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Distribution patterns and diversity of riverine fishes of the Lake Victoria Basin, Kenya

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Abstract

The Lake Victoria Basin (LVB) is a global hotspot of aquatic biodiversity, but aquatic ecosystems are under threat from multiple stressors. Most studies on fish have focused on Lake Victoria, while patterns of fish diversity, distribution, and assemblage structure in influent rivers remain poorly understood. To assess threats and conservation status of riverine fishes, we used sampling surveys and searches of published and gray literature to compile data on diversity, distribution, and abundance. In total, 72 fish species were found to inhabit Kenyan rivers and associated wetlands and lakes (excluding Lake Victoria). Low-order streams (first to third order) in headwaters of rivers are species-poor and dominated by small-bodied cyprinids (*Enteromius* spp.) and clariids (*Clarias* spp.). A small number of fishes are endemic to rivers, and species turnover across river basins is low. Species dominance is high, with 10 species accounting for >90% of all individuals and weights. Two cyprinid species (*Labeobarbus altianalis* and *Labeo victorianus*) account for >65% of all individuals and weights (biomass) per unit effort. Most species occur in small numbers and low biomass is insufficient to sustain a commercial riverine fishery. A review of the literature continues to indicate a reduction in migratory runs of potamodromous fishes from Lake Victoria into influent rivers, although some species, such as *L. victorianus* and *L. altianalis*, also maintain stenotopic populations in rivers. Most of the exotic fishes introduced in Lake Victoria, such as *Oreochromis nilotics*, *Oreochromis*, *Coptodon zillii*, *Coptodon rendalli, and Gambusia affinis*, have invaded and established themselves in rivers, thereby posing a threat to riverine populations. Although this study focuses on Kenyan rivers, the distribution patterns of fishes reflect other rivers of the LVB and have broad implications on threats to riverine biodiversity in other regions undergoing development around the world.

KEYWORDS
biodiversity, fisheries, potamodromous, species richness, tropical rivers

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1 | INTRODUCTION

Biodiversity in freshwater ecosystems is under threat from human activities due to the combined effects of multiple stressors such as pollution and habitat degradation, flow regulation, introduction of nonnative species, and climate change (Knouft & Ficklin, 2017; Strayer & Dudgeon, 2010; Vörösmarty et al., 2010). At the same time, adequate data on freshwater biodiversity are generally unavailable, especially in tropical areas despite the high levels of species diversity and endemism (Balian, Segers, Martens, & Lévéque, 2007; Dudgeon et al., 2006). In rivers, overfishing and blockage of migratory routes through damming and excessive water abstractions have placed great stress on riverine populations globally (Dudgeon et al., 2006; Grill et al., 2019). The result has been a massive reshaping of communities, with higher rates of change occurring in the tropics (Araújo et al., 2013; Collen et al., 2014).

The Lake Victoria Basin (LVB) drains some of the most agriculturally productive and densely populated areas in East Africa. Studies in the LVB have linked deterioration in aquatic environmental conditions to human activities (Hecky, Mugidde, Ramlal, Talbot, & Kling, 2010; Verschuren et al., 2002). As a result of rapid human population growth, ecosystem alteration has been driven by land-use and land cover changes and increased agricultural production, which has been accompanied by heightened fertilizer use (Mati, Mutie, Gadain, Home, & Mtalo, 2008; Verschuren et al., 2002). The once expansive wetlands along the lake and river margins have been encroached upon, and vast areas have been drained or degraded (Masese, Raburu, & Kwena, 2012; Rongoei, Kipkemboi, Okeyo-Owuor, & Van Dam, 2013). Streams and rivers have undergone a considerable transformation with increases in concentrations of nutrients and suspended sediments (Masese & McClain, 2012). Changes in the natural flow regime of some rivers have also occurred due to land-use and land cover changes (Mango, Melesse, McClain, Gann, & Setegn, 2011). These developments contribute to a host of rapidly evolving multiple stressors that threaten the biodiversity and functioning of ecosystems in the LVB (Masese et al., 2018; Dutton, Subalusky, Hamilton, Rosi, & Post, 2018).

With the changing biophysical environment in the LVB, the degree to which biodiversity and ecosystem structure and function in streams and rivers have been affected is largely unknown but of concern. However, assessment of changes in fish community characteristics in the rivers has been inconsistent, while long-term studies have focused on Lake Victoria. Some earlier studies have shown that the biomass of most of the migratory fishes was declining, with a shift in communities toward the dominance of exotic and a few indigenous species (Manyala & Ochumba, 1990; Ochumba & Manyala, 1992; Ogutu-Ohwayo, 1990).

Long-term studies are needed to better understand the impacts of human activities on diversity, population characteristics, and conservation status of riverine fishes. In the LVB, long-term studies on distribution and population characteristics of riverine fish populations are lacking. Some of the earliest studies on riverine fishes were done in the lower reaches of major rivers (Nzoia and Kagera) and focused on large and economically important species such as *Labeo victorianus*, *Clarias gariepinus*, and *Labeobarbus altianalis* (e.g., Cadwalladr, 1965; Whitehead, 1959a, 1959b), and feeding and food composition (e.g., Balirwa, 1979; Corbet, 1961; Okedi, 1971; Welcomme, 1969). Studies on fish species distributions focused on individual rivers and did consider the entire river length from the upper to lower reaches (e.g., Balirwa & Bugenyi, 1980; Ochumba & Manyala, 1992). The only comprehensive studies on fish distribution in Kenyan rivers have only focused on three major rivers: Nzoia, Nyando, and Sondu-Miriu (Mugo & Tweddle, 1999; Raburu & Masese, 2012). In addition to their limited coverage, most of these studies are old and do not capture the potential effects of the changing environment on communities and ecosystem functioning as a result of increasing human development in the catchments (Achieng', Masese, & Kaunda-Arara, 2020). Nevertheless, threats associated with the life history of many fishes have been persistent. A report by the International Union of Conservation of Nature (IUCN) indicated that the LVB is likely to experience unprecedented loss of critical species due to various threats, including, but not limited to, pollution, climate change, invasive species, and mechanized farming (Darwall, Smith, Lowe, & Vié, 2005). This and other reports (Sayer, Máiz-Tomé, & Darwall, 2018) focused on fishes in Lake Victoria and lacked information on the diversity, distribution, and population characteristics of riverine fishes necessary in evaluating population trends and conservation status.

Studies are needed to evaluate the diversity, distribution, and population characteristics of riverine fishes to determine the full extent of human activities on aquatic biodiversity. These data are vital for effective management and conservation of species, biomonitoring of environmental change, and assessment of the status and viability of riverine fisheries as a resource for human populations and commercial fisheries. For the LVB, these data are also necessary to evaluate current riverine environments as refuges for remnants of fishes and populations that have declined or disappeared from catches in Lake Victoria. The objectives of this study are therefore to (1) determine the species diversity, composition, and endemism of riverine fishes in the LVB, Kenya; (2) determine spatial (between rivers) and longitudinal (along rivers) distributions of fishes in the rivers; (3) determine the yield (abundance and biomass [weights]) and fishery potential of fish species in riverine environments; and (4) assess the conservation status of the fishes according to the IUCN Red List to inform their conservation.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted on rivers draining into the Kenyan part of the LVB, which include the Sio, Nzoia, Yala, Nyando, Sondu-Miriu, Kuja-Migori, and Mara Rivers, and the streams that drain directly into the lake: Awach, Kibos, and Kisian (Figure 1). The annual rainfall displays a bimodal distribution, with two distinct rainy and dry seasons (both short and long), especially in the upper catchment (Kizza, Rodhe, Xu, Ntale, & Halldin, 2009). In the lower basin, the short rains

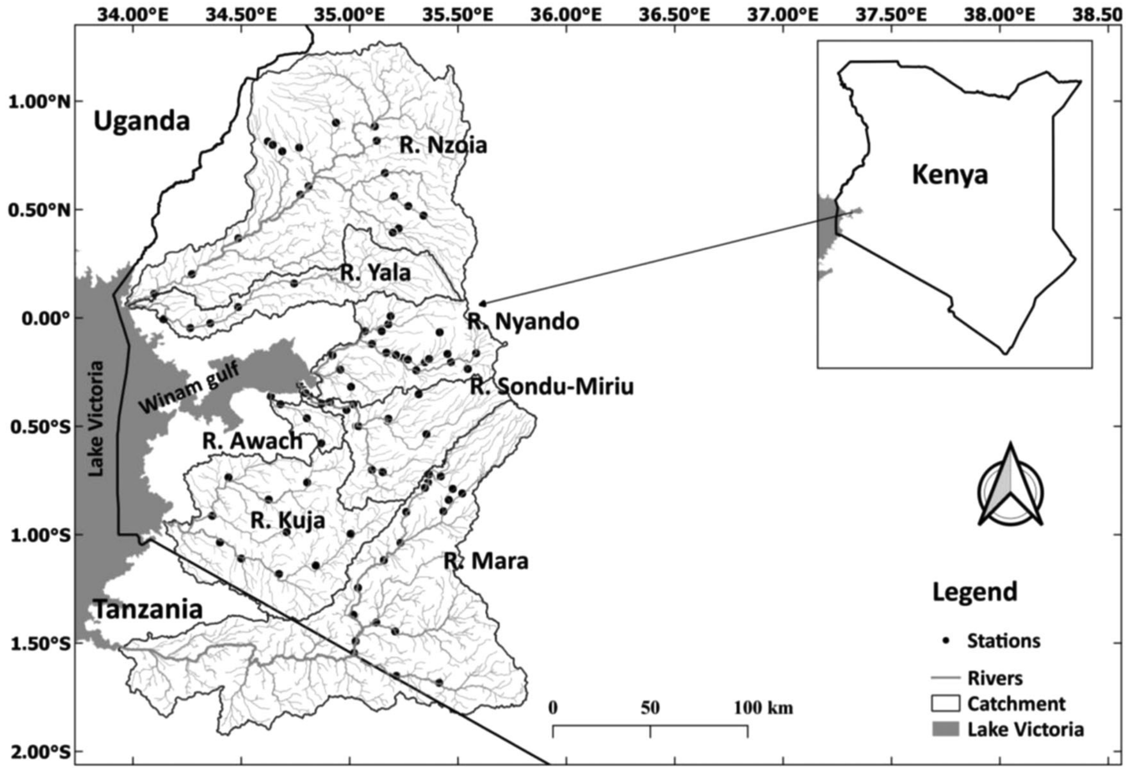

FIGURE 1 Map of the Kenyan part of the Lake Victoria Basin with an indication of sampling sites in the major rivers

are uneven and poorly distributed. Mean annual rainfall ranges from about 800 mm in the lowlands and southern lakeshore areas to a maximum of around 2200 mm in the highlands, with a catchment average of 1200 mm.

The Mau Forest Complex is the major source of rivers draining into the Kenyan part of the LVB. Most streams in the upper reaches of the catchment are small and rocky, with a moderate to high gradient. Some have natural habitat and good water quality, whereas others have suffered from a combination of the expansion of croplands, excessive livestock grazing and access, human settlement, and discharge of wastewater (Masese & McClain, 2012; Mati et al., 2008). In the middle and lower reaches, rivers are wider and deeper, with more fine sediment, although rocky sections and stable substrate still predominate in some areas. Most of the lowland streams and rivers are impacted by habitat degradation and water pollution, urban influences, and discharges from agroprocessing industries (Ojwang, Kaufman, Soule, & Asila, 2007; Scheren, Zanting, & Lemmens, 2000). Most of the floodplain and river mouth wetlands, which are important breeding grounds for migratory fish and can be important habitat for endemic species, have either been converted to other uses (e.g., farming and grazing, forest plantations) or degraded (Rongoei et al., 2013).

2.2 | Fish sampling and other data sources

The study uses fish data collected over the past 20 years in different rivers in the LVB, Kenya. Fish sampling was done using a generator-powered electrofisher (Smith-Root Type VI-A) during both baseflow (January to March) and high-flow (May to July) periods. For standardization, a 100-m long river reach was sampled, starting from the downstream end, and the time taken was noted. The effort was made to sample all habitats available relative to their prevalence. Captured fish were kept in buckets filled with river water until they were identified, counted, and weighed (g). A subsample of each species was preserved in 75% ethanol for confirmation of species identifications in the laboratory, and the remaining fish were returned to the point of capture.

Specimen identifications were done at species level using several taxonomic guides (Eccles, 1992; Greenwood, 1962; Skelton, 1993; Whitehead, 1960) except for haplochromine cichlids and small-bodied cyprinids whose taxonomy is unclear. Names used are as given in Eschmeyer, Fricke, and van der Laan (2016), and Fishbase (Froese & Pauly, 2018). Noting that the generic taxonomy of certain African cyprinids long known as *Barbus* is currently in flux, we instead use the genus *Enteromius* for the small diploid smiliogastrin cyprinids formerly of the genus *Barbus*, and for the large hexaploid species, we use *Labeobarbus* (Skelton, 2016; Van Ginneken, Decru, Verheyen, & Snoeks, 2017).

Data from a variety of other fish sampling techniques were also used to supplement the occurrence and distribution of fishes. Sampling methods included kick nets, fishing nets, and angling, depending on the river characteristics of the study areas. In addition to the fish sampling surveys, quantitative (abundance, weight, and catch per unit effort) and qualitative (occurrence and distribution) data were sourced from gray literature (research and consultancy reports, theses), unpublished raw data sets, and publications on riverine fishes of the LVB, Kenya.

2.3 | Data analysis

Species occurrence (presence–absence) and distribution data were summarized for each river using the number of species (*S*), the total number of individuals, biomass, and relative abundance of each species. Several catchment-scale diversity indices were calculated for each river basin by summing species-specific abundances across sites. Shannon's diversity index (H') was derived as a measure of diversity (Magurran, 2004), and an associated $H'/H'_{\max}$ index (Pielou, 1975) was used as a measure of evenness. The reciprocal form of the Simpson index (1/*D*s) (Simpson, 1949) was used as a measure of species richness. We used Hill's number (i.e., gamma diversity; Hill, 1973) and Fisher's alpha (Fisher, Corbet, & Williams, 1943) as extra measures of fish diversity. Hill's number was calculated as the ratio between H' and 1/*D*s.

Longitudinal patterns in species distribution were generated according to river order (Strahler, 1957). Sites were categorized into low-order headwater streams (first to third order), mid-order streams in the middle reaches (fourth to sixth order), and large river sites (seventh order and above), including river mouth wetlands and floodplains. A fourth category included low-order streams that drain directly into Lake Victoria. To determine preferences in longitudinal (upper, middle, and lower reaches of rivers) distribution of species along the rivers, and to identify species responsible for differences in fish communities along rivers, similarity percentage (SIMPER) analysis was used. SIMPER is a strictly pairwise analysis between two-factor levels or categories using a Bray–Curtis dissimilarity matrix (Clarke & Warwick, 2001), and in this case, comparisons were made between upper and middle reaches, upper and lower reaches, and middle and lower reaches.

Abundance and biomass data were used to estimate the relative importance of different species to fish communities in the rivers and the potential of the riverine fishery. Catch composition in numbers and weight (kg), as well as the frequency of occurrence (FRQ; i.e., whether the species was present or not irrespective of abundance), were estimated using the Pasgear II version 2.10 software (Kolding & Skålevik, 2011). Each value was also given in percentage of the total (note that the percentage frequency of occurrence [%FRQ] does not add to 100 as the total is the total number of settings). As a measure of relative abundance or commonness of each species (*i*) in the catch composition, an index of relative importance (%IRI), was used (Kolding, 1989):

$$\%\mathrm{IRI} = \frac{(\%W_i + \%N_i) - \%F_i}{\sum_{j-1}^{s}(\%W_j + \%N_j) - \%F_j} - 100,$$

where $\%W_i$ and $\%N_i$ are the percentage of weight and number of each species of the total catch, respectively; $\%F_i$ is percentage frequency of occurrence of each species in the total number of settings, and *S* is the total number of species.

3 | RESULTS

3.1 | Species diversity, composition, and endemism

While conducting this study, we identified numerous published synonyms and misidentifications of species (Table S1). Examples of misidentifications of fishes that do not occur in the LVB include *Bagrus bajad*, *Alcolapia grahami*, and *Labeobarbus oxyrhynchus*. We found a total of 72 fish species in Kenyan rivers of the LVB, belonging to 17 families and 37 genera (Table S2). Despite the high number of exotic fishes that have been introduced into Kenya, nine occur in the LVB rivers (*Oreochromis niloticus*, *Oreochromis leucostictus*, *Coptodon zillii*, *Coptodon rendalli*, *Gambusia affinis*, *Micropterus salmoides*, *Lates niloticus*, *Salmo trutta*, *and Oncorhynchus mykiss). O. niloticus and O. leucostictus were widespread in the lower and middle reaches of many rivers, while L. niloticus occur in the lower reaches of some rivers, including Mara, Sondu-Miriu, and Nzoia.*

The species richness of cichlids was low (nine indigenous and four introduced). Instead, non-cichlids dominated with 59 species, of which 29 are endemic, and 1 endemic genus (Table S1). Abundance was also dominated by non-cichlids (96% of all individuals caught), with indigenous cichlids accounting for 2.4% and exotics 1.6%. Cyprinidae dominated families in both the number of species (15) and relative abundance (86.5%). They were followed by Cichlidae (9 species; 1.5%) and Clariidae (6 species; 6.8%). Mormyridae was represented by five species, but these were less abundant (0.24%) than Mochokidae, which had four species but with higher relative abundance (1.6%). There were five single species families (Bagridae, Centrarchidae, Centropomidae, Mastacembelidae, and Protopteridae) and five families with two species (Alestidae, Anabantidae, Poeciliidae, Salmonidae, and Schilbeidae). The genera *Zaireichthys* (Amphilidae), *Chiloglanis* (Mochokidae), and *Aplocheilichthys* (Poeciliidae) are endemic to rivers, and no previous records exist of their occurrence in Lake Victoria.

Except for dominance, all diversity indices considered were positively correlated with species richness and were higher in major rivers, such as Mara, Nzoia, Sondu-Miriu, and Yala, as compared with the small streams (Awach, Kibos, and Kisian) draining directly into Lake Victoria (Table 1). The Shannon diversity index was higher (>1.9) in major rivers than in the small streams (<1.3). Similar trends were obtained using the Simpson index (1/*Ds*), with higher values in major rivers (>4.0) compared with the small streams (≤2.5). There were limited responses in Hill's number and Pielo's evenness across river basins, with a range from 2.0 to 2.9 and 0.5 to 0.7, respectively. In contrast, Fisher's alpha diversity index showed a wider range (0.8–5.6) and clear differences between the major rivers (>3) and the small streams (<1.3), capturing the low number of fishes (range, 4–7) in these streams, but with high numerical dominance by one or two

TABLE 1 The diversity indices of fish communities in rivers of the Lake Victoria Basin, Kenya

	Streams and rivers							
Diversity indices	**Awach**	**Kibos**	**Kisian**	**Mara**	**Nyando**	**Nzoia**	**Sondu-Miriu**	**Yala**
Number of species	6	7	4	41	37	48	49	36
Dominance	0.41	0.49	0.61	0.22	0.17	0.14	0.17	0.24
Simpson index (1/*D*)	2.45	2.05	1.64	4.54	5.81	6.91	5.80	4.13
Shannon index (*H'*)	1.22	0.98	0.75	1.94	2.20	2.41	2.21	1.95
Pielou's Evenness (*J'*)	0.68	0.50	0.54	0.64	0.66	0.71	0.67	0.60
Hill's number (gamma diversity)	2.02	2.08	2.18	2.34	2.64	2.87	2.63	2.11
Fisher-alpha diversity	0.97	1.23	0.77	3.12	3.67	5.55	4.39	4.65

Note: Catchment-scale indices were calculated by summing species-specific abundances for each species per river. Hill's number was calculated as the ratio between *H'* and 1/*D*.

species; *L. altinalis* formed >60% of all individuals caught in these streams. Indeed, dominance in the small streams was more than twice (>0.4) the level in most of the major rivers (≤0.25).

The Sondu-Miriu had the highest number of fishes (49), closely followed by Nzoia (48), then Mara (41), Nyando (37), Yala (36), Kuja-Migori (34), and Sio (28) (Table S2). Species richness was low among streams draining directly into the lake and ranged between four (Kisian) and seven (Kibos), but abundance was high for species such as *L. victorianus* and *L. altianalis*, which have disappeared from the lake. There was low species turnover or endemism among rivers and the numerically dominant species had cosmopolitan basin-wide distribution. Patterns of endemism in rivers differed considerably from those of species richness, with 1–4 endemic species occurring in the headwaters of the major rivers. However, recent surveys have

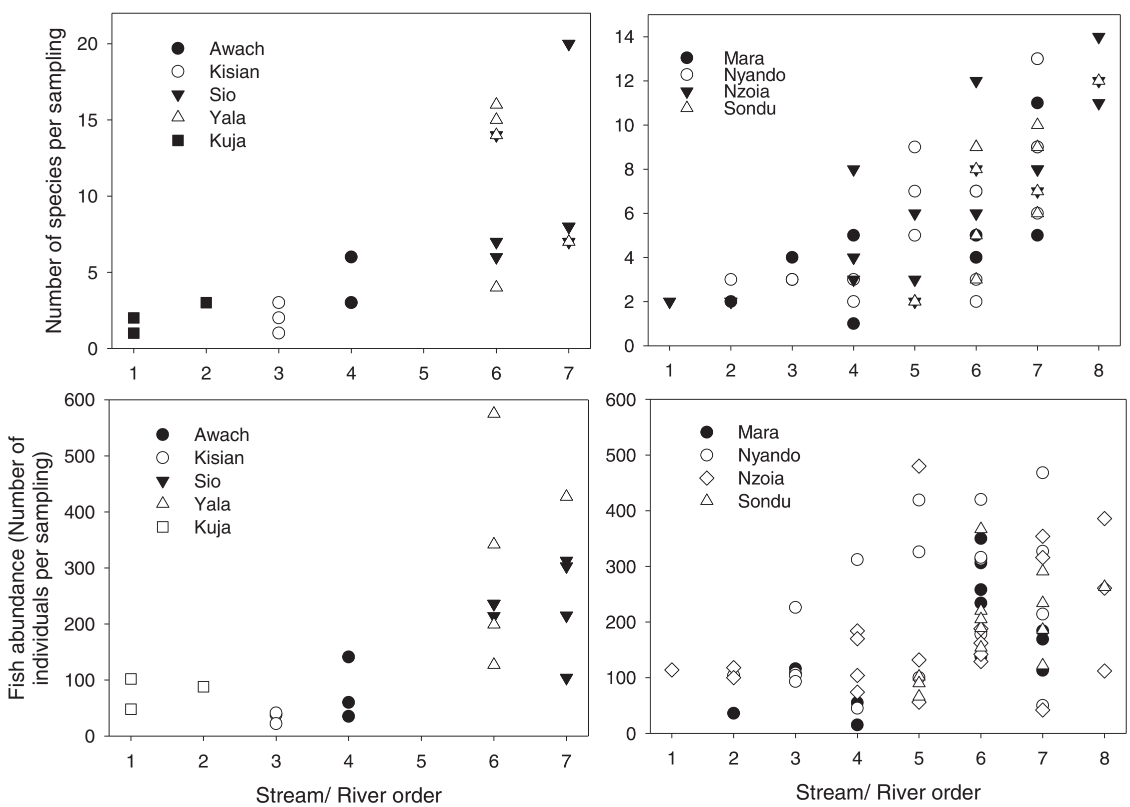

FIGURE 2 Occurrence and longitudinal trends in the number of fishes (upper panels) and total abundance (lower panels) per sampling in rivers of the Lake Victoria Basin, Kenya. To avoid overlap in distributions, rivers have been separated into medium-sized (left panels) and large (right panels) rivers. Note the difference in *y*-axis scale for the number of species (upper panels)

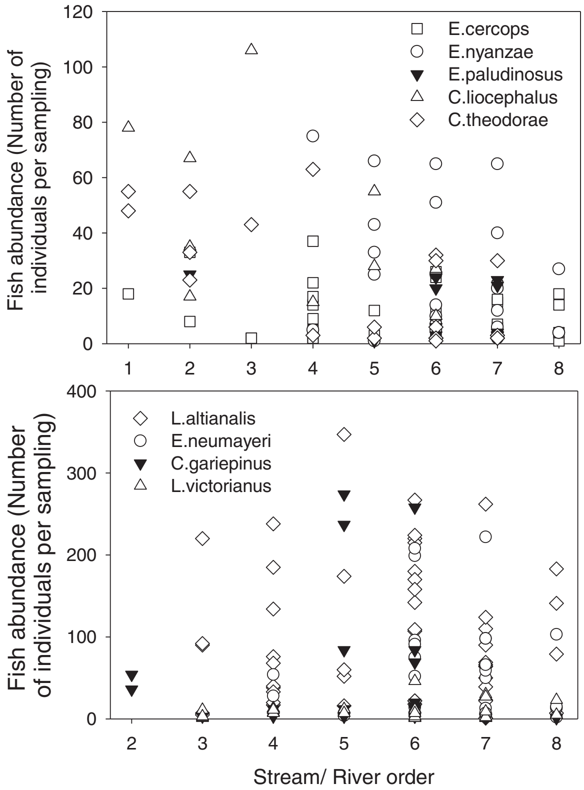

FIGURE 3 Distribution of most abundant and cosmopolitan fishes in riverine ecosystems of the Lake Victoria Basin, Kenya. To avoid overlap in distributions, fishes have been separated into moderately abundant (top panel) and most abundant (lower panel) fishes. Note the difference in *y* axis scale between the upper and lower panels

recorded undescribed species among the small-bodied cyprinids (genus *Enteromius*), many of which may be endemic to certain rivers.

3.2 | Longitudinal patterns of fish distribution and potamodromy

There was an increase in the number of species and abundance with river order (longitudinal gradient) for all river systems in the LVB (Figures 2 and 3). First-order streams in the forested upper reaches hardly recorded any fishes, but those in the lowlands draining into large rivers or the lake (lakeshore streams) recorded at least four species of fish. Generally, low-order (first to third order) specialists in the headwaters of major rivers were small-sized cyprinids and clariids such as *Enteromius neumayeri*, *Enteromius paludinosus*, *Clarias theodorae*, and *Clarias liocephalus* (Figure 3). Cyprinidae also dominated mid-order (fourth to sixth order) streams in terms of species richness and abundance. Other diverse and abundant families included Mochokidae and Mormyridae. In the lower reaches (>6th order), no family was particularly dominant, but families Cichlidae, Mochokidae, and Mormyridae gained prominence and were caught more often.

SIMPER analysis identified fish species that distinguished the three river reaches (upper, middle, and lower; Table 2). Currently, 12 fishes are restricted to the upper and middle reaches of the major rivers, while approximately 30–40 species occur in the lower reaches, including river mouths and floodplain wetlands (Table S2). We grouped fishes into four groups according to their longitudinal distribution: (1) rheophilic small-bodied *Enteromius and Clarias* species that were restricted to the upper reaches (Table 2); (2) species that showed wide biotope preferences in the middle reaches, including *Labeobarbus* sp. and *Labeo* sp., Amphilidae spp., and many *Enteromius* spp.; (3) migratory species with a wide preference of biotopes and tolerance to changes in water quality in the middle and lower reaches. This was the most diverse and abundant group and included most of the catfishes such as *C. gariepinus*, *Schilbe* spp., and amphiliids, and some of the introduced cichlids, such as *O. niloticus* and *Coptodon* spp.; (4) the fourth group of fishes was confined to the lower reaches, floodplains and river mouth wetlands, satellite lakes, and some occurred in seasonal depressions and ponds. Species here included most of the cichlids (e.g., *Oreochromis esculentus*, *Oreochromis variabilis; Haplochromis spp.), anabantids, most of the mormyrids, and all killifishes (Nothobranchiidae).*

We recorded at least 13 potamodromous fishes in the LVB, especially cyprinids, characoids, and siluroids. The major migratory species include *L. victorianus* and *L. altianalis* (Cyprinidae), *Schilbe intermedius* (Schilbeidae), *Synodontis victoriae*, and *Synodontis afrofischeri* (Mochokidae), *Bagrus docmak* (Bagridae), *C. gariepinus* (Clariidae), and several *Enteromius* spp.

3.3 | Fish abundance, biomass, and the riverine fishery

A total of 9210 individuals were collated from different sources to determine the relative abundance and biomass of fishes (Table 3). A total of 43 fishes had available abundance data (number of individuals), but the remaining species (29) were recorded from reports and publications lacking such data. Species dominance was remarkably high, with two species forming >65% of all individuals: *L. altianalis* (50.4%) and *L. victorianus* (17.1%; Table 3). Only 10 species formed >90% of all individuals in the rivers: *E. neumayeri* (6.2%), *Enteromius nyanzae* (5.6%), *C. liocephalus* (3.0%), *Enteromius cercops* (2.9%), *C. gariepinus* (2.7%), *C. theodorae* (1.4%), *E. paludinosus* (1.2%), O. *niloticus* (1.2%), and *Enteromius kerstenii* (1.2). Most species occurred in small numbers, with 19 species forming a combined <1% of all individuals.

4 | DISCUSSION

4.1 | Patterns of fish diversity and endemism

A total of 72 fishes, including nine cichlid species, were recorded for the major rivers of the LVB, Kenya. This diversity is quite low compared with Lake Victoria, which has over 500 recorded cichlid species (Lowe-McConnell, 1987; Witte et al., 1992). Despite the high

TABLE 2 SIMPER contributions to percentage dissimilarity in fish species distributions between the upper reaches and middle reaches, upper reaches and lower reaches, and upper reaches and lower reaches of tributaries of the Lake Victoria Basin, Kenya, based on presence–absence data

	SIMPER % contribution			Mean abundance		
Fish species	Upper vs. middle reaches	Upper vs. lower reaches	Middle vs. lower reaches	Upper reaches	Middle reaches	Lower reaches
Enteromius neumayeri	6.8	5.2	2.0	0.50	0.16	–
Clarias gariepinus	5.4	5.4	3.5	0.10	0.44	0.57
Labeobarbus altianalis	5.4	3.8	2.4	0.43	0.62	0.50
Labeo victorianus	4.2	6.3	3.7	0.13	0.35	0.63
Enteromius cercops	4.8	4.7	3.2	0.07	0.37	0.50
Clarias liocephalus	4.4	3.0	0.4	0.26	0.02	–
Clarias theodorae	3.9	1.6	1.9	0.13	0.19	–
Enteromius paludinosus	3.3	2.2	1.7	0.20	0.16	0.13
Enteromius kerstenii	3.3	3.1	2.5	0.20	0.19	0.32
Enteromius jacksonii	3.2	1.4	1.6	0.10	0.14	–
Enteromius nyanzae	2.9	3.6	3.0	0.07	0.23	0.44
Mastacembelus frenatus	2.6	3.2	2.9	–	0.23	0.38
Oreochromis variabilis	2.2	2.4	2.5	–	0.19	0.32
Oreochromis niloticus	1.7	2.2	2.3	–	0.16	0.25
Enteromius apleurogramma	1.7	2.0	1.7	0.07	0.07	0.19
Labeo cylindricus	1.6	0.6	0.7	0.07	0.09	–
Babrus docmak	1.5	2.3	2.2	–	0.14	0.25
Oreochromis leucostictus	1.5	1.4	1.8	–	0.14	0.19
Zaireichthys sp.	1.5	0.6	0.5	0.07	0.07	–
Coptodon zillii	1.4	0.7	1.0	–	0.09	0.06
Schilbe intermedius	1.4	0.6	1.1	–	0.12	0.06
Chiloglanis somerini	1.3	0.5	0.5	–	0.07	–
Mormyrus kanumme	1.1	2.4	2.1	–	0.07	0.25
Barbus spp.	1.1	0.3	0.5	0.03	0.07	–
Lates niloticus	1.1	3.8	3.1	–	0.09	0.32
Pseudocrenilabrus multicolor	1.0	1.1	0.8	0.06	0.05	–
Synodontis victoriae	1.0	1.7	1.8	–	0.09	0.19
Enteromius jacksonii	0.9	1.9	1.9	–	0.09	0.25
Labeobarbus oxyrhynchus	0.8	0.3	0.3	0.03	0.05	–
Synodontis afrofischeri	0.7	1.4	1.5	–	0.07	0.19
Zaireichthys rotundiceps	0.7	0.4	0.1	0.03	0.02	–
Haplochromis spp.	0.6	2.1	2.0	–	0.07	0.25
Coptodon rendalli	0.5	1.4	1.4	–	0.05	0.13
Clarias alluaudi	0.4	1.5	1.1	–	0.03	0.13
Astatoreochromis alluaudi	0.4	0.0	0.3	–	0.05	–
Schilbe mystus	0.4	0.3	0.6	–	0.05	0.06

(Continues)

TABLE 2 (Continued)

Fish species	SIMPER % contribution			Mean abundance		
	Upper vs. middle reaches	Upper vs. lower reaches	Middle vs. lower reaches	Upper reaches	Middle reaches	Lower reaches
Gnathonemus longibarbis	0.4	0.6	0.6	–	0.02	0.00
Lacustricola bukobanus	0.2	0.6	0.4	–	–	0.06
Astatotilapia sp.	0.2	1.1	0.9	–	–	0.13
Marcusenius victoriae	0.2	0.5	0.3	–	–	0.06
Rastrineobola argentea	0.2	4.2	3.3	–	0.02	0.32
Hippopotamyrus grahami	0.0	0.9	0.7	–	–	0.13
Enteromius yongei	0.0	0.5	0.4	–	–	0.06
Garra dembeensis	0.0	0.3	0.3	–	–	0.06
Clarias werneri	0.2	0.0	0.0	0.03	–	
Propterus aethiopicus	0.0	1.2	1.0	–	–	0.13

Note: Mean abundances of fishes are presented for each river reach; upper, middle, and lower. (–) represents the absence of a species in the reach. Abbreviation: SIMPER, similarity percentage.

number of exotic fishes that have been introduced into Kenya (Seegers, De Vos, & Okeyo, 2003), this study recorded only nine exotic species in the LVB rivers. Most exotic species (except *L. niloticus*, *M. salmoides*, *S. trutta*, and *O. mykiss*) were caught in large numbers and in various size classes, indicating established populations. While *L. niloticus* is fairly common in rivermouths of many large rivers, *M. salmoides* was only reported in the Sondu-Miriu River nearly three decades ago (Ochumba & Manyala, 1992), and no recent records exist for *S. trutta* and *O. mykiss* in the streams of Cherangani Hills and Mt. Elgon where they were introduced.

A decline in occurrence and distribution of *L. altianalis*, *L. victorianus*, *O. variabilis*, *Mormyrus kannume*, and *B. docmak*, which were once economically important for the fisheries of lower reaches of many rivers, has occurred (Balirwa & Bugenyi, 1980; Cadwalladr, 1965; Ochumba & Manyala, 1992). Most of these species have also disappeared from the lake (Nyamweya et al., 2016; Ogutu-Ohwayo, 1990; Outa, Yongo, Keyombe, Ogello, & Namwaya, 2020). Even in rivers, *M. kannume* and *B. docmak* occur in very low numbers (Masese, own data; O'Brien, 2016), which can be attributed to their high sensitivity to water pollution and habitat degradation (Raburu & Masese, 2012; Toham & Teugels, 1998).

Species richness differed among major rivers, ranging from 28 species in Sio River to 48 and 49 species for the Nzoia and Sondu-Miriu Rivers, respectively. The small streams draining directly into the lake had low species richness (4–7 species), but very high numerical dominance of one or two species. The diversity indices used were largely in agreement regarding differences in fish diversity and richness among rivers and between the major rivers and small streams (Table 1). The low values of the Shannon diversity index (<2.5) indicate widespread degradation affecting fish communities in all rivers. Small streams seemed to be more affected by having depauperate communities with high dominance of a few species (mainly *L. altianalis*). *L. altianalis* was one of the species showing increased abundance and distribution in the rivers, an indication that it is not highly affected by ongoing human-mediated environmental and ecological changes (Masese & McClain, 2012; Raburu & Masese, 2012). Hill's number (gamma diversity) was not able to capture variability in species diversity among rivers. Lack of variability in Hill's number across the LVB rivers indicates the similarity of fish communities (Jost, 2007), especially in terms of abundance of common species. On the contrary, Fisher's alpha diversity showed clear differences among rivers, suggesting that it is less sensitive to the numerical dominance of fish communities by a few common species, hence, better suited at assessing anthropogenic influences on the diversity of fishes in the LVB rivers.

While the Kenyan rivers are not as speciose as Rwandan or Burundian rivers (Banyankimbona, Vreven, Ntakimazi, & Snoeks, 2012; De Vos, Snoeks, & van den Audenaerde, 2001; Kishe-Machumu et al., 2018), there are potentially many undescribed endemic species, particularly in the headwaters. The Nzoia River has two undescribed *Enteromius* spp. (Mugo & Tweddle, 1999), and a recent survey in the Mara River collected potentially undescribed *Enteromius* spp. (O'Brien, 2016). Other studies in the LVB have also identified cases of river-specific endemism (Achieng' et al., 2020), highlighting the potential for local extinctions in the face of widespread environmental changes in the catchments of most rivers.

4.2 | Longitudinal patterns in fish distribution and potamodromy

There was a general increase in species and abundance of fishes with stream order. While several species had a cosmopolitan longitudinal distribution, some fishes limited their occurrence to either the upper

TABLE 3 Catch composition and IRI among common riverine fishes of the Lake Victoria Basin, Kenya

Species	No.	% No.	Weight (kg)	% Weight	FRQ	% FRQ	IRI	% IRI
Labeobarbus altianalis	4645	50.43	217.6	47.5	13	6.2	603	56.0
Labeo victorianus	1577	17.12	91.5	20.0	11	5.2	193	17.9
Enteromius neumayeri	573	6.22	4.5	1.0	10	4.7	34	3.2
Enteromius nyanzae	514	5.58	1.8	0.4	11	5.2	31	2.9
Enteromius cercops	265	2.88	0.8	0.2	12	5.7	17	1.6
Clarias liocephalus	262	2.84	5.9	1.3	3	1.4	6	0.5
Clarias gariepinus	243	2.64	91.7	20.0	12	5.7	129	11.9
Clarias theodorae	130	1.41	2.9	0.6	7	3.3	7	0.6
Enteromius paludinosus	110	1.19	0.4	0.1	10	4.7	6	0.6
Oreochromis variabilis	109	1.18	7.8	1.7	8	3.8	11	1.0
Enteromius kerstenii	107	1.16	0.3	0.1	9	4.3	5	0.5
Synodontis victoriae	87	0.94	1.9	0.4	6	2.8	4	0.4
Enteromius apleurogramma	68	0.74	0.1	0	9	4.3	3	0.3
Schilbe intermedius	62	0.67	1.4	0.3	6	2.8	3	0.3
Bagrus docmak	47	0.51	8.8	1.9	8	3.8	9	0.9
Oreochromis niloticus	45	0.49	2.8	0.6	5	2.4	3	0.2
Afromastacembelus frenatus	43	0.47	1.2	0.3	6	2.8	2	0.2
Enteromius jacksonii	42	0.46	0.3	0.1	5	2.4	1	0.1
Labeo cylindricus	32	0.35	5.5	1.2	1	0.5	1	0.1
Lates niloticus	31	0.34	2.8	0.6	5	2.4	2	0.2
Synodontis afrofischeri	30	0.33	0.5	0.1	5	2.4	1	0.1
Pseudocrenilabrus multicolor	22	0.24	0.1	0	5	2.4	1	0.1
Coptodon rendalli	20	0.22	2.9	0.6	6	2.8	2	0.2
Rastrineobola argentea	19	0.21	0.11	0	2	0.9	0	0
Labeobarbus oxyrhynchus	17	0.18	0.73	0.2	1	0.5	0	0
Gambusia	17	0.18	0.02	0	1	0.5	0	0
Schilbe mystus	15	0.16	0.33	0.1	1	0.5	0	0
Mormyrus kannume	10	0.11	1.9	0.4	3	1.4	1	0.1
Astatotilapia sp.	10	0.11	0.07	0	4	1.9	0	0
Oreochromis leucostictus	9	0.10	0.9	0.2	3	1.4	0	0
Astatoreochromis alluaudi	7	0.08	0.1	0	5	2.4	0	0
Coptodon zillii	7	0.08	0.13	0	3	1.4	0	0
Gnathonemus longibarbis	6	0.07	0.32	0.1	2	0.9	0	0
Haplochromis sp.	4	0.04	0.01	0	2	0.9	0	0
Chiloglanis sp.	4	0.04	0.01	0	2	0.9	0	0
Hippopotomyrus graham	4	0.04	0.06	0	1	0.5	0	0
Chiloglanis somerini	4	0.04	0.01	0	1	0.5	0	0
Amphilius jacksonii	3	0.03	0.04	0	3	1.4	0	0
Zaireichthys rotundiceps	3	0.03	0.01	0	2	0.9	0	0

(Continues)

TABLE 3 (Continued)

Species	No.	% No.	Weight (kg)	% Weight	FRQ	% FRQ	IRI	% IRI
Enteromius yongei	3	0.03	0.003	0	1	0.5	0	0
Clarias werneri	2	0.02	0.04	0	1	0.5	0	0
Marcusenius victoriae	1	0.01	0.005	0	1	0.5	0	0
Lacustricola bukobanus	1	0.01	0.001	0	1	0.5	0	0
Total	9210	100	458.3	100	–	–	1078	100

Note: FRQ is the frequency of occurrence or the number of occasions where the fish was present in the survey; % FRQ is the percentage of total occasions when the species is present.

Abbreviations: FRQ, frequency of occurrence; IRI, index of relative importance.

reaches or lower reaches. Rheophilic species, mainly small-bodied species among genus *Enteromius* and *Clarias*, occurred in the upper reaches, while those in the middle and lower reaches comprised of species with broad biotope preferences, including large-bodied cyprinids, catfishes of family Aphilidae, and a large number of small-sized *Enteromius* spp. In the lower reaches, fishes occurred in a broad diversity of habitats, including floodplains and river mouth wetlands, satellite lakes, and depressions that fill with water during the rainy season. Species in this group included most of the cichlids, anabantids, mormyrids, and all the killifishes (Nothobranchiidae), which prefer deeper habitats with low oxygen levels and slow-moving water (Raburu & Masese, 2012; Sayer et al., 2018).

Fish migrations between Lake Victoria and influent rivers (potamodromy) is a salient feature of fish communities in the LVB (Lowe-McConnell, 1987; Manyala, Bolo, Onyang'o, & Rambiri, 2005). While not as renowned as their marine counterparts, which migrate thousands of kilometers from oceans into influent rivers to spawn (Naiman, Bilby, Schindler, & Helfield, 2002), there are at least 13 potamodromous fishes among cyprinids, characoids, and siluroids known to migrate between Lake Victoria and its influent rivers and floodplains for spawning. The major migratory species include *L. victorianus*, *L. altianalis*, several *Enteromius* spp., *S. intermedius*, *S. victoriae*, *S. afrofischeri*, *B. docmak*, and *C. gariepinus* (Cadwalladr, 1965; Manyala et al., 2005; Whitehead, 1959a). Some species have been recorded to move 80 km or more up the Nzoia River from Lake Victoria (Whitehead, 1959a, 1959b). However, the numbers of migrating fishes have notably reduced (Cadwalladr, 1965; Whitehead, 1959a), and some species, such as *L. victorianus* and *L. altianalis*, have resident stenotopic populations in rivers (Chemoiwa et al., 2013; Ojwang et al., 2007).

4.3 | Fish abundance, biomass, and the riverine fishery

Although all fishes in the LVB rivers are edible, only a small number of species, such as *L. altianalis*, *L. victorianus*, *C. gariepinus*, mormyrids, and squeaker catfishes can sustain a commercial fishery (Table 3 and Figure 4). However, reduced yields in the riverine fisheries have been noted for over 70 years (Cadwalladr, 1965; Ochumba & Manyala, 1992; Owiti, Kapiyo, & Bosire, 2013; Waswala-Olewe, Okuku, & Abila, 2014; Whitehead, 1959a). The once-lucrative riverine commercial fishery in the lower reaches of major rivers has essentially collapsed and has been replaced with a subsistence fishery employing traditional gear, hook, and line, and occasionally seining using makeshift nets, such as mosquito nets (Figure S1).

The collapse of the commercial riverine fishery has been attributed to overfishing, water pollution, habitat degradation, use of poor fishing methods that target gravid females in river mouths of major rivers during spawning runs, and the introduction of exotic species in Lake Victoria. Declining stocks due to overfishing were first reported by Graham (1929), and by the mid-20th century, rivers had already started experiencing drastic declines in all fishes (Cadwalladr, 1965). From Lake Victoria, *L. altianalis*, along with *L. victorianus* and other big catfishes, constituted a substantial part of the catch in a fishery that was dominated by *Tilapia esculentus* before the 1950s (Balirwa et al., 2003; Cadwalladr, 1965). The introduction of the carnivorous *L. niloticus* in the late 1950s not only led to a reduction of haplochromine stocks but also the other large fishes, including *L. victorianus* and *L. altianalis*.

4.4 | Conservation status of fish species

The LVB, as a center of biodiversity, has been recognized in previous surveys and reports (Darwall et al., 2005; Sayer et al., 2018). While most of the fishes in this study (44 of 67 species, or 65.7%) are listed as "least concern," the IUCN Red List (IUCN, 2018) shows that the Kenyan rivers of the LVB host several fishes of great conservation concern (Table S2). These include the critically endangered *L. victorianus* and non-haplochromine cichlids (*O. esculentus* and *O. variabilis*), the near-threatened *Nothobranchius serengetiensis*, and the critically endangered *Xenoclarias eupogon*. Some of Lake Victoria's threatened *Haplochromis* spp. also occur in some rivers, although they are classified as not assessed due to lack of data.

Despite low endemism in the LVB rivers reported in this study, there is no substitutability among river systems as no one river system supports all the LVB fish diversity in healthy and sustainable

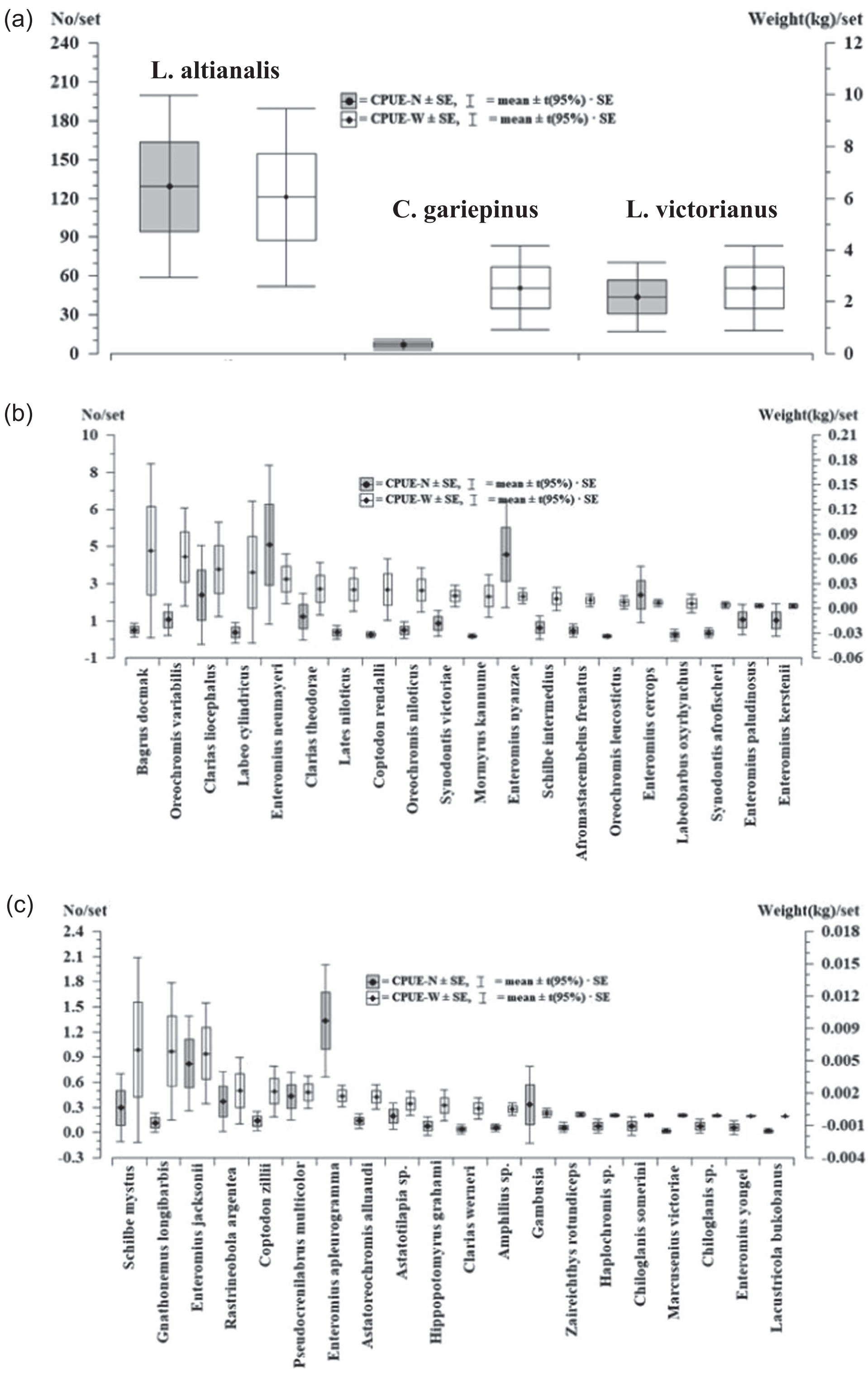

FIGURE 4 Catch per unit effort (CPUE) in terms of numbers or abundance (CPUE-N ± *SE*) and weight or biomass (CPUE-W ± *SE*) for riverine fishes of the Lake Victoria Basin, Kenya. Most fishes have extremely low numbers and weights, and have been separated into (a) most abundant, (b) moderately abundant, and (c) least abundant species. No, number per sampling effort (set)

populations. Moreover, there is increasing evidence of potentially new species in most river systems (Mugo & Tweddle, 1999; O'Brien, 2016), including a confirmed case of *Labeobarbus bynni* in River Awach in the Kano Plains (S. W. Agembe, personal communication, February 18, 2020). Thus, the protection of one river system cannot preserve all fishes, especially as most river systems suffer from different types and levels of human disturbances (Ojwang et al., 2007; Sayer et al., 2018). Many fragile aquatic habitats have been degraded or lost, such as temporary wetlands and small streams that drain directly into the lake, some of which harbor threatened and endemic species (Wildekamp, Watters, & Shidlovskiy, 2014). Inshore waters of Lake Victoria, river mouth wetlands, and lowland sections of major rivers are important refugia for numerous native fishes that have disappeared from the lake (Balirwa et al., 2003; Chapman, Chapman, Nordlie, & Rosenberger, 2002). Similarly, the satellite lakes such as Lake Kanyaboli, Sare, and Namboyo have been identified as important habitat, harboring endangered species, especially the haplochromine cichlids (Aloo, 2003). Thus, fragile aquatic ecosystems in the lower reaches of the rivers and around the lake must be protected to sustain fishes and other aquatic biodiversity.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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