticus*, *Oreochromis leucostictus*, *Clarias gariepinus*, *Protopterus aethiopicus*, *L. pelagica*, and *Lacustricola vitschumbaensis*) were depicted as abundant. These species, apart from *L. pelagica*, which is restricted to the open deep waters of Lake Edward, and *L. vitschumbaensis*, which is restricted to the inshore areas, especially those associated with river mouths, were found throughout the lakes. The abundance of these species, in general, decreased from the inshore to offshore areas and was highest in the following habitats: shallow areas, river mouths, sheltered bays and vegetated and swampy fringes (Worthington, 1932). However, the western shoreline of Lake Edward has some deep nearshore areas, lacking the preferred habitats of these species. As a result, *P. aethiopicus* is absent in these areas and the abundance of others is remarkably low (Poll & Damas, 1935). Worthington (1932) demonstrated the general decrease of abundance from the inshore habitats towards the offshore habitats using *O. niloticus* in Lake Edward. Catch rates of the species from experimental gillnets diminished from 120 fish per net at the mouth of Kazinga Channel (Figure 1) to 2–3 fish per net at a site about

TABLE 2 Fish species in lakes Edward and George.

Family	Trophic group (for *Haplochromis* spp.)	Species	George	Edward	Distribution and habitat use in Lakes Edward and George	Main diet
Anabantidae		*Ctenopoma muriei* (Boulenger, 1906)	X	X	Vegetated fringes and river mouths	Insect larvae and crustacea
Bagridae		*Bagrus docmak* (Fabricius, 1775)	X	X	Abundant in Lake George and shallow waters of Lake Edward; mainly in closed bays and river mouths	Fish, detritus and insects
Cichlidae		*Astatoreochromis alluaudi* (Pellegrin, 1904)	X	X	Inshore areas and river mouths	Insect larvae
		***Coptodon zillii* (Gervais, 1848)	X	X	Vegetated fringes	Higher plant materials
	Detrivores	***Haplochromis aeneocolor* (Greenwood, 1973)	X	X	Papyrus swamp edges	Detritus
		**Haplochromis akika* (Lippitsch, 2003)	X	X	Papyrus shores	Detritus (based on morphology)
		**Haplochromis eduardii* (Regan, 1921)	–	X	Insufficient data	Detritus (based on morphology)
	Insectivores	**Haplochromis elegans* (Trewavas, 1933)	X	X	Sandy shoals and papyrus shores	Insect larvae and adults
		**Haplochromis engystoma* (Trewavas, 1933)	–	X	Insufficient data	Insect larvae (based on morphology)
		**Haplochromis labiatus* (Trewavas, 1933)	–	X	Inshore habitats	Insect larvae
		**Haplochromis lobatus* (Vranken et al., 2020)	–	X	Inshore habitats	Insect larvae
		**Haplochromis angustifrons* (Boulenger, 1914)	X	X	Offshore habitats	Insect larvae
		**Haplochromis macropsoides* (Greenwood, 1973)	X	X	Sublittoral habitats	Insect larvae and adults
		**Haplochromis oregosoma* (Greenwood, 1973)	X	X	Sublittoral habitats	Possibly phytoplankton, morphology suggests insects
		Haplochromis schubotzi (Boulenger, 1914)	X	X	Sublittoral and offshore habitats	Insect larvae
		**Haplochromis schubotziellus* (Greenwood, 1973)	X	X	Muddy bays and near papyrus fringes	Insects
	Phytoplanktivores	**Haplochromis nigripinnis* (Regan, 1921)	X	X	Shallow offshore habitats	Phytoplankton
		**Haplochromis vicarius* (Trewavas, 1933)	–	X	Insufficient data	Phytoplankton (based on morphology)
	Phytoplanktivores (Algae scrapers-epilithic)	**Haplochromis serridens* (Regan, 1925)	–	X	Insufficient data	Aufwuchs on rocks (based on morphology)
		**Haplochromis fuscus* (Regan, 1925)	–	X	Insufficient data	Aufwuchs on rocks (based on morphology)

(Continues)

TABLE 2 (Continued)

Family	Trophic group (for *Haplochromis* spp.)	Species	George	Edward	Distribution and habitat use in Lakes Edward and George	Main diet
	Phytoplanktivores (Algae scrapers-epiphytic)	**Haplochromis limax* (Trewavas, 1933)	X	X	Vegetated shores	Aufwuchs on plants and lake substrate
	Molluscivores (Pharyngeal crushers)	**Haplochromis mylodon* (Greenwood, 1973)	X	X	Inshore and offshore habitats	Gastropods and insects
		**Haplochromis pharyngalis* (Poll and Damas, 1939)	X	X	Rocky shores	Gastropods and some insect larvae)
	Molluscivores (Oral shellers)	**Haplochromis concilians* (Vranken et al., 2020)	–	X	Inshore habitats over sand	Gastropods
		**Haplochromis erutus* (Vranken et al., 2020)	–	X	Inshore and offshore habitats	Gastropods
		**Haplochromis planus* (Vranken et al., 2020)	–	X	Inshore and offshore habitats	Ostracods
	Zooplanktivores	**Haplochromis pappenheimi* (Boulenger, 1914)	X	X	Upper water layers in offshore habitats	Zooplankton
	Piscivores	**Haplochromis mentatus* (Regan, 1925)	X	X	Mostly in shallow waters offshore	Fish (based on morphology)
		**Haplochromis latifrons* (Vranken et al., 2022)	–	X	Offshore habitats	Fish (based on morphology)
		**Haplochromis rex* (Vranken et al., 2022)		X	Over sandy substrates	Fish (based on morphology)
		**Haplochromis simba* (Vranken et al., 2022)	–	X	Inshore areas over hard substrates	Fish (based on morphology)
		**Haplochromis glaucus* (Vranken et al., 2022)	–	X	Over sandy substrates	Fish (based on morphology)
		**Haplochromis aquila* (Vranken et al., 2022)	–	X	Inshore areas over muddy substrates	Fish (based on morphology)
	Piscivores (Microdontic)	*Haplochromis squamipinnis* (Regan, 1921)	X	X	Offshore, muddy shore and papyrus fringes	Fish
		**Haplochromis kimondo* (Vranken et al., 2022)	–	X	Over sandy substrates	Fish (based on morphology)
		**Haplochromis falcatus* (Vranken et al., 2022)	–	X	Over sandy substrates	Fish (based on morphology)
		**Haplochromis curvidens* (Vranken et al., 2022)	–	X	Inshore areas	Fish (based on morphology)
		**Haplochromis pardus* (Vranken et al., 2022)	–	X	Inshore areas	Fish (based on morphology)
		**Haplochromis quasimodo* (Vranken et al., 2022)	X	X	Offshore, benthic areas in shallow and deep waters	Fish (based on morphology)
	Piscivores (Paedophages)	**Haplochromis gracilifur* (Vranken et al., 2019)	–	X	Inshore waters	Fish eggs and larvae
		**Haplochromis molossus* (Vranken et al., 2019)	X	X	Inshore habitats	Fish eggs and larvae
		**Haplochromis paradoxus* (Lippitsch and Kaufman, 2003)	X	X	Inshore and offshore areas	Fish larvae
		**Haplochromis relictidens* (Vranken et al., 2019)	X	X	Inshore habitats	Fish eggs and larvae
		**Haplochromis taurinus* (Trewavas, 1933)	X	X	Inshore habitats	Fish eggs and larvae

(Continues)

TABLE 2 (Continued)

Family	Trophic group (for *Haplochromis* spp.)	Species	George	Edward	Distribution and habitat use in Lakes Edward and George	Main diet
	Parasite eaters	**Haplochromis eduardianus* (Boulenger, 1914)	X	X	Inshore and sublittoral habitats	Presumably parasites
		Oreochromis leucostictus (Trewavas, 1933)	X	X	Common everywhere in Lake George and inshore waters of Lake Edward	Higher plant material and detritus
		Oreochromis niloticus (Linnaeus, 1758)	X	X	Found throughout Lakes Edward and George. In Lake Edward, the typical habitat is shallow inshore waters, found only occasionally in open waters and deep steep western shores	Detritus, higher plant material, diatoms and insects
Clariidae		*Clarias gariepinus* (Burchell, 1822)	X	X	Found throughout the lakes, especially in river mouths and papyrus fringes	Fish, insects, higher plant material and detritus
		Clarias liocephalus (Boulenger, 1898)	X	X	Papyrus fringes of the Kazinga Channel and Lake George	Dipteran larvae and plant material
		Heterobranchus longifilis (Valenciennes, 1840)	–	X	Insufficient data	Insufficient data
Cyprinidae		*Enteromius kerstenii* (Peters, 1868)	X	X	Inshore areas and river mouths	Diptera larvae
		Enteromius cf. mimus (Boulenger, 1912)	X	X	Inshore areas and river mouths	Diptera larvae
		Enteromius alberti (Poll, 1939)	X	X	Inshore areas and river mouths or sources	Diptera larvae
		Labeo forskalii (Rüppell, 1835)	–	X	Only in Lake Edward. Deep clear waters close to the western shore and in rocky shorelines	Insufficient data
		Labeobarbus altianalis (Boulenger, 1900)	X	X	Common in river mouths particularly that of the Semliki river	Fish, detritus and insects
Mormyridae		*Mormyrus kannume* (Forsskål, 1775)	X	X	Papyrus fringes and river mouths	Insect larvae
		Pollimyrus nigricans (Boulenger, 1906)	X	X	Inshore and offshore waters	Dipteran larvae
Procatopodidae		**Laciris pelagica* (Worthington, 1932)	–	X	Endemic in open waters	Zooplankton
		Lacustricola vitschumbaensis (Ahl, 1924)	X	X	Inshore and river mouths	Dipteran larvae and emergents
Protopteridae		*Protopterus aethiopicus* (Heckel, 1851)	X	X	Vegetated/swampy fringes and shallow areas	Fish, mollusks, insects, Ostracoda, higher plant material and detritus

Note: X denotes presence. Notes on habitat and trophic ecology are from Worthington (1932), Poll and Damas (1935), Greenwood (1973), Gwahaba (1975), Dunn (1975), Yatuha et al. (2013), Cox (2018), Kusters (2019), Vranken et al. (2019) and Vranken, Steenberge, Kayenbergh et al. (2020), Vranken, Steenberge, Snoeks (2020), Vranken, Steenberge, Balagizi et al. (2020). Species with an asterisk are endemic to the Lake Edward system. Species with two asterisks are introduced.

Source: The list was adopted from Decru et al. (2020) and Maetens et al. (2020) for all species apart from *Haplochromis* spp. (*Cichlidae*). *Haplochromis* spp. were based on Greenwood (1973), Vranken et al. (2019), Vranken, Steenberge, Kayenbergh et al. (2020), Vranken, Steenberge, Snoeks (2020), Vranken, Steenberge, Balagizi et al. (2020) and Vranken et al. (2022).

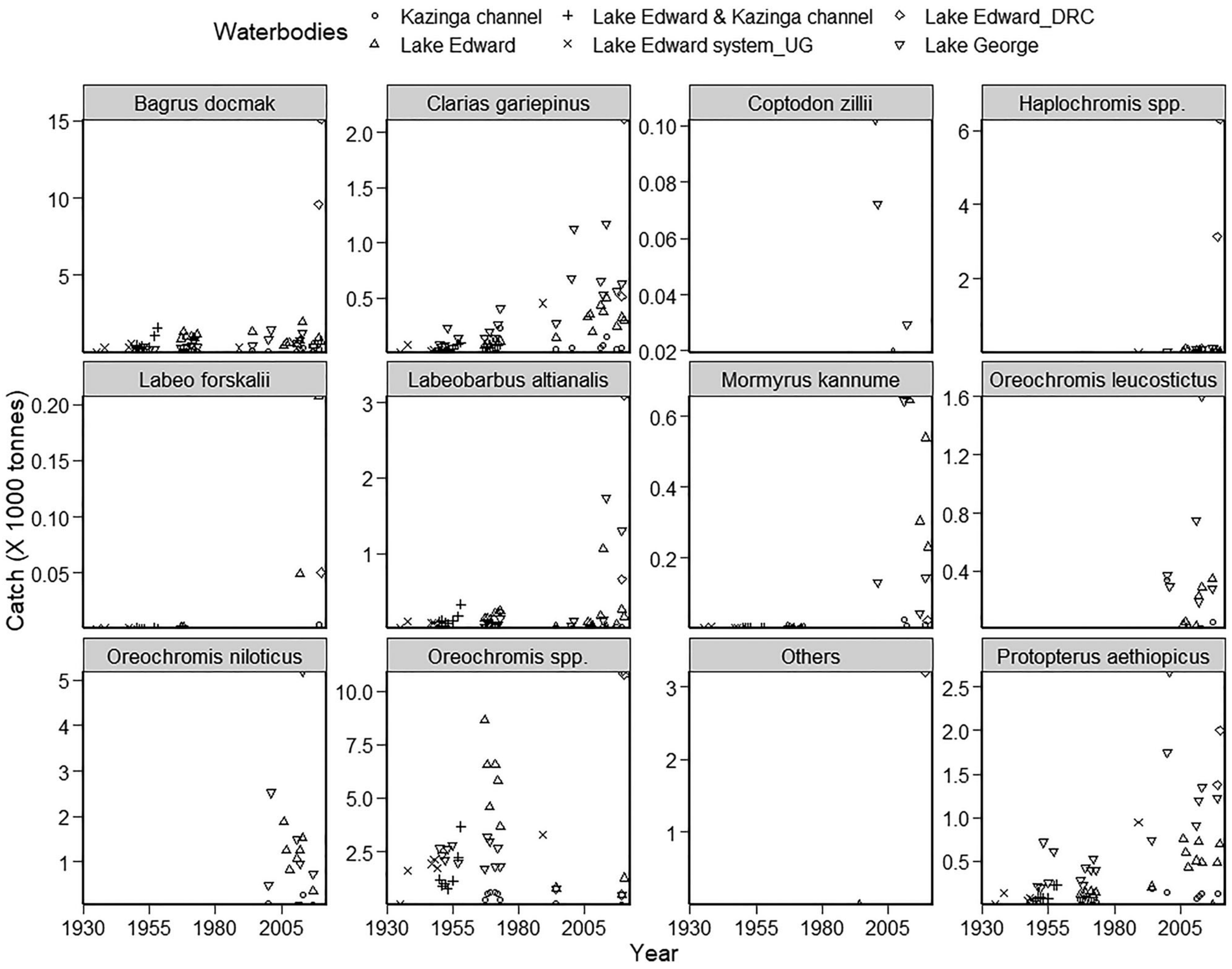

FIGURE 2 Annual catches of exploited fish species or species groups in lakes Edward, George, and the Kazinga Channel. Each graph shows catches for a specified species or species group in different water bodies: Lake Edward in Uganda (LE_UG), Lake George (LG), the Kazinga Channel (KC), Lake Edward (Uganda) and the Kazinga Channel (LE_UG_KC), Lake Edward in the Democratic Republic of the Congo (LE_DRC), lakes Edward (Uganda), George and the Kazinga Channel (LE_System_UG). Two or more water bodies are combined where available data was not segregated by waterbody. Lake Edward is shared between Uganda and the Democratic Republic of Congo (DRC). For more clarity, separate graphs were made for each species or species groups (Online Resource 1 Figures S1–S12). *Source*: Data obtained from Game and Fisheries Department (1935, 1938, 1947, 1948, 1949, 1950, 1951, 1952, 1953, 1955, 1957, 1958, 1959, 1967, 1968, 1969, 1994), Okaranon and Kamanyi (1989), Fisheries Department (1971, 1972, 1973), Lubala et al. (2018), NBI (2020, 2021) and National Fisheries Resources Research Institute (NaFIRRI).

8 mil offshore.

Worthington (1932) and Poll and Damas (1935) did not provide notes on distribution and abundance for species of *Haplochromis*. However, the distribution of *Haplochromis* spp., in general, was like that of the non-*Haplochromis* species that were not restricted to inshore or offshore habitats (Worthington, 1932). Subsequent studies provided more information on the habitat use, distribution and abundance of all described fish species, reaffirming earlier observations and providing more information on *Haplochromis* spp. For instance, in Lake George, Gwahaba (1975) found that most of the species (15 species), including most of the *Haplochromis* spp. known at the time, *Astatoreochromis alluaudi* and *Enteromius kerstenii*, were more abundant within 100 m from the shoreline and only found beyond that distance, occasionally. Gwahaba (1994) showed that species found in all regions of the lake moved freely between inshore and offshore regions, and in addition, some *Haplochromis* spp. moved to deeper parts of the lake during the day, reflected in lower catch rates near the surface. The preferred habitats for *Haplochromis* spp. in Table 2 are based on areas where they were found to be more abundant in Lake George or recorded in Lake Edward.

Recent studies have showed that the distribution of the fish species in the water bodies mirrors the pattern observed in the past. For instance, NaFIRRI (2008) recorded six species of non-*Haplochromis*: *B. docmak*, *L. altianalis*, *C. gariepinus*, *O. leucostictus*, *O. niloticus* and *P. aethiopicus*. All these species were recorded in the inshore sites, but only *B. docmak* and *P. aethiopicus* were also recorded in the offshore sites. The study recorded 14 taxa of *Haplochromis* spp. in offshore sites. In each site, three fleets of gillnets of mesh sizes 1–8 in were set

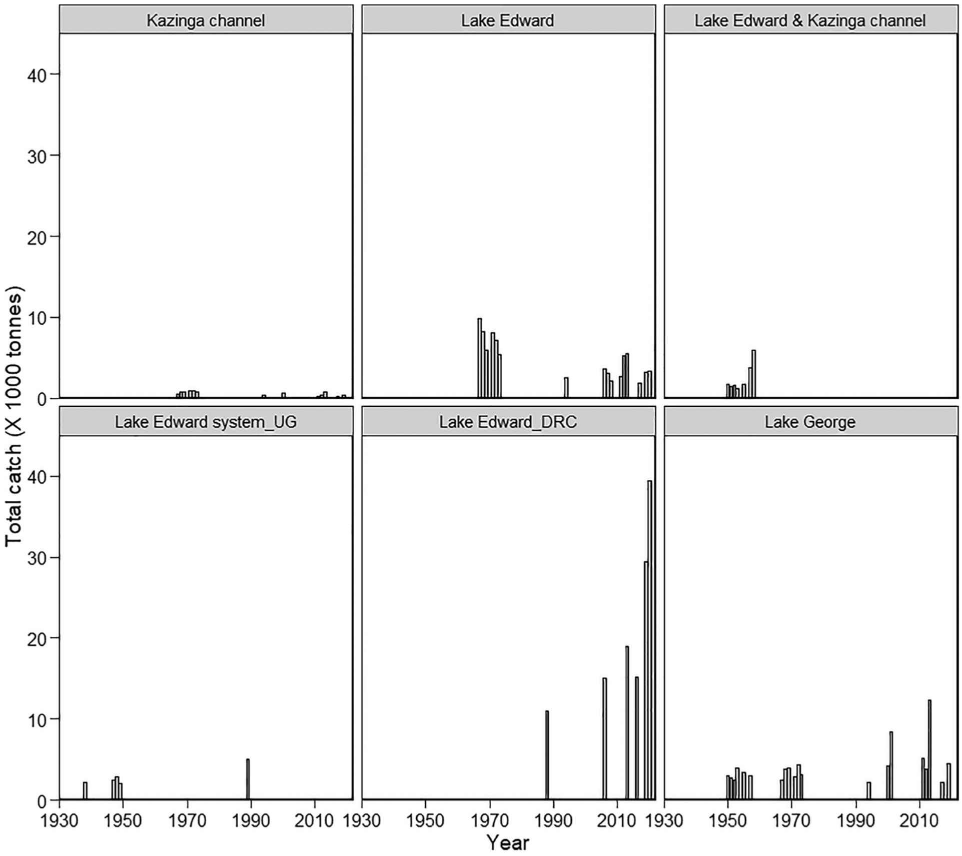

FIGURE 3 Total annual catches of exploited fish species or species groups in lakes Edward, George and the Kazinga Channel. Two or more water bodies are combined where available data was not segregated by waterbody. Lake Edward is shared between Uganda (UG) and the Democratic Republic of Congo (DRC). *Source*: Data obtained from Game and Fisheries Department (1935, 1938, 1947, 1948, 1949, 1950, 1951, 1952, 1953, 1955, 1957, 1958, 1959, 1967, 1968, 1969, 1994), Okaranon and Kamanyi (1989), Fisheries Department (1971, 1972, 1973), Lubala et al. (2018), NBI (2020, 2021) and National Fisheries Resources Research Institute (NaFIRRI).

at varying distances from the shoreline. The study showed that, generally, species diversity in the lake decreased from the shoreline, in conformity with earlier studies (Worthington, 1932).

The habitat use of fish species is best studied by tracking the movement of tagged individuals. Mbalassa et al. (2015) attempted this approach on *C. gariepinus* in Lake Edward. Observations indicated that the species predominantly used littoral areas, river channels, and wetlands as general habitats and spawning areas, and to a less extent, pelagic areas, consistent with earlier observations.

Attempts have been made using more quantitative fishing experiments to estimate the abundance of the fish species in Lakes Edward and George. These experiments involve the capture of fish mainly using gillnets in sites selected to represent diverse habitats in the waterbodies (Ogutu-Ohwayo et al., 1997; NaFIRRI, 2008). Due to the selective nature of the gillnets, multiple mesh-sizes are used to capture fish in many size classes. The capture of fish is followed by systematic identification and enumeration to acquire data on the abundance. Measures of abundance from the experiments show a dominance of cichlids (*Cichlidae*). In Lake George, Ogutu-Ohwayo et al. (1997) showed that the cichlids comprised 91.4% of the lake's fish biomass, based on the relative weight from experimental catches. Haplochromines (*Haplochromis* spp.) formed 54.1% of the relative biomass followed by *O. leucostictus* (30.7%) and *O. niloticus* (6.7%). Earlier, Gwahaba (1975) determined the biomass of fish in Lake George, reporting total fish biomass as 29 gm^{-2}. *Haplochromis nigripinnis* comprised most of the fish biomass (40%) in the lake, followed by *O. niloticus* (18%), *H. angustifrons* (15%), *P. aethiopicus* (9%), *C. gariepinus* (7%), *O. leucostictus* (4%), *B. docmac* (4%), *H. squamipinnis* (3%), *Aplocheilichthys* (now *Lacustricola)* (2%), and *H. pappenheimi* (0.1%). These observations suggested that other fish species belonging to Cyprinidae, Mormyridae, Anabantidae and some cichlids such as *Coptodon zillii* were less abundant in the lake.

In Lake Edward, NaFIRRI (2008) showed that haplochromines comprised 95.9% of the fish community by number. The six non-haplochromine species captured accounted for only 4.1% by number. By weight, the haplochromines accounted for 76.4% and non-haplochromines 23.6%. Furthermore, the most dominant species, among the haplochromines, was *H. nigripinnis*, whereas the most dominant non-haplochromine species was *B. docmak*. The dominance of the haplochromines in Lake Edward was also demonstrated by a recent experimental fishing expedition conducted in 2019 in which the haplochromines comprised ~90% of the fish community by number (LEAF, 2019). It is important to note that gillnets, the fishing gear on which these observations are best, is highly selective for species and size, although multiple mesh sizes are used to target all species and size classes.

3.4 | Life history characteristics of the fish species

3.4.1 | Reproductive biology

Life history characteristics of fish species determine how vulnerable or resilient the species and the ecosystem services they support are to fishing pressure and environmental change (McKinney, 1997; Pitcher et al., 2013). For data-poor fisheries, these characteristics may be the only information available to define fish stock status and support decision-making. The characteristics are also direct or indirect inputs into ecosystem models and comprehensive stock assessments. We established that not many studies have examined the life history and biological characteristics of the populations of the fish species occurring in lakes Edward and George.

The reproductive biology of fishes is examined through aspects such as sex ratio, size at maturity, fecundity and timing and location of spawning. Sex ratios were available for six species of commercial importance (Table 3). Sex ratios reported for species in Lake Edward by NaFIRRI (2008) seemingly differed from the expected male:female ratio of 1:1, probably because few specimens (4–26) were examined. Estimates of size at first maturity (L_{M50}) were available for only 4 of the 8 fish species of commercial importance (Table 3).

Estimates of fecundity (absolute) in the lakes were only retrieved for *O. leucostictus* at a range of 230–718 eggs from 5 specimens (Ogutu-Ohwayo et al., 1997). Using the distribution of the young, Gwahaba (1973) provided information on the spawning behaviour and habitats of selected species in Lake George and the Kazinga Channel. *O. niloticus* spawns throughout the year, with peak spawning in the wet season associated with a higher proportion of fish with active gonads and young fish. *B. docmak* and *L. altianalis* predominantly use sandy bottoms for spawning. In Lake Edward, spawning locations for *C. gariepinus* were determined as marginal wetlands, river channels, littoral zones, and river mouths (Mbalassa et al., 2015). However, generally, species in the two lakes spawn in shallow nearshore habitats (Gwahaba, 1975).

3.4.2 | Growth and mortality rates

Fish growth parameters include von Bertalanffy growth parameters (Von Bertalanffy, 1938), age at a given size and longevity, whereas mortality rates include total, natural, and fishing mortality rates. This information was found to be limited for the populations of the fish species in the water bodies. No estimates existed for mortality rates of the exploited fish species in the water bodies and only *O. niloticus* in Lake Edward had estimates of length and weight at infinity based on observed maximum length (49 cm) and weight (2.0 kg), that is 51.6 cm and 2.7 kg, respectively (Vakily, 1989). Substantial information on the growth of the fishes was available only as Fulton's condition factor (*K*), and coefficients (*b*) of length–weight relationships (Table 4.

3.5 | Trophic ecology

Table 2 synthesizes available information on the trophic ecology of the fish species in Lakes Edward and George. Worthington (1932) and Poll and Damas (1935) provided insights into the food of some of the species in the two lakes. *Labeobarbus altianalis* was suggested to be omnivorous, with fish remains, mollusks, chironomids, macrophytes and detritus present in its stomachs. *Clarias gariepinus* was defined as a predatory species, feeding mainly on fish and to a lesser extent, macroinvertebrates, macrophytes, algae, detritus and, probably, zooplankton. The species fed on a variety of fish species including *Oreochromis* spp., *Haplochromis* spp., *Barbus* spp. (now *Enteromius* spp. or *L. altianalis*) and *L. pelagica*. *Protopterus aethiopicus* was omnivorous. In nine stomachs with food examined for the species, six were found with fish remains, and each of the three remaining ones with either mollusks, chironomid larvae or plant materials. This data suggested that fish was the main diet of the species. All stomachs of Mormyridae examined contained chironomid larvae. The food of *L. pelagica* was reported as zooplankton.

In Lake George and the Kazinga Channel, the diet of *O. niloticus* was found to be predominantly phytoplankton and zooplankton (Worthington, 1932). In the Kazinga channel, near Lake Edward, the composition in the diet of the species shifted, with the zooplankton and phytoplankton taxa more abundant in Lake George, and the Kazinga channel becoming replaced by those more abundant in Lake Edward. In the open water of the lake, the species fed on macrophytes and Chaoboridae, but to a lesser extent than zooplankton and phytoplankton. Worthington (1932) remarked that the food of *Haplochromis* spp. was diverse and observed the presence of molluscivores, planktivores and piscivores, based on the morphology of mouth parts, jaws and teeth. Dunn (1975) provided more information on the main food organisms of the fish species in Lake George, including *Haplochromis* spp. (Table 2). Trewavas (1983) suggested that the diet of *O. leucostictus* was dominated by phytoplankton.

Until 2008, information on the diet of the species was qualitative without the quantification of the relative importance of diet items. Although NaFIRRI (2008) also listed the main food of *C. gariepinus* and *P. aethiopicus* as insects and mollusks, respectively, the relative importance of food organisms of *B. docmak* and *O. niloticus* were quantified. Odonata at 47.6% dominated the diet of *B. docmak* followed by fish (mainly haplochromines) at 35.2%, with the rest comprised Chironomidae, *Chaoborus* spp. and Ephemeroptera. The food items of *O. niloticus* were dominated by algae (76.7%), followed by zooplankton (12.1%) and detritus (11.3%).

Between 2015 and 2020, more studies on the trophic ecology of the fish species were conducted under HIPE (human impacts on ecosystem health and resources of Lake Edward), a project implemented to study the aquatic ecosystems in the Lake Edward system (Borges et al., 2021). The studies integrated stomach contents analysis with stable

TABLE 3 Reproductive biology of the commercial fish species in lakes Edward, Gorge, and the Kazinga channel.

Species	Sex ratio (Male: Female)	L_{M50} (cm) Total length	Sampling event year	Water body	Reference
Oreochromis niloticus	–	20	1997	Lake George	Ogutu-Ohwayo et al. (1997)
	10:4 (12)	–	2007/2008	Lake Edward	NaFIRRI (2008)
	–	21	2011/2013		Bassa et al. (2015)
	1:0.88 (942)	20.5	1972	Lake George	Gwahaba (1973)
	–	25.2	1957–1959	Lake George	Fry and Kimsey (1960)
	1:1.6 (751)	–	1930/31	lakes Edward and George	Worthington (1932)
	–	20 (24)		Lakes Edward, George and the Kazinga Channel	Kamanyi (1996)
Bagrus docmak	~1:2 (26)	–	2007/2008	Lake Edward	NaFIRRI (2008)
	–	35–39 FL	1997	Lake George	Ogutu-Ohwayo et al. (1997)
	–	34.5	2011/2013		Bassa et al. (2015)
	1:1.3 (150)	–	1930–31	lakes Edward and George	Worthington (1932)
	–	35–39 FL (50–54)		Lakes Edward, George and the Kazinga Channel	Kamanyi (1996)
Clarias gariepinus	10:3 (8)	–	2007/2008	Lake Edward	NaFIRRI (2008)
	1:0.7 (104)	–	1930–31	lakes Edward and George	Worthington (1932)
Oreochromis leucostictus	10:3 (9)	–	2007/2008	Lake Edward	NaFIRRI (2008)
	–	15	1997	Lake George	Ogutu-Ohwayo et al. (1997)
Protopterus aethiopicus	1:1 (4)	–	2007/2008	Lake Edward	NaFIRRI (2008)
	–	56	2011–2013		Bassa et al. (2015)
	–	55–59	1997	Lake George	Ogutu-Ohwayo et al. (1997)
	–	55–59 (75–79)		Lakes Edward, George and the Kazinga Channel	Kamanyi (1996)
	1:1 (17)	–	1930/31	lakes Edward and George	Worthington (1932)
Labeobarbus altianalis		21.1 FL (male)	2015	Lake Edward	Aruho et al. (2018)
		35.4 FL (Female	2015		Aruho et al. (2018)
	10:3 (23)	–	2007/2008		NaFIRRI (2008)
	1:2.5 (228)	–	–		Worthington (1932)

Note: Values alongside sex ratios in parenthesis are number of fish examined. L_{M50} stands for size at first maturity, the length at which 50% of individuals in a fish population are mature.

isotopes. Excluding synthetic materials, 21, 19, 13, 6, 16 and 14 items were identified in the stomachs of *C. gariepinus*, *P. aethiopicus*, *O. niloticus*, *O. leucostictus*, *B. docmak*, and *L. altianalis*, respectively, indicating that the diet of the species was diverse (Cox, 2018; Kusters, 2019). In broader terms, the diet items of these species were found to lie in six major groups: detritus, phytoplankton, higher plant material, zooplankton, macroinvertebrates, and fish. Using prey specific abundance and frequency of occurrence (Amundsen et al., 1996), the most frequent and dominant of these diet items or broad groups were determined for each of the species (Table 2).

Stable isotope analyses provided more information on the trophic ecology of the fish species. The fish species community in Lake Edward were found to have higher nitrogen isotope ratios and lower carbon isotope ratios than in Lake George and the Kazinga Channel (Cox, 2018). Higher nitrogen ratios in fish are linked with a higher concentration of DIN in waterbodies (Qu et al., 2021). However, this may not explain the higher ratios in Lake Edward compared to Lake George and the Kazinga Channel because the former has the least concentration of DIN (Stoyneva-Gärtner et al., 2020). Therefore, the differences in isotope ratios could be attributed to the incorporation of higher trophic level organisms into diet of the fish species in Lake Edward.

The variety of diet items for the different species or species groups were combined to form a diet matrix useful in ecosystem models based on Ecopath with Ecosim (EwE), the most common modelling platform for aquatic ecosystems (Christensen et al., 2008). The matrix (Online Resource 1; Table S1) comprises predators (columns in Online Resource 1 Table 1) and their diet composition. The diet composition shows the proportion each prey (rows in Online Resource 1; Table S1) contributes to the overall diet of a predator, relative to the contribution of others (Christensen et al., 2008). The sum of the diet composition should be equivalent to one which was true for only five species or species groups. For the others, the sum was indicated as NA for

TABLE 4 Estimates of some growth parameters for selected fish species in the lake Edward system.

Species	Length–weight coefficients	Fulton's condition factor (K)	Sampling year	Waterbody	Reference
Oreochromis niloticus	$a = 0.015$; $b = 3.09$	–	1997	Lake George	Ogutu-Ohwayo et al. (1997)
	–	2.2	2008	Lake Edward	NaFIRRI (2008)
	–	2.0–2.3	1930–1931	lakes Edward and George	Worthington (1932)
	$a = 0.023$; $b = 2.954$	–	1989	Lake Edward, DRC	Vakily (1989)
Oreochromis leucostictus	$a = 0.013$, $b = 3.13$	–	1997	Lake George	Ogutu-Ohwayo et al. (1997)
	–	1.9	2008	Lake Edward	NaFIRRI (2008)
Labeobarbus altianalis	$a = 0.0000021$; $b = 3.27$	–	2013	Lake Edward and the Kazinga channel	Ondhoro et al. (2017)
	–	1.5	2008	Lake Edward	NaFIRRI (2008)
	–	1.0–1.1	1930–1931	lakes Edward and George	Worthington (1932)
Clarias gariepinus	–	0.8	2008	Lake Edward	NaFIRRI (2008)
	–	0.6–0.8	1930–1931	lakes Edward and George	Worthington (1932)
Bagrus docmak	–	1.2	2008	Lake Edward	NaFIRRI (2008)
Protopterus aethiopicus	–	0.4	2008	Lake Edward	NaFIRRI (2008)

Note: Length–weight coefficients: *a* represents the intercept, whereas *b* represents the slope of the length–weight regression.

predators whose diet composition was only qualitative, and less than one where some diet items could not be attributed to specific species or species groups in the matrix. These two issues indicated a knowledge gap in trophic ecology in the waterbodies.

3.6 | Fisheries

Lakes Edward, George, and the Kazinga Channel support fisheries from which riparian communities in Uganda and the DRC derive livelihoods. By the 1930s, fisheries exploitation was occurring although fishing effort and corresponding catches were small (Poll & Damas, 1935; Worthington, 1932) (Figures 2–3). According to Worthington (1932), *Oreochromis* spp. were the main targeted group, although *L. altianalis*, *C. gariepinus*, *B. docmak*, *P. aethiopicus*, *M. kannume*, and *L. forskalii* were also caught. The study of Worthington (1932) also noted that by 1931, fishing effort was small and restricted to inshore areas and a few fishing villages because of inadequate fishing craft to access the open waters, poor road network and area closures. As a result, the catches at the most active landing sites on lakes Edward and George in Uganda were small, ~100 fishes per day. The most active site on Lake George had 16 fishermen operating three fishing craft, whereas the most active site on Lake Edward was in DRC (Kamande; Figure 1) with several fishing boats including one with an outboard engine.

Since 1935, the initial targeted species or groups of species (*B. docmak*, *C. gariepinus*, *L. forskalii*, *L. altianalis*, *M. kannume*, *P. aethiopicus*, *O. niloticus*, and *O. leucostictus*) persisted in catches (Figure 2). Others appeared in catches later (*Haplochromis* spp. from the 1980s and *C. zillii* from 2000) (Figure 2). Species of commercial importance are *B. docmak*, *L. altianalis*, *P. aethiopicus*, *C. gariepinus*, *O. leucostictus*, *O. niloticus*, and *M. kannume* (Decru et al., 2020; Lubala et al., 2018; NaFIRRI, 2019; Petit, 2006). Generally, species extant in the water bodies (Table 2) but not in catches are less abundant. *Haplochromis* spp., which are the most dominant in the waterbodies by biomass (Gwahaba, 1975), are not dominant in catches because they are not a preferred target species. Described as rare (Poll & Damas, 1935; Worthington, 1932), the presence and persistence of *M. kannume* and *L. forskalii* in catches are noteworthy (Figure 2).

Fisheries of Lakes George and Edward have developed steadily since the 1930s, associated with an increase in the number of fishers and fishing efficiency, utilizing gillnets and longlines (Dunn, 1972) (Figure 3). In these water bodies, *Oreochromis* spp. initially comprised most of the catches (Figure 4; Online Resource 2), contributing 38.4%–82.2%. The development of the fisheries, however, was accompanied by changes in species composition in the catches. In the Ugandan part of Lake Edward, the contribution of *Oreochromis* spp. reduced from 87.7% in 1967 to 14.6% in 2019 (Figure 4; Online Resource 2), whereas in Lake George, their contribution decreased from 91.8% in 1950 to 11.0% in 2019 (Figure 4; Online Resource 2), and from 79.1% in 1969 to 6.85% in 2019 in the Kazinga Channel (Figure 4; Online Resource 2). In the DRC (Lake Edward), the contribution of *Oreochromis* spp. reduced from 78% in 1970 to 26% in 2016 (Figure 4; Online Resource 2). The decline in the contribution of *Oreochromis* spp. suggests that species in this group, particularly *O. niloticus* which is of higher abundance and importance in the fisheries than *O. leucostictus*, became heavily exploited around the 1970s. In Uganda, this decline in *Oreochromis* spp. coincided with a decline in total catches (Figure 3). In response, fishers redistributed fishing effort to *B. docmak*, *P. aethiopicus*,

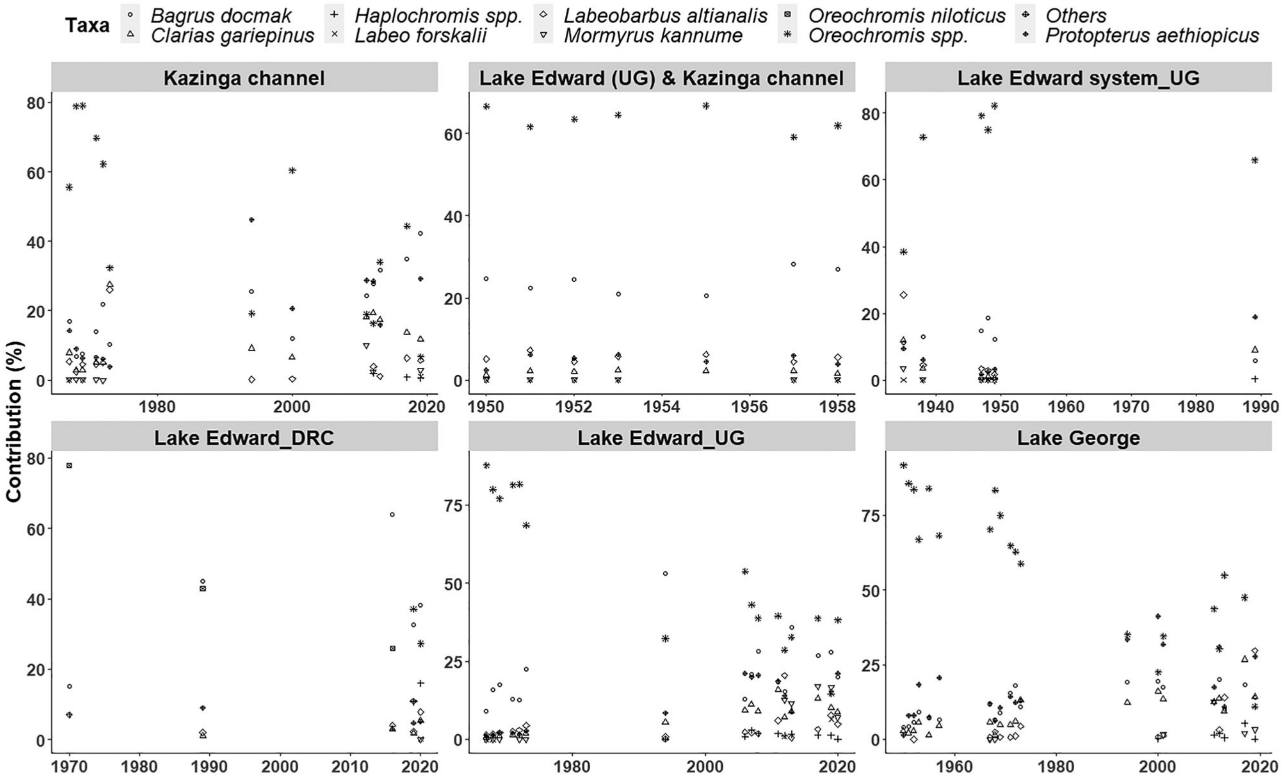

FIGURE 4 Catch composition (%) by water body or a combination of water bodies. Two or more waterbodies were combined for some periods when data was not segregated by waterbody. Lake Edward is shared between Uganda and the Democratic Republic of the Congo (DRC). Online Resource 2 provides data on which this figure was based. *Source*: Data adopted from Game and Fisheries Department (1935, 1938, 1947, 1948, 1949, 1950, 1951, 1952, 1953, 1955, 1957, 1958, 1959, 1967, 1968, 1969, 1994), Okaranon and Kamanyi (1989), Fisheries Department (1971, 1972, 1973), Lubala et al. (2018), NBI (2020, 2021) and National Fisheries Resources Research Institute (NaFIRRI).

and *C. gariepinus*. This shift in target fisheries was followed by an increase in catches of these species in lakes Edward and George (Figure 2), especially for *C. gariepinus* (Online Resource 1; Figure S2) and *P. aethiopicus* (Online Resource 1; Figure S12).

Where substantial long-term data was available, total catches for fish species or water bodies illustrated a general increase, followed by a decrease to a relatively stable level (Figures 2 and 3; Online Resource 1; Figures S1–S12). The trend in catches of Lake Edward in the DRC is an exception that is discussed in the following.

The CAS conducted in 2019 and 2020 provided catch estimates for the part of Lake Edward in the DRC that were enormously inconsistent with previous catches in the country, and the known estimates of maximum sustainable yield (MSY) (NBI, 2020, 2021). The estimates of the catches, as depicted in Figures 2 and 3, were much higher than expected. Total catches were estimated at 29,347 t for 2019 and 39,411 t for 2020. Dominated by *B. docmak* and *Oreochromis* spp. (Figure 4; Online Resource 2), these estimates showed that the actual catches in the DRC could be more than twice the previous catches (Figures 2 and 3) and known estimates of MSY. Estimates of MSY are a range of 14,000–16,000 t per year for the whole lake, 11,000–12,000 t for the DRC and 3000–4000 t for Uganda (Vakily, 1989).

Despite the inconsistency, the estimates of catches for 2019 and 2020 (NBI, 2020, 2021) could be believed, given that past authors acknowledged gross underestimation of catches (Petit, 2006; Vakily, 1989) and these estimates were derived from the first comprehensive CAS in the DRC. Several issues hinder the proper monitoring of the fisheries resources of Lake Edward in the DRC. Fishing activities in the part of the lake are managed by multiple stakeholders (Lubala et al., 2018; Vakily, 1989). Due to lack of coordination, these stakeholders, if they do, only report catches from fish landing sites within their jurisdictions and selected fishing gears (Petit, 2006). A substantial part of the fishery is controlled by rebel groups and for safety reasons, this part is rarely, if at all, monitored (Petit, 2006). Research studies also restrict data collection to safe landing sites and have substantial methodological limitations. For instance, Lubala et al. (2018) sampled only four safe landing sites to determine annual catches, and the approach used to derive lake-wide estimates from the observations made at the sampled sites was not indicated. NBI (2020, 2021), on the other hand, engaged multiple stakeholders in the DRC, sampled many (10) fish landing sites and used standardized approaches for CAS (LVFO, 2005). These estimates were corroborated with estimates from an independent monitoring exercise by the Congolese Institute for Nature Conservation-Virunga National Park (ICCN-PNVI) that began in 2019 to record daily catches in four landing sites. Using data from this monitoring exercise, Omombo et al. (unpublished) estimated total catches in the DRC as 28,427 t for 2019, 29,338 t for 2020 and 22,868 t for 2021.

The inconsistency of the estimates of 2019 and 2020 with the known estimates of MSY could be explained by the origin of the MSY estimate. Vakily (1989) derived the MSY from a model that relates the morphoedaphic index (MEI) of a water body with its fish yield (Schlesinger & Regier, 1982). In the model, the MEI, derived from a ratio of total dissolved solids (TDS) and mean depth, is directly proportional to MSY. Environmental changes such as eutrophication that increase TDS and decrease mean depth should increase MEI, and consequently, MSY (Ryder, 1965). Given that Lake Edward has become more nutrient-enriched (Stoyneva-Gärtner et al., 2020), its current MSY based on the model should be higher. However, this is not the case. Recalculating the MSY using recent estimates of TDS (derived from mean conductivity from Stoyneva-Gärtner et al. (2020) using a function by Rusydi (2018) that correlates TDS and conductivity) and mean depth (Hamilton et al., 2022) generated a value (16,550 t), close to that of Vakily (1989). This finding suggests that TDS may not be a good predictor of fish yield in the lake. Therefore, the MSY value by Vakily (1989), compared to the catches of 2019 and 2020, was probably an underestimate. In addition, research efforts before 2019 as suggested by Vakily (1989) and Petit (2006) underestimated catches in the DRC. For this reason, the pattern in catches differs from that in the Ugandan part of Lake Edward and Lake George (Figure 3). Actual catches in the past could have been more than the values determined for 2019 and 2020. These catch levels account for the high fishing effort which has increased remarkably on the lake as indicated by the number of fishers and fishing boats (Figure 5).

Lakes Edward and George have had a long history of fisheries management. In Uganda, the leading role of fisheries management has always been a responsibility of a designated government agency. In the DRC, management responsibilities are mainly shared among different stakeholders with different spatial or functional jurisdictions (Lubala et al., 2018; Petit, 2006; Vakily, 1989). Some fishing areas are controlled by rebel groups that encourage illegal fishing, discourage monitoring and contest management measures by the government (Marijnen, 2022; Petit, 2006). The earliest report we retrieved for the agency responsible for fisheries management in Uganda was from 1935 (Game and Fisheries Department, 1935), the time the fisheries on the water bodies were developing. The department practiced active management, taking precautions to prevent overfishing. Management practices included recording catches, licensing, enforcement of fishing regulations and setting minimum mesh size. These practices showed that management aimed at controlling fishing effort directly through different measures, an approach that is still followed on these water bodies today. Over time, these management measures became ineffective, especially in the DRC, as reflected in the proliferation of fishing effort (Figure 5), the use of illegal fishing gear and the capture of immature fish (Bassa et al., 2014; Dunn, 1975; Lubala et al., 2018; Petit, 2006). These unsustainable fishing practices are depicted in declining catches and reduced average weight of individuals in the catches for most species (Figure 6).

In response to unsustainable fishing practices, Uganda intensified the enforcement of fisheries regulations since 2018 to end illegal fishing practices and methods (NPA, 2019). Since then, illegal activities have significantly reduced, and catches have improved on lakes Edward and George (NBI, 2020). Fishers from the DRC are increasingly crossing into Uganda to exploit the opportunities of the improved enforcement on Lake Edward, resulting in fatal crashes and frequent arrests by Uganda's military, which coordinates the enforcement (Kyalwahi, 2021; Marijnen, 2022).

4 | DISCUSSION

Reliable data is an important requirement for sustaining inland fisheries and the ecosystem services they support (Cooke et al., 2016). The first of the 10 steps of the Rome Declaration for responsible inland fisheries calls for the enhanced acquisition of accurate and complete data on inland fisheries, including at local scales (FAO and MSU, 2016). The availability of data is envisaged to spur global assessments of the inland fisheries, akin to those of marine fisheries and stimulate inclusion into global governance processes. Required actions at local scales according to the Rome Declaration include data collection, monitoring, and assessment of fisheries. In all these actions, standard methodologies are recommended and all forms of inland fisheries, including subsistence, recreational and illegal and unregulated fisheries should be covered.

This review showed that Lakes Edward and George have been subjected to research surveys, providing data and information on aspects of water quality, extant taxa, the abundance of biotic communities, life history of fish species, trophic ecology, fishing effort and fish catches. However, substantial gaps exist. First, all the aspects examined lacked adequate time series data. Unlike aspects such as water quality, extant fish species, fishing effort and fish catches which had recent data, data available on abundance of all biotic communities and life history parameters (Tables 3 and 4) require updating. In addition, the commercial fish species in the waterbodies lacked values on fish mortalities and von Bertalanffy growth parameters which are important life history characteristics (King & McFarlane, 2003). Information available on trophic ecology was mainly qualitative (Table 2; Online Resource 1; Table S1), indicating the need for quantifying diet composition of all the fish species or species groups in the water bodies. In fisheries, apart from the uncertainty in the catches of DRC, there is absence of fisheries management reference points, benchmarks used to measure the status of exploited fisheries (ICES, 2017).

Lack of adequate time series and presence of aspects that require updating or consideration in research can be explained by lack of established monitoring programmes for regular data collection, a characteristic of most inland fisheries (Cooke et al., 2016; Plisnier et al., 2022). Routine monitoring programmes with a wide scope covering all aspects of aquatic ecosystem health and fisheries have been recommended on water bodies in the region, including lakes Edward and George, to sustain data collection efforts and avoid the data gaps (Plisnier et al., 2022). In these water bodies, monitoring programmes could be designed to fill all the established data gaps above. Studies of substantial magnitude on these water bodies such as Stoyneva-Gärtner et al. (2020) and NaFIRRI (2008) considered spatial variations

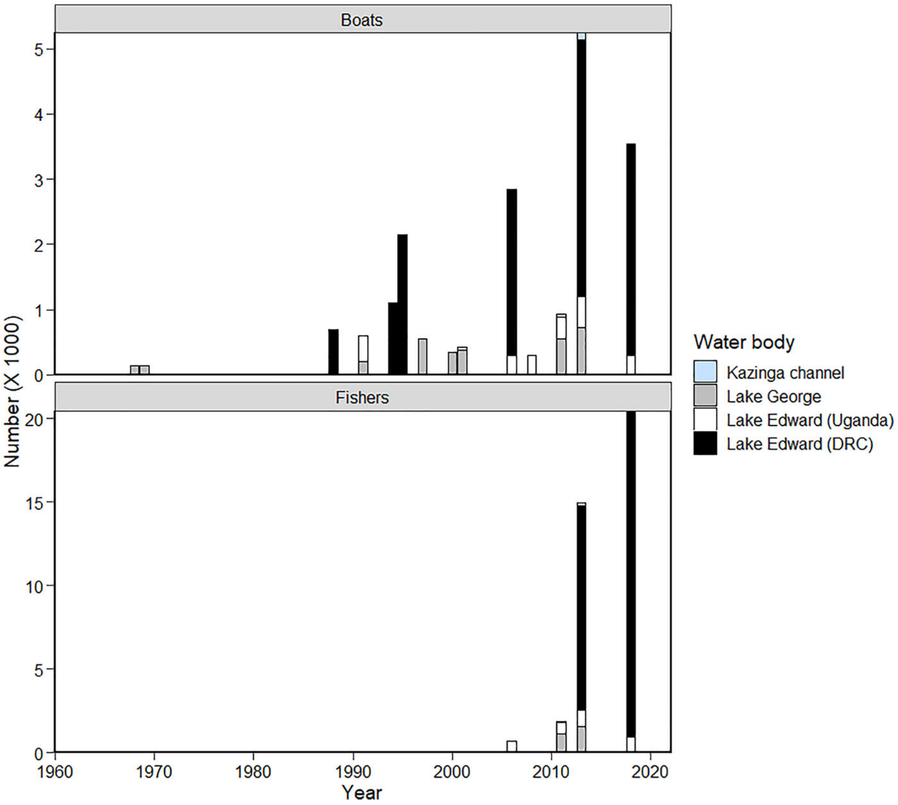

FIGURE 5 Number of fishers and boats on lakes Edward, George and the Kazinga Channel. *Source*: (Fishers) Data adopted from: Lubala et al. (2018) and National Fisheries Resources Research Institute); (Boats) Data adopted from: Vakily (1989), Petit (2006), NaFIRRI (2015), Lubala et al. (2018) and NBI (2019).

in parameters studied. This should be maintained in the routine monitoring programmes. In Lake Edward, these studies were biased to the Ugandan part of Uganda (Online Resource 1; Figure S13). The absence of the part of the lake in the DRC in these studies is conspicuous probably due to unrest in the region that makes sampling difficult (Marijnen, 2022). This issue seems to have been the reason why for instance, Stoyneva-Gärtner et al. (2020) sampled only one site in DRC compared to 16 sites in Uganda. Where possible, the monitoring programmes should consider this part of the lake to ensure a complete understanding of the spatial variations.

Routine data collection is required most on the aspects of fisheries using fishery-dependent surveys to obtain data on catch and fishing effort preferably on an annual basis. In DRC, these could help ascertain the catches observed in 2019 and 2020. Data collection using fishery-dependent surveys could be improved by using personnel placed at fish landing sites, observers and fishers' records (FAO, 1999). High costs of observation programmes and low literacy levels among fishers in the area make personnel stationed at landing sites the most viable option. In the past, such personnel recorded catches on the water bodies in Uganda (Game and Fisheries Department, 1935), whereas, in the DRC, the personnel exist at some landing sites, although they do not measure catches directly but record fishers' declarations which is problematic (Petit, 2006). Actualizing this approach could be preceded by selecting representative sites whose estimates could be extrapolated to generate lake-wide estimates. This is because landing sites on the waterbodies are many and dispersed (Figure 1), making it difficult to place personnel at each site to collect data. To improve the completeness of data, data collection efforts should incorporate measurements of individual fish size (length and weight) and always aim at disintegrating the catches data by species. Catches by illegal segments of the fisheries are not properly recorded (Dunn, 1972; Ogutu-Ohwayo, 1997; Petit, 2006). Modalities should be devised to reflect these catches in records.

Fishery-independent surveys are required to supplement the data from fishery-dependent surveys and cover aspects of the abundance of biotic communities, the life history of fish, fish trophic ecology and water quality. Data on abundance, preferably absolute biomass, is required for biotic communities including fish, invertebrates, macrophytes, and phytoplankton. Fish biomass is best derived using swept area (trawling) and hydroacoustic methods (Silliman and Gutsell, 1958). In the region, these methods are not common and may occur only in larger lakes such as Lake Victoria (Hydro-acoustics Regional Working Group, 2019). Using these methods in lakes Edward and George needs the acquisition of infrastructure in terms of, for example research vessels which are costly. For this reason, we are certain that it will take time to apply these methods in these waterbodies. Fishery-independent surveys should occur annually with standardized methods to provide adequate time series data to assess ecosystem

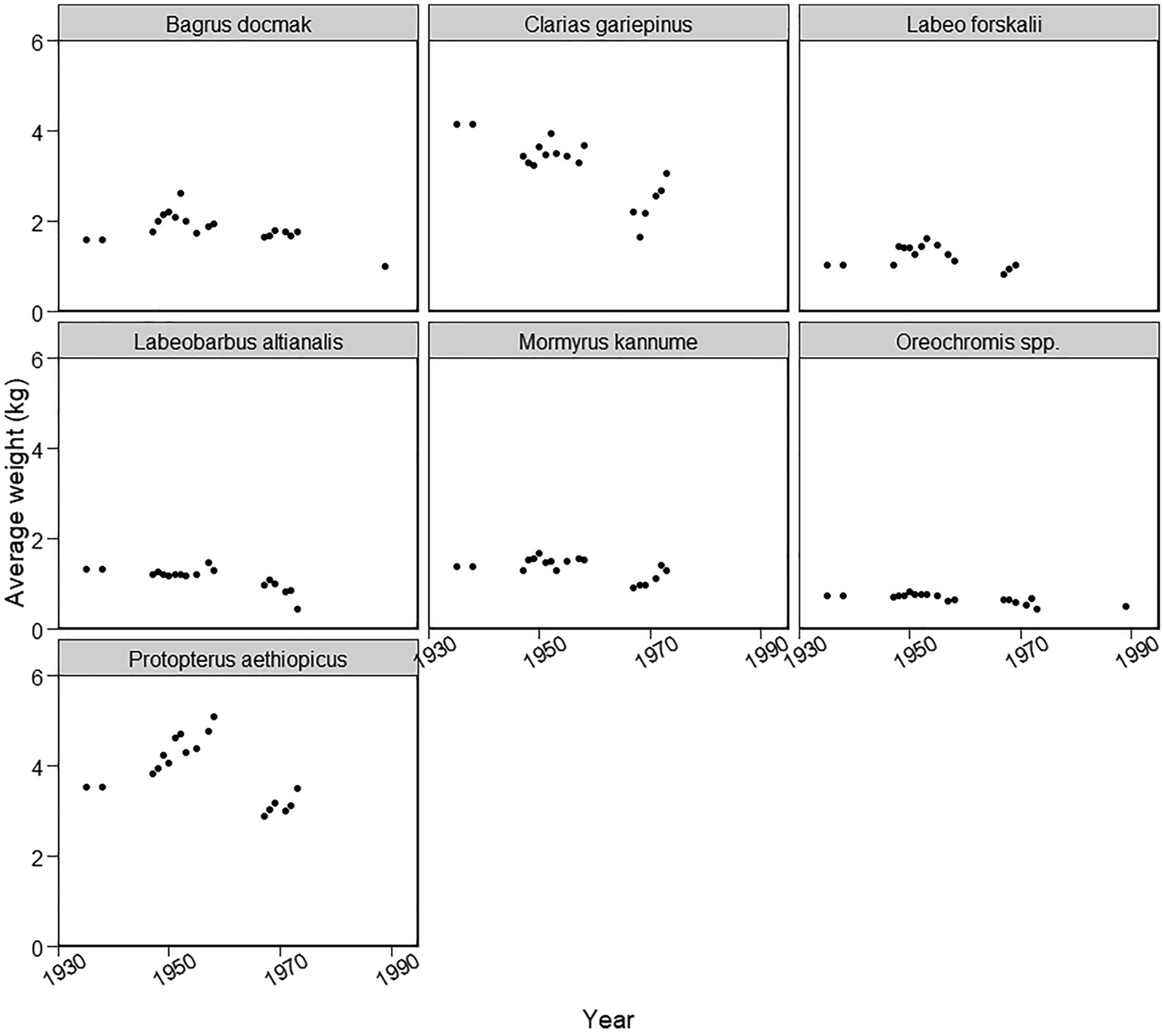

FIGURE 6 Changes in average weight of individuals in catches. Values are aggregations for lakes Edward, George and the Kazinga Channel. *Source*: Data adopted from Reports by the Game and Fisheries Department (1935, 1938, 1947, 1948, 1949, 1950, 1951, 1952, 1953, 1955, 1957, 1958, 1959, 1967, 1968, 1969, 1994), Fisheries Department (1971, 1972, 1973) and Ssentongo (1992).

and fisheries status (Froese et al., 2020). In these fishery-independent surveys, efforts should be made to design the methods in a way that facilitates the comparison of results with those from studies in the past. For water quality, methods and sensitivity of instruments for some parameters may have changed in response to technological advances (Zainurin et al., 2022). As result, temporal comparisons should be made cautiously.

Life history parameters of fish are key for monitoring and management of exploited fish species yet in these waterbodies, the parameters are either missing or require updating. Data from the proposed fishery-dependent and fishery-independent surveys should be integrated to obtain more reliable estimates of these parameters. In the short term, gillnet surveys (fishery-independent) could be integrated with fishery-dependent surveys to update existing estimates of growth, size at maturity and coefficients of length–weight relationships (Tables 3 and 4). Only data-poor approaches could be applicable for determining von Bertalanffy growth parameters and mortalities using this data. The most used of these methods is the electronic length frequency analysis (ELEFAN) which generates growth parameters from length–frequency data (Pauly & David, 1981). Data needs for this method are monthly data collections, preferably for 1 year, covering all size spectrums and populations of species of interest. Sampling commercial catches to supplement fishery-dependent surveys could contribute to data completeness for this approach.

The exploited fish species in the waterbodies also lacked fisheries management reference points meaning that stock assessment in the past neglected a critical stage where the fishery-dependent and -independent data is used to define the status of fish stocks using fisheries management reference points (Caddy & Mahon, 1995). The reference points are used to establish rules for harvest control and to evaluate management measures. We found this stage lacking, with the stock assessment process ending at the estimation of catches, life history parameters and fishing effort, defined as either the number of boats or fishers. The absence of this stage suggests that management occurs with inadequate guidance. In addition, uncertainty exists on the actual status of exploited fish species and the limits or targets adequate to sustain and rebuild the fisheries. In response, available data could be subjected to stock assessments using appropriate methods for data-poor fisheries to generate the fisheries management reference points. A variety of data-poor methods that for example use only length–frequency data, and catches exist (Froese et al., 2017, 2018, 2020; Newman et al., 2015). In future, the reference points should be generated annually, simultaneous with the fishery-dependent and -independent surveys, which we have also recommended to occur annually.

With intensifying fishing pressure and emerging issues such as oil exploitation (Verheyen et al., 2016), Lakes Edward and George could benefit from Ecosystem-based Fishery Management (EBFM) which is promoted as the best option for fisheries management (Pikitch et al., 2004). Positive outcomes have been reported for inland fisheries, for example in Indonesia, Brazil and Laos, where elements of EBFM have been incorporated in management (Butorac et al., 2020; Ditya et al., 2022; Koning et al., 2020). Supporting EBFM requires ecosystem modelling to describe and quantify interactions among ecosystem elements (functional groups), assess the impacts of environmental change and fishing, and evaluate management options (Essington & Punt, 2011; Plagányi, 2007). Acknowledging the significance of climate change to fisheries (Allison et al., 2009), the EBFM is also the best means to adapt the fisheries to impacts of climate change (Holsman et al., 2020). The development of operational ecosystem models of lakes Edward and George to support decision-making should be considered in research.

Modelling efforts could focus on using EwE, the most common framework for modelling aquatic ecosystems (Colléter et al., 2015). Many EwE models exist for most of the African Great Lakes (Musinguzi et al., 2017), but Lake Edward has never been considered for ecosystem modelling using EwE, whereas one model of the 1970s exists for Lake George (Moreau et al., 1993). Despite the gaps in data, this review showed that minimum information required to define functional groups for the models is available. The data available on water quality and primary production (Table 1), fish life history and biological characteristics (Section 3.2), biomass of invertebrates (Section 3.1), trophic ecology (Table 2; Table S1) and catches (Section 3.5) could be sufficient to derive model parameters or as direct inputs into the models. However, updating the data on these aspects through the data collection efforts recommended above could improve the outputs of the models. The available data could be supplemented with data from nearby water bodies, especially Lake Victoria, which is a common practice in ecosystem modelling globally (Christensen et al., 2008). Lake Victoria is appropriate in this case because it is the most studied lake in the region and shares many fish species with lakes Edward and George.

AUTHOR CONTRIBUTIONS

Laban Musinguzi: Conceptualization; data curation; formal analysis; methodology; project administration; visualization; writing—original draft; writing—review and editing. **Nathan Vranken**: Data curation; writing—review and editing. **Vianny Natugonza**: Visualization; writing—review and editing. **William Okello**: Conceptualization; funding acquisition; project administration; supervision; writing—review and editing. **Maarten van Steenberge**: Conceptualization; funding acquisition; methodology; supervision; writing—review and editing. **Jos Snoeks**: Conceptualization; funding acquisition; methodology; project administration; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

No, I declare that the authors have no conflicts of interest.

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ETHICS STATEMENT

The research conducted in this work did not involve direct contact with animals which may require approval.

DATA AVAILABILITY STATEMENT

Data used in this article is provided in tables, Online Resource 2, and on figshare at https://doi.org/10.6084/m9.figshare.22013312.v3 and https://doi.org/10.6084/m9.figshare.24480898.v1.

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PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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