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Fish populations and biomass in headwater streams of the Lake Tumba Landscape, DR Congo, 2007–2011

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Abstract

The fish biodiversity in the Congo River and its tributaries is extremely rich but the information on fish communities in the headwaters in terms of catch and biomass estimates is rare. Fishes in the running and stagnant waters in this region are of vital importance as a food resource for local residents. This study aimed to describe the fish community, catch, and biomass in the three headwater streams Bambou, Lebomo, and Bongo in the Lake Tumba Landscape (LTL) of the Democratic Republic of the Congo. Such information is of vital importance as a benchmark to understand the sustainability of the fish population for future generations of residents of the LTL. The field data were collected from 2007 through 2011, including dry and wet seasons. Here we present the results of this systematic, multi-annual study which was the first for fishes in streams of this region. In total, 50 species of 15 families were found in the nutrient-poor brown waters of these streams where high concentrations of humic acids cause a low pH. Among abundant species occurring in all three streams were the cyprinid *Enteromius holotaenia* (Boulenger, 1904), the mormyrid *Marcusenius moorii* (Günther, 1867), the alestids *Clupeocharax schoutedeni* Pellegrin, 1926 and *Bryconaethiops boulengeri* Pellegrin, 1900, and the clariid *Clarias angolensis* Steindachner, 1866. Bongo Stream was distinguished from the others by a rich abundance of *Alestopetersius compressus* (Poll et Gosse, 1963). The presence of several species at low pH (between 5.0 and 5.5) is new information that lowers the bottom of the pH interval for these species compared to earlier reports. The maximum total length (TL) of some other species was by 5–20 percentage points higher than those reported earlier. The median weight per unit effort (WPUE) in the streams varied between 30 and 115 g per hour during the dry seasons and between 18 and 86 g per hour during the wet seasons. The fish biomass in the streams varied between 0.05 and 0.7 g · m^{-2} with a median 0.14 g · m^{-2}. This relatively low value compared to other tropical headwaters may be a result of the low pH and dark color of these headwaters. The results of the study serve as a reference point to which future monitoring of fish fauna can be compared for sustainable management of the LTL.

Keywords

acidity, catch, Congo River, fish biomass, fish species, headwaters, humic water, multi-annual data

Introduction

The Congo River and its tributaries, covering an area of about 4 000 000 km^2, is the world's second-largest drainage basin after the Amazon River. It's ichthyofauna is extremely rich—to a large extent incompletely known (Shumway et al. 2003; Harrison et al. 2016). In the central basin of the Congo River catchment, the UN Central African Forest Initiative (CAFI) has designated the 65 700 km^2 Lake Tumba Landscape (LTL) as one of twelve priority conservation areas in Africa (Twagirashyaka and Inogwabini 2009). The primary focus for the area is on the freshwater ecosystem, and the LTL is also a Ramsar site (Ramsar n.d.). The LTL has a tropical rainforest climate. Many of the waters in the LTL have high concentrations of dissolved organic matter with humic acids which color the water brown and lower the pH (Matthes 1964; Zanga et al. 2019).

Fishes in the running and stagnant waters are of vital importance as a food resource for the local residents of the LTL; 85% of the protein in their diet derives from fishes (Carpe n.d.). There are indications that the sustainability of the fish population in the landscape is compromised by changes in land use, and in some areas also by overfishing (Brummett et al. 2011). Freshwater ecosystems are sensitive to the clearing of forests for agriculture, overgrazing by livestock, and logging activity since these actions can all cause soil erosion and increase water turbidity (Bojsen and Barriga 2002; Chimwanza et al. 2006; Weijters et al. 2009). In tropical streams that are poor in nutrients, many fish species depend largely on food from terrestrial sources (Welcomme and de Merona 1988). Therefore, the destruction of forests may result in a decline in aquatic productivity (Lorion and Kennedy 2009). Another alarming issue is the use of nonselective fishing methods such as dynamiting, plant toxins, or mosquito nets. These practices have a basis in pervasive poverty, problematic governance, and lack of knowledge that could be overcome to improve the sustainable productivity of the fishery. Despite the high diversity of fish in the region, ichthyological studies are scarce, especially those with quantitative, multi-annual catch statistics. The majority of published results of ichthyological studies of the LTL have focused on Lake Tumba, and its species (e.g., Marlier 1958; Matthes 1964) but there was one focusing on quantitative aspects (Zanga et al. 2019).

Some important fish studies have been performed on other parts of the Congo River basin. For example, the fish fauna of the largest tributary, the Lualaba River, and its associated waters has been documented by several expeditions (e.g., Banister and Bailey 1979). Other examples include a comprehensive study on the ichthyofauna of three northeastern tributaries of the middle Congo and their headwaters (Decru et al. 2017), and studies on the lower Congo River (e.g., Hanssens 2009; Lowenstein et al. 2011). In some sections of the middle Congo River with a high proportion of acid brown waters, species in the Salonga and Luilaka rivers have been reported (Inogwabini 2005). In a later investigation, a number of sites along these rivers and the connecting Yenge River were more intensely inventoried together with water chemistry (Monsembula Iyaba and Stiassny 2013). An important article about fishes in streams was published by Matthes (1964), who for two months in 1959 fished 34 sites upstream of the Ruki River, a left bank tributary to the Congo River. Further fish studies have been conducted on growth rates of single species (Mbadu Zebe et al. 2010) and the impact of environmental variables on fish growth in the Congo basin (Pwema Kiamfu et al. 2011). The streams of the LTL, situated in the middle Congo area, have received less attention although they are important for the livelihoods of local residents. A single survey carried out in August 2010 to identify fish species is the only previous study in Bambou and Lebomo streams (Stiassny and Mamonekene unpublished*).

The presently reported study was undertaken on three LTL headwater streams, Bambou, Lebomo, and Bongo, to improve knowledge of community structure and diversity of the LTL fish fauna. These streams were investigated systematically over a period of 3–5 years, with a special focus on the catch and biomass data. We describe the stream fish community composition and biomass with the aim to compare variation within and between streams over years and seasons. The relations to water quality are explored, and comparisons are made with previous studies from the Congo River basin. The information presented in this paper will increase our knowledge on the fish biomass in central African waters that are relatively poor in nutrients, low in pH, and high in dissolved organic matter.

Material and methods

Characteristics of investigated streams. The investigated streams Bambou, Lebomo, and Bongo are situated in the Mai-Ndombe province in the central part of the Democratic Republic of the Congo (Fig. 1). This area has a humid tropical climate with dry seasons (usually from mid-May to mid-September as well as shorter periods from January to March) as well as wet seasons that vary in onset dates and duration. In the Köppen climate classification system, this is Af, i.e., a tropical rainforest climate (Peel et al. 2007). Seasons were nominally classified as wet for months February to May, and dry for months May to July since it was not possible to measure water level frequently due to logistical reasons in more than one of the streams during two of the five study years. Small streams (catchments), like the three studied here, are affected by occasional, local heavy showers and dry periods which diminish seasonality. The mean annual precipitation in the province is about 1600 mm (DRC Ministry of Planning 2005).

The stream catchments were estimated from satellite images and their area ranged from 90 to 180 km^2 (Table 1). The topography of the area is rather flat and the agriculture practiced in the catchments is a small-scale but extensive type of slash-and-burn. The land adjacent to the streams is sparsely populated with villages at some distance. The area around Bambou and Lebomo streams is populated by some 15 000 people living in 15 villages. The riparian area around Bambou is an 80 m broad gallery forest with trees, roots, and stones on the riverbank. The riparian area of the Lebomo was formerly

* Stiassny MLJ, Mamonekene V (n.d.) Fish diversity in the Lake Tumba Landscape. (Study in August 2010). Unpublished report.

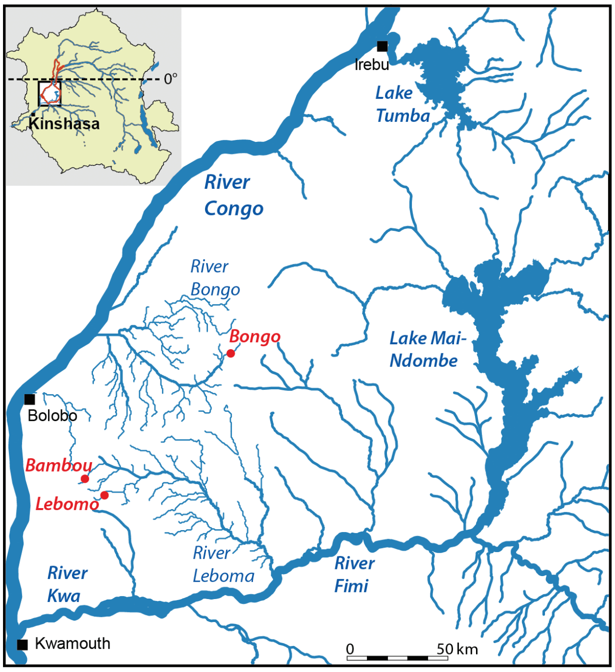

Figure 1. The sites investigated on the streams Bambou, Lebomo, and Bongo in the Lake Tumba Landscape, DR Congo. Based on a map from WWF (G. Tshimanga). The inserted map shows the Congo basin with the Ramsar area 1784 delimited in red.

Table 1. Basic physical and chemical data for the streams investigated in the headwater streams of the Lake Tumba Landscape, DR Congo. Drainage area data based on satellite images. Median width and depth with ranges in brackets. Chemical values presented as medians with ranges in brackets.

Character	Stream		
	Bambou	**Lebomo**	**Bongo**
Landscape type	Forest, savannah	Grassland, savannah	Mature forest
Land use	Natural	Ranching	Logging
Coordinates	2.29ºS, 16.30ºE	2.57ºS, 16.55ºE	1.95ºS, 17.10ºE
Bottom substrate	Sand, pebble	Sand, stone	Mud, boulder
Elevation [m]	440	380	340
Drainage area [km^2]	90	100	180
Number of measurements	8	8	6
Width [m]	7.6 (3.7–12.5)	7.7 (6.3–9.9)	8.5 (4.6–17.0)
Depth [m]	0.4 (0.17–1.4)	0.7 (0.38–0.97)	0.6 (0.18–1.15)
Number of measurements	10	10	4
pH	5.0 (4.8–5.8)	6.4 (6.0–6.8)	5.7 (5.5–5.8)
Color [mg Pt· L^{-1}]	120 (30–120)	50 (10–90)	55 (40–60)
TOC [mg · L^{-1}]	10.6 (4.5–12)	3.8 (0.8–8.9)	5.9 (4.5–6.5)
$NO_{2,3}$-N [µg · L^{-1}]	70 (2–91)	52 (1–140)	300 (280–340)
Total P [µg · L^{-1}]	41 (26–54)	35 (5–63)	69 (61–79)

Elevation is above the sea level. Pt = Platinum, TOC = Total organic carbon.

used for cattle ranching. Mixed grassland savannah and forests cover the catchments of Bambou and Lebomo streams while the Bongo catchment is a mixed mature forest that is subjected to selective logging of blackwood (the endangered tree *Millettia laurentii*). This is evident from trails left by timber transport. The area close to the stream is very rugged with steep slopes. A waterfall of approximately 25 m in height lies in the highest section of the investigated part of Bongo Stream. The bottom substrate and the presence of aquatic vegetation were assessed in each transect by the use of a 1-m^2 wooden square frame. The bottom substrate of Bambou and Lebomo streams comprised sand and stones, while Bongo with its deeper water has clayey sediments in addition to stones.

Sampling and analysis. The study period was 2007–2011. In each stream 10 transects set approximately 200 m from each other were delineated. The total length covered was 1800 m. Five transects were placed upstream and five downstream of the existing bridges to facilitate subsequent sampling. In Bongo two transects became located upstream of the 25 m high waterfall and eight downstream. Width and depth were measured every meter by a stick at the ten fishing transects in each stream on eight occasions in Bambou and Lebomo, and six in Bongo. For each transect, a mean of three central depth values was used in order to avoid possible “pits”. Due to the heavy workload during fishing, this was done on other occasions close to fishing days.

An apparent visual observation of water color was recorded during a total of 53 days where the water was classified as white, clear, or brown as established for Amazonian waters by Sioli (1965).

Samples for water chemistry were collected at the bridge location on ten occasions in Bambou and Lebomo and on four occasions in Bongo. The samples were sent to the accredited water chemistry laboratory at the Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden, and analyzed using standardized methods (International standards, ISO and European standards, EN).

Fishing was carried out in a way that allowed separation of catches between day (08:00–16:00 h or 18:00 h) and night (18:00–06:00 h). There was a variation in the times for setting and harvesting of the fishing gear which was set out up to five times a day at 08:00, 12:00, 14:00, 16:00, and/or 18:00 h. During the daytime, harvesting occurred two or four hours after nets were set. Nighttime fishing nominally started at 18:00 h and continued until 06:00 h the following morning. The total number of fishing days was 176 of which 68 occurred during the dry seasons and 106 in wet seasons (Table 2). However, the number of fishing days varied between streams. Fishing was done more frequently on Bambou and Lebomo streams than on the more distant Bongo stream due to logistic problems with transport. Two sets of five different gillnets with mesh-size 1, 1.5, 2, 2.5, or 3 cm, 1 m high and 10 m long, were used on each 200 m transect. The nets were stretched perpendicular to the stream reach. Some transects (13%) were one to a few meters wider than 10 m, and thus not fully covered by the net. The nets were held up by ropes fastened to stones and anchored to the stream bed with sinks touching the bottom. Further-more, to be able to catch fish of various sizes, lines with hooks of sizes 16, 14, and 12 were also used (the hook size decreased with increasing hook number). Lines with a total of 100 hooks baited with earthworms were set out from the riverbank between the nets crossing the river. However, hook sampling was used with less regularity than nets due to logistic reasons (Table 2). Out of a total of 176 fishing days, nets were used on 150 days, including occasions combined with hooks. Hooks were used separately or in combination with nets on 64 days. On site, each fish specimen was identified, weighed, and its total length (TL) was measured. The weighing was done up to the nearest 1 g (except for measurements before 2009, which were done up to 10 g accuracy), and TL was measured up to the nearest 1 mm. Every fish was assigned to a site, fishing time, and fishing gear. Events with no catch were also noted and included in the calculations of catch. After identification and measurement, live fish from hook fishing were in two cases returned to the stream whereas dead fish were used as food for the staff.

The number of sampling events varied between years but always included periods of the nominally dry and wet seasons. The streams were not fished during either the times of lowest or highest water levels as illustrated for Bambou Stream (Fig. 2). This was due both to transport difficulties at times of high precipitation and the need to avoid interfering with fishing by the local inhabitants. During the dry season when the water level drops in the streams, women were observed to use baskets to remove water from the pools and then use scoop baskets (ecopage) to catch fish.

An overview of the Congolese fish fauna has never been compiled and identification keys are lacking for the majority of regions and taxonomic groups (Decru et al. 2017). In the presently reported study, the first identifications of the specimens were made using FishBase (Froese and Pauly 2021) and local support. Specimens that were not identified in the field were given a vernacular name and photographed and three fish of each species were preserved in ethanol for later confirmation. Melanie Stiassny (American Museum of National History), during her visit to the station at Malebo (Bambou Stream), inspected the collection and helped to identify some specimens. Unfortunately, specimens kept at the station at Malebo (Bambou Stream) were inadequately preserved and later discarded. Based on photos, a number of species could later be verified or in some cases re-identified by specialists during a visit to the Royal Museum for Central Africa and the KU Leuven University in Belgium. Later, an additional check with the specialists was done. Photos may, however, not reflect all details that could be decisive for a correct determination. The procedures used may have had an impact on the species' determinations. In cases of apparent inaccuracy, specimens were only identified up to the genus level.

Weight (catch) was calculated as a daily sum of catches for all fishing gear and species. The Weight Per Unit Effort (WPUE) and number of fish per hour (NPUE) were calculated with respect to actual fishing hours. Different subsets of fishing time and gear were used in order to obtain detailed, comparable subsets as specified for each statistical analysis.

In order to assess the total fish biomass in each stream, fishing was performed repeatedly during 4–12 days with the aim of achieving total fish depletion in the study area. The fishing gear was harvested 3–4 times per day and set up again immediately after each harvest, covering a 24-h period, until no or low catch was re-

Table 2. Fishing days by stream, season, and gear for the headwater streams of the Lake Tumba Landscape, DR Congo.

Stream	Year	Season	Hook	Net	Net and hook	Total fishing days
Bambou	2007	Wet	—	12	—	12
Bambou	2008	Dry	—	5	—	5
Bambou	2008	Wet	4	14	—	18
Bambou	2009	Dry	—	2	—	2
Bambou	2010	Dry	—	7	3	10
Bambou	2010	Wet	4	6	—	10
Bambou	2011	Wet	3	7	—	10
Bambou	**Total**		**11**	**53**	**3**	**67**
Bongo	2008	Dry	1	7	—	8
Bongo	2008	Wet	—	7	1	8
Bongo	2009	Dry	1	6	—	7
Bongo	2009	Wet	—	6	—	6
Bongo	2010	Dry	—	2	4	6
Bongo	2010	Wet	—	3	5	8
Bongo	**Total**		**2**	**31**	**10**	**43**
Lebomo	2008	Dry	—	3	4	7
Lebomo	2008	Wet	—	7	—	7
Lebomo	2009	Dry	7	5	1	13
Lebomo	2009	Wet	—	5	—	5
Lebomo	2010	Dry	—	3	7	10
Lebomo	2010	Wet	7	7	1	15
Lebomo	2011	Wet	—	4	5	9
Lebomo	**Total**		**14**	**34**	**18**	**66**
Total			**27**	**118**	**31**	**176**

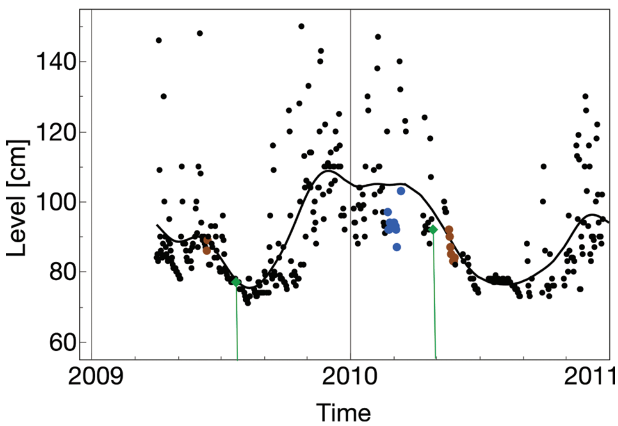

Figure 2. Water level recordings from Bambou Stream, the Lake Tumba Landscape, DR Congo. Fishing days indicated as blue markers for the wet season and brown markers for the dry season. Black markers indicate level recording days with no fishing. Line is a cubic smoothing. The green dots and vertical lines indicate the two dates with pH-measurements.

corded, indicating complete or nearly complete removal of fish from the study area for the size of fish caught by the used mesh sizes.

Statistical analyses. Data handling and univariate statistical calculations were done in JMP® 14.0.0. Non-metric multidimensional scaling (NMDS) was used for visual representation and to compare the similarity in community composition for daytime (08:00–18:00 h) net-sampled fish abundances (NPUE). Only daytime catches were included in this analysis as not in all sites both day- and night-time catches were done. Differences between streams and seasons (groups) were tested with an analysis of similarities (ANOSIM, Clarke 1993), using the R statistic to test differences between groups (R = 0 means no difference, R = 1 means total dissimilarity between groups). The Bray–Curtis distance measure was used for separating groups. The ANOSIM and NMDS analyses were computed using the PRIMERv6 software (PRIMER-E Ltd, Plymouth, UK).

Results

Stream characteristics. Bambou Stream was the shallowest with a mean maximum depth of 0.5 m while the other streams were about 0.7 m deep on average (range in Table 1). The water depth did not vary significantly ($P > 0.05$) between dry seasons (0.5–1.8 m; mean 0.9 m) and rainy seasons (0.6–2.1 m; mean 1.1 m) when considering all the transects.

The streams were of similar width (Table 1) varying from 3.7 to 17 m along the study transects. The seasonal variation in the width was largest in Bongo where it could increase in width by 7.2 m to 9.8 m along the 1.8 km study reach during wet seasons (data not illustrated). The smallest seasonal variation in stream width of only 0.1 m was recorded in Lebomo. According to the visual water observations, white (turbid) water was always associated with the wet season while clear and brown waters were recorded during both wet and dry seasons.

Bambou and Bongo are tropical blackwaters with high concentrations of humic acids coloring the water deep brown (measured as total organic carbon (TOC) and water color) and causing a low pH of around 5 (Table 1). Lebomo Stream was slightly less colored and had a pH above 6. The groundwater level is likely higher during rainy seasons resulting in higher concentrations of humic matter reaching the streams from more superficial organic soils. Two pH values from Bambou Stream (green dots and vertical lines in Fig. 2); July 2009 with a pH of 5.8, and April 2010 with pH 4.8 illustrate events influenced by the water flow from the drainage area. The latter sample with the lower pH was also associated with a higher TOC concentration. Bambou and Lebomo were nutrient-poor streams with low concentrations of nitrogen and low to medium concentrations of Total-P (Table 1). Bongo was more nutrient rich with a maximum nitrogen concentration of 340 $\mu g \cdot L^{-1}$ and a total phosphorus concentration of around 70 $\mu g \cdot L^{-1}$.

Fish occurrence, abundance, size, and frequency. A total of 2028 fish individuals representing 50 species were caught in this study. The majority of specimens were identified up to the species level, however, ten could be identified up to genus only (Table 3). Sixteen species appeared in all streams while six or seven species were unique for each stream making a total of 19 unique species (Table 3). The 50 species were distributed over 15 families with species richness of 31 in Bambou, 36 in Lebomo, and 29 in Bongo. As the study period progressed, the cumulative species curves for each stream leveled off and approached a plateau (Fig. 3).

When considering the number of specimens per family caught in the three streams, the pattern varied slightly. Alestids stand out markedly with 26% of the total number of caught fish specimens belonging to just four species (Table 3). Two of these species (*Clupeocharax schoutedeni* Pellegrin, 1926, and *Bryconaethiops boulengeri* Pellegrin, 1900) occurred frequently in all streams. The alestid, *Alestopetersius compressus* (Poll et Gosse, 1963) was only caught in Bongo, where it was the most common species (22% of total abundance, Table 4). In all streams, cyprinids, clariids, and mormyrids, with 18%, 16%, and 15% of the total fish abundance respectively, were also families with high specimen abundance. Some species among cyprinids and clariids were caught in large numbers and occurred in all streams such as *Enteromius holotaenia* (Boulenger, 1904) with 13% of the total catch, and *Clarias angolensis* Steindachner, 1866, with 9%. Seventy-five percent of all fish caught belonged to the aforementioned four families. An overview of species with an abundance of 20 specimens or more caught in each stream is provided in Table 4. These common species accounted for more than 80% of all fish caught in Bambou and Bongo, and over 70% in Lebomo. Species unique to a stream were usually caught in small numbers, and sometimes just a single specimen. The exception was the high abundance of *Alestopetersius compressus* in Bongo exclusively caught by net (22% of total catch). Several taxa caught by net were also caught by hook. There were, however, six species captured only by the hook and just as single individuals *Protopterus dolloi* Boulenger, 1900, *Mormyrops anguilloides* (Linnaeus, 1758), *Channalabes apus* (Günther, 1873), *Clarias gabonensis* Günther, 1867, *Malapterurus melanochir* Norris, 2002, and *Microctenopoma nanum* (Günther, 1896).

Compared to thirteen other studies of fish fauna found in the Congo River basin (Table 5) three more species for the basin were recorded: the mormyrid *Marcusenius dundoensis* (Poll, 1967), the anabantid *Ctenopoma multispine* Peters, 1844, and the clariid *Platyclarias machadoi* Poll, 1977. Of those, *Ctenopoma multispine* and *Platyclarias machadoi* were present in all of our study streams, with the latter found in large numbers in Bambou (9% of total catch).

Table 3. Summary table for species caught in the headwater streams of the Lake Tumba Landscape, DR Congo. Total number and measured maximum total length (TL) of each species. The FishBase data (FB) on maximum (TL) or standard length (SL) are provided for comparison (Froese and Pauly 2021).

FAMILY	Number of fish sampled			TL max	FB TL max	FB SL max
Species	Bambou	Lebomo	Bongo	[cm]	[cm]	[cm]
PROTOPTERIDAE						
Protopterus dolloi Boulenger, 1900	0	0	2	82	130	
POLYPTERIDAE						
Polypterus ornatipinnis Boulenger, 1902	5	0	0	40	60	
Polypterus polli Gosse, 1988	1	0	0	22.2		32.1
MORMYRIDAE						
Brienomyrus sp.	1	0	9	15.5		
Campylomormyrus sp.	0	4	2	22		
Cyphomyrus psittacus (Boulenger, 1897)	11	0	0	20.5	30	
Gnathonemus petersii (Gunther, 1862)	0	5	0	23.6	35	
Heteromormyrus sp.	0	0	5	20.5		
Hippopotamyrus sp.	16	2	2	17		
Marcusenius dundoensis (Poll, 1967)	4	3	0	21		12.3
Marcusenius moorii (Günther, 1867)	16	6	94	20		21.4
Mormyrops anguilloides (Linnaeus, 1758)	0	1	0	37	150	
Mormyrops sp.	16	3	25	17.1		
Mormyrus caballus Boulenger, 1898	3	0	0	18.5	50	
Myomyrus macrodon Boulenger, 1898	0	9	0	24	24	
Petrocephalus christyi Boulenger, 1920	1	4	3	13	7.7	
Petrocephalus simus Sauvage, 1879	0	2	1	12.1	12	
Pollimyrus adspersus (Günther, 1866)	0	1	0	8	9.8	
Pollimyrus sp.	2	1	35	15.5		
Pollimyrus tumifrons (Boulenger, 1902)	2	14	0	19	11.2	
ALESTIDAE						
Alestopetersius compressus (Poll et Gosse, 1963)	0	0	152	11.5		7.8
Brycinus sp.	0	0	1	6.5		
Bryconaethiops boulengeri Pellegrin, 1900	96	52	18	24	25	
Clupeocharax schoutedeni Pellegrin, 1926	127	84	3	20	25	
DISTICHODONTIDAE						
Mesoborus crocodilus Pellegrin, 1900	3	3	0	29.5	26.5	
Phago boulengeri Schilthuis, 1891	1	0	0	14	17	
HEPSETIDAE						
Hepsetus microlepis (Boulenger, 1901)	5	2	12	38	26.7	
CYPRINIDAE						
Enteromius holotaenia (Boulenger, 1904)	171	25	77	17.5		12
Raiamas christyi (Boulenger, 1920)	42	43	0	19	17.7	
CLARIIDAE						
Channallabes apus (Günther, 1873)	0	2	0	29	41.6	
Clarias angolensis Steindachner, 1866	22	7	146	40	35	
Clarias gabonensis Günther, 1867	1	3	0	21	36	
Clarias jaensis Boulenger, 1909	1	11	8	29	48,3	
Clarias platycephalus Boulenger, 1902	3	3	19	43	37.6	
Clarias sp.	0	1	0	14.5		
Platyclarias machadoi Poll, 1977	73	12	7	26.2	20.1	
MALAPTERURIDAE						
Malapterurus melanochir Norris, 2002	0	1	2	14		98
Malapterurus sp.	0	0	1	11		
CLAROTEIDAE						
Parauchenoglanis balayi (Sauvage, 1879)	117	5	0	19.5	39	31.7
Parauchenoglanis pantherinus (Pellegrin, 1929)	2	0	0	17		29.2
Parauchenoglanis punctatus (Boulenger, 1902)	12	58	0	38		41.0
SCHILBEIDAE						
Schilbe marmoratus Boulenger, 1911	0	69	35	21		21.7
MOCHOKIDAE						
Euchilichthys royauxi Boulenger, 1902	0	1	2	12.5	22	
Synodontis sp.	0	0	1	12.5		
ANABANTIDAE						
Ctenopoma multispine Peters, 1844	14	5	8	15	14	
Microctenopoma nanum (Günther, 1896)	0	0	1	9.2		6.7
CICHLIDAE						
Hemichromis elongatus (Guichenot, 1861)	44	14	13	22		18.7
Hemichromis stellifer Loiselle, 1979	41	5	22	12.6		10
Pelmatochromis nigrofasciatus (Pellegrin, 1900)	0	2	0	7.3		11.6
MASTACEMBELIDAE						
Mastacembelus congicus Boulenger, 1896	1	5	0	36.5		43.5
Total number of species	31	36	29			

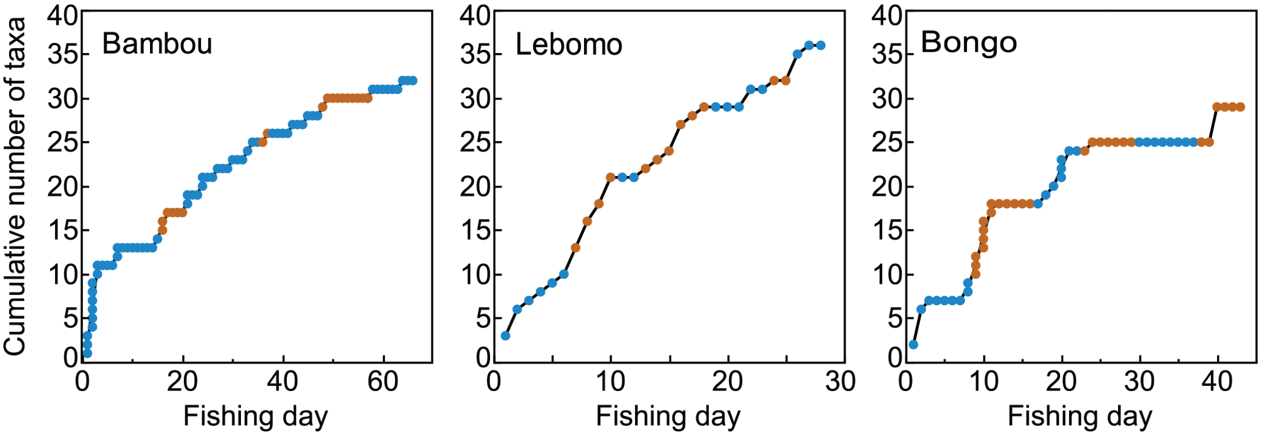

Figure 3. Species cumulative curves from the whole study period in three headwater streams of the Lake Tumba Landscape, DR Congo. Blue dots indicate wet season, brown dots dry season.

Table 4. Major species (caught in numbers ≥20) sorted by abundance for each stream for the headwater streams of the Lake Tumba Landscape, DR Congo. Percentages are compared to the total abundance in each stream.

Bambou		Lebomo		Bongo	
Species	**[%]**	**Species**	**[%]**	**Species**	**[%]**
Enteromius holotaenia	20	*Clupeocharax schoutedeni*	18	*Alestopetersius compressus*	22
Clupeocharax schoutedeni	15	*Schilbe marmoratus*	15	*Clarias angolensis*	21
Parauchenoglanis balayi	14	*Parauchenoglanis punctatus*	12	*Marcusenius moorii*	13
Bryconaethiops boulengeri	11	*Bryconaethiops boulengeri*	11	*Enteromius holotaenia*	11
Platyclarias machadoi	9	*Raiamas christyi*	9	*Schilbe marmoratus*	5
Hemichromis elongatus	5	*Enteromius holotaenia*	5	*Pollimyrus* sp.	5
Raiamas christyi	5			*Mormyrops* sp.	4
Hemichromis stellifer	5			*Hemichromis stellifer*	3
Clarias angolensis	3				

As expected, larger species tended to be caught with a hook rather than with a net. There was a difference in total length (TL) between catches with the two gears (Wilcoxon $P < 0.0001$). The median TL was 15.3 cm for hook fishing and 12.5 cm for nets. The largest species caught only by the hook was *Protopterus dolloi* in the Bongo stream with a maximum TL of 82 cm. Large species caught by net and reaching lengths of about 40 cm were *Polypterus ornatipinnis* Boulenger, 1902, *Hepsetus microlepis* (Boulenger, 1901), and *Parauchenoglanis punctatus* (Boulenger, 1902). There was a lack of small individuals due to the available fishing gear. The shortest fish caught was 6.3 cm TL.

The maximum TL of three species in this study exceeded the maximum TL recorded in FishBase (Froese and Pauly 2021) by up to a factor of 1.7 (Table 6). For one species, *Enteromius holotaenia*, only standard length (SL) was available in FishBase. We suggest a TL of 17.5 cm be added in FishBase for *E. holotaenia*, based on the maximum TL from this study (Table 6).

The high waterfall in Bongo most probably impeded some species from moving upstream. Only six species were found upstream from the 25 m high waterfall: *Alestopetersius compressus*, *Clarias angolensis*, *Clarias platycephalus* Boulenger, 1902, *Enteromius holotaenia*, *Marcusenius moorii* (Günther, 1867), *Mormyrops* sp. They were all found downstream of the waterfall as well.

Visual water color and fish occurrence. *Enteromius holotaenia*, *Hemichromis elongatus* (Guichenot, 1861), *Cyphomyrus psittacus* (Boulenger, 1897), *Bryconaethiops boulengeri*, and *Platyclarias machadoi* were species caught in the largest numbers during periods with brown water. Species almost totally lacking during brown water phases were *Alestopetersius compressus* in Bongo, *Schilbe marmoratus* Boulenger, 1911 and *Parauchenoglanis punctatus* in Bongo and Lebomo, as well as *Marcusenius moorii* in all streams. Species not caught during periods of brown water were roughly equally abundant during white and clear water phases.

Influence of pH on fish occurrence. Twenty-seven species in the streams occurred at pH 5, seven species were added when the pH was 5.5, and six species at pH 6 (Table 7). A comparison with pH ranges from FishBase (Froese and Pauly 2021) suggest that several species are present in much lower pH ranges than have previously been reported (Table 7).

Diurnal differences. Comparisons of NPUE and WPUE between day and night catches were inconclusive (Wilcoxon non-parametric test). The majority of species were caught during the daytime and *Hemichromis elongatus*, *Alestopetersius*

Table 5. Species list from the presently reported study compared with published records from other streams/rivers in the Congo River drainage area.

FAMILY	**Reference study**													**Total**
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**No.**
PROTOPTERIDAE														
Protopterus dolloi	–	x	x	–	x	x	x	–	–	–	–	–	x	6
POLYPTERIDAE														
Polypterus ornatipinnis	–	–	x	–	x	x	–	x	–	–	–	–	–	4
Polypterus polli	–	–	–	–	–	x	–	–	–	–	–	–	–	1
MORMYRIDAE														
Cyphomyrus psittacus	–	x	–	x	x	x	–	x	–	–	–	–	x	6
Gnathonemus petersii	L	x	x	–	x	x	–	x	x	–	x	–	x	9
Marcusenius dundoensis	–	–	–	–	–	–	–	–	–	–	–	–	–	0
Marcusenius moorii	B L N	x	x	–	x	x	–	x	–	x	x	x	x	10
Mormyrops anguilloides	–	x	x	x	x	x	–	x	–	–	–	–	x	7
Mormyrus caballus	–	x	x	x	x	x	–	x	–	–	x	–	–	7
Myomyrus macrodon	–	–	–	x	–	–	–	–	–	–	–	–	–	1
Petrocephalus christyi	–	x	–	–	x	x	–	x	x	–	x	–	x	7
Petrocephalus simus	–	–	–	–	–	x	x	–	–	x	–	x	–	4
Pollimyrus adspersus	–	–	–	–	x	x	–	–	–	–	–	–	–	2
Pollimyrus tumifrons	–	–	–	–	–	x	–	–	–	–	–	–	–	1
ALESTIDAE														
Alestopetersius compressus	–	–	–	–	–	x	–	–	–	–	–	–	–	1
Bryconaethiops boulengeri	B	x	x	–	x	x	x	x	x	x	x	–	x	11
Clupeocharax schoutedeni	–	x	x	–	–	–	–	–	–	–	–	–	x	3
DISTICHODONTIDAE														
Mesoborus crocodilus	–	–	x	–	–	x	–	x	x	–	x	–	x	6
Phago boulengeri	–	x	–	–	x	x	x	x	–	–	x	–	x	7
HEPSETIDAE														
Hepsetus microlepis	–	–	x	–	x	x	–	–	x	x	x	–	x	7
CYPRINIDAE														
Enteromius holotaenia	–	–	–	–	–	x	–	–	x	x	x(cf)	–	–	4
Raiamas christyi	B(cf)	–	–	–	–	x	x	–	x	x	x	x	x	8
CLARIIDAE														
Channallabes apus	B	x	x	x	x	x	–	–	–	–	x	–	x	8
Clarias angolensis	–	x	x	x	x	x	–	–	–	–	x	x	x	8
Clarias gabonensis	–	x	x	x	x	x	–	–	x	x	–	x	x	9
Clarias jaensis	–	–	–	–	–	–	–	–	–	x	–	–	–	1
Clarias platycephalus	B	x	x	–	x	x	–	–	–	–	–	x	–	5
Platyclarias machadoi	–	–	–	–	–	–	–	–	–	–	–	–	–	0
MALAPTERURIDAE														
Malapterurus melanochir	–	–	x	–	–	x	–	–	–	–	–	–	x	3
CLAROTEIDAE														
Parauchenoglanis balayi	–	–	–	x	x	x	–	–	–	x	–	–	–	4
Parauchenoglanis pantherinus	–	–	–	–	–	–	–	–	–	x	–	–	–	1
Parauchenoglanis punctatus	N	x	x	–	x	x	–	x	–	–	x	x	x	9
SCHILBEIDAE														
Schilbe marmoratus	–	x	x	–	x	x	–	x	x	–	x	–	x	8
MOCHOKIDAE														
Euchilichthys royauxi	–	–	–	–	–	x	–	–	–	–	–	–	–	1
ANABANTIDAE														
Ctenopoma multispine	–	–	–	–	–	–	–	–	–	–	–	–	–	0
Microctenopoma nanum	B L	x	x	–	x	x	x	–	–	x	x	–	x	9
CICHLIDAE														
Hemichromis elongatus	B N	–	x	x	x	x	–	x	x	x	x	x	–	10
Hemichromis stellifer	B	–	–	x	x	–	–	–	x	–	x	x	–	6
Pelmatochromis nigrofasciatus	–	–	x	–	x	x	–	–	–	–	x	–	x	5
MASTACEMBELIDAE														
Mastacembulus congicus	–	–	–	–	x	x	–	x	–	–	x	–	–	4
Total number	10	17	20	10	24	32	6	14	11	12	19	9	20	

Reference studies: 1 = Stiassny and Mamonekene unpublished (See footnote on page 196) Fish diversity in the Lake Tumba Landscape. (Study in August 2010). Unpublished report.) (Lake Tumba Landscape); 2 = Zanga et al. 2019 (Lake Tumba); 3 = Inogwabini 2005 (Salonga National Park); 4 = Wamuini Lunkayilakio et al. 2010 (Inkisi, Lower Congo); 5 = Monsembula Iyaba et al. 2013 (N'sele River); 6 = Decru et al. 2017 (NE tributaries to Congo River); 7 = Matthes 1964 (Ikela area); 8 = Mbimbi Mayi Munene and Stiassny 2011 (Kwilu River, Kasai region); 9 = Liyandja et al. 2019 (Musolo River catchment); 10 = Mamonekene and Stiassny 2012 (Ogowe and Kouilou rivers); 11 = Ibala Zamba et al. 2019 (Lefini River); 12 = Batiabo Mikembi et al. 2019 (Loua River); 13 = Stiassny et al. 2021 (Mfini River). X = species found; minus sign = species not found, B = found in Bambou Stream, L = found in Lebomo Stream, N = found in Ngampoko Stream, cf = the species was not fully identified in the article. Total No. denotes the total number of studies reporting a fish.

Table 6. Presently reported species from headwater streams of the Lake Tumba Landscape, DR Congo with lengths considerably larger than maximum total length (TL) recorded in FishBase (FB, Froese and Pauly 2021).

Species	No. of fish caught	Median TL [cm]	Max TL [cm]	FB TL (SL) [cm]	Max TL/ FB TL
Clarias angolensis	175	19.5	40	35	1.1
Enteromius holotaenia	273	12.0	17.5	na (12)	na
Raiamas christyi	85	15.6	23.8	17.7	1.3
Pollimyrus tumifrons	16	16.0	19	11.2	1.7

SL = standard length, na = not available.

Table 7. Fish species list with lowest recorded pH from the presently reported study from headwater streams of the Lake Tumba Landscape, DR Congo confronted with the data on pH range from FishBase (Froese and Pauly 2021).

FAMILY Species	Lowest pH	pH from FishBase
PROTOPTERIDAE		
Protopterus dolloi	5.5	na
POLYPTERIDAE		
Polypterus ornatipinnis	5.0	na
Polypterus polli	5.0	na
MORMYRIDAE		
Cyphomyrus psittacus	5.0	6.8–7.2
Gnathonemus petersii	6.0	6.0–8.0
Marcusenius dundoensis	5.0	na
Marcusenius moorii	5.0	na
Mormyrops anguilloides	6.0	na
Mormyrus caballus	5.0	na
Myomyrus macrodon	6.0	na
Petrocephalus christyi	5.0	na
Petrocephalus simus	5.5	na
Pollimyrus adspersus	6.0	na
Pollimyrus tumifrons	5.0	na
ALESTIDAE		
Alestopetersius compressus	5.5	na
Bryconaethiops boulengeri	5.0	na
Clupeocharax schoutedeni	5.0	6.0–7.5
DISTICHODONTIDAE		
Mesoborus crocodilus	5.0	na
Phago boulengeri	5.0	na
HEPSETIDAE		
Hepsetus microlepis	5.0	na
CYPRINIDAE		
Enteromius holotaenia	5.0	6.0–6.5
Raiamas christyi	5.0	6.5–7.0
CLARIIDAE		
Channallabes apus	6.0	6.0–8.0
Clarias angolensis	5.0	7.0–9.0
Clarias gabonensis	5.0	7.0–9.0
Clarias jaensis	5.0	na
Clarias platycephalus	5.0	na
Platyclarias machadoi	5.0	na
MALAPTERURIDAE		
Malapterurus melanochir	5.5	na
CLAROTEIDAE		
Parauchenoglanis balayi	5.0	na
Parauchenoglanis pantherinus	5.0	na
Parauchenoglanis punctatus	5.0	na
SCHILBEIDAE		
Schilbe marmoratus	5.5	6.5–7.5
MOCHOKIDAE		
Euchilichthys royauxi	5.5	na
ANABANTIDAE		
Ctenopoma multispine	5.0	6.0–7.5
Microctenopoma nanum	5.5	na
CICHLIDAE		
Hemichromis elongatus	5.0	na–7.0
Hemichromis stellifer	5.0	na
Pelmatochromis nigrofasciatus	6.0	na
MASTACEMBELIDAE		
Mastacembelus congicus	5.0	na

na = not available.

compressus, *Mormyrops* sp., *Marcusenius moorii*, and *Platyclarias machadoi* were always day-time catches. Only one species was solely caught during the night, and this was *Myomyrus macrodon* Boulenger, 1898 in Lebomo. No other species were regularly caught in significant quantities during night-time in any stream, but all those caught at night belonged to the family Mormyridae.

Fish catches. A compilation of net catches in each stream between years and seasons with day-time fishing effort is given in Table 8. NPUE was significantly higher during dry seasons in Lebomo and Bongo (Wilcoxon P = 0.04 and 0.004, respectively). For Bongo, WPUE was significantly higher also during dry seasons (Wilcoxon P = 0.02).

ANOSIM analysis of community composition based on NPUE data from daytime net fishing clustered the streams separately from each other (ANOSIM P = 0.001, Global R = 0.583, Fig. 4). ANOSIM did not indicate seasonal differences in community composition based on NPUE (seasons: P = 0.693, Global R = 0.078).

Estimation of fish biomass. The median fish biomass for all streams and occasions combined was 0.14 $g \cdot m^{-2}$. The biomass varied from 0.05 to 0.21 $g \cdot m^{-2}$ in Bambou, from 0.14 to 0.70 $g \cdot m^{-2}$ in Bongo, and from 0.05 to 0.43 $g \cdot m^{-2}$ in Lebomo (Table 9). Only in one stream was total fish depletion achieved, i.e. no fish caught on the last fishing day, while in the other streams up to 4% of the total catch was still added on the last day of fishing.

Discussion

Species distributions in the streams. During the presently reported study, we identified 31, 36, and 29 species in Bambou, Lebomo, and Bongo, respectively. Thanks to intense and prolonged fishing during both day and night these values are likely to be close to the total number of species present that could be caught with the net meshes and hook sizes used (Fig. 3). The count of species does, however, miss smaller-sized ones due to the fishing gear. The shortest fish caught was 6.3 cm.

Table 8. Compilation of comparable catch statistics of the presently reported study from headwater streams of the Lake Tumba Landscape, DR Congo during daytime net-fishing period (08.00–16.00/18.00) with all 10 nets (transects).

Stream	No. of fishing days		NPUE [no. $\cdot h^{-1}$]		WPUE [$g \cdot h^{-1}$]	
	Dry	Wet	Dry	Wet	Dry	Wet
Bambou	12	18	1.4	2.6	30	86
Lebomo	26	25	0.9	0.5	38	18
Bongo	19	17	2.8	1.0	115	69
Total	**57**	**60**				

Dry and Wet refer to the respective seasons. Number of fishing days and median values for number of fish per hour (NPUE) and weight of catch per hour (WPUE) for seasons classified as dry or wet.

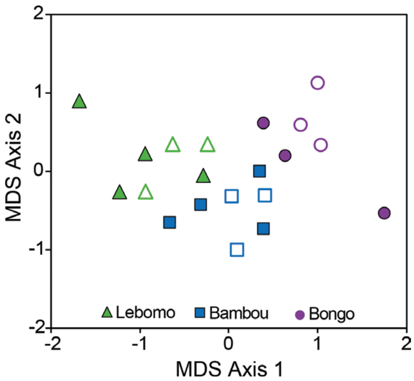

Figure 4. Non-metric multidimensional scaling (MDS) ordinations showing differences in community structure between streams and seasons of the presently reported study in three headwater streams of the Lake Tumba Landscape, DR Congo. Filled markers represent wet seasons, open markers dry seasons.

Table 9. Estimation of fish biomass of the presently reported study from three headwater streams of the Lake Tumba Landscape, DR Congo.

Stream	Year	Season	Gear	Fishing days	Fishes caught	Stream width [m]	Biomass [g·m^{-2}]
Bambou	2010	Dry	n	4	40	7.23	0.115
Bambou	2010	Wet	n	5	44	8.03	0.212
Bambou	2011	Wet	n	4	22	8.79	0.045
Bongo	2010	Dry	nh	5	166	7.22	0.707
Bongo	2010	Wet	nh	8	33	9.37	0.135
Lebomo	2008	Dry	n	7	105	8.02	0.253
Lebomo	2009	Dry	nh	5	55	7.75	0.137
Lebomo	2009	Wet	n	10	22	7.56	0.066
Lebomo	2010	Dry	nh	10	31	8.01	0.083
Lebomo	2010	Wet	n	5	21	8.18	0.054
Lebomo	2011	Wet	nh	9	90	7.79	0.425
Median					40		0.135

Fishing gear n = net, nh = net and hook.

Stiassny and Mamonekene (unpublished*) also fished in two of these streams and caught only two species of smaller size: *Aphyosemion cognatum* Meinken, 1951 with a maximum recorded TL of 5 cm, and *Epiplatys multifasciatus* (Boulenger, 1913) with a TL of 6 cm (Froese and Pauly 2021). Their fishing gear involved rotenone which kills all specimens independent of size and therefore covers also the smallest species. Compared to the number of species found in earlier studies in the Congo River tributaries, the species richness of our study was relatively low. For example, in the Lualaba River and connected waters of Upemba National Park, 131 species were recorded (Banister and Bailey 1979), three Congo Basin tributaries recorded 187 to 246 species (Decru et al. 2017), in streams of Salonga National Park 56 (Inogwabini 2005) to 152 species (Monsembula Iyaba and Stiassny 2013) were found. The reason for the low richness in our study streams is most likely that these streams are short headwater streams compared to the other studies that investigated larger sections of each river. Headwater streams do often have lower richness than downstream sections of a river (Matthews 1986; Decru et al. 2017) which we suggest to be the main reason for the relatively low richness in our study together with the finding that they were very acidic which we discuss further below.

Many of the fish species of our study have been found in similar streams in the region (Table 5). One of the most abundant species in our study, *Enteromius holotaenia* is recorded as widespread in the Congo River area in FishBase (Froese and Pauly 2021). This species was, however, not regularly noted in the river fish stocks from the study areas summarized in Table 5 except in the northeastern tributaries of the Congo River and in the Republic of Congo (Mamonekene and Stiassny 2012; Decru et al. 2017; Ibala Zamba et al. 2019). Another species frequently found in our study, *Clupeocharax schoutedeni*, is classified as vulnerable in the IUCN Red List of threatened species, due to its continuing decline in areal distribution and its only occasional appearance in parts of the Congo River basin where it is considered endemic (IUCN 2021). The rich occurrence of *Clupeocharax schoutedeni* in our study streams is therefore valuable information along with additional records from Salonga National Park and Lake Tumba (Monsembula Iyaba and Stiassny 2013; Zanga et al. 2019). The dominant occurrence of *Alestopetersius compressus* in Bongo has not been recorded in the other streams of the Lake Tumba Landscape (Table 5) but it occurred in many of the northeastern tributaries of the Congo River that includes both headwaters and lower reaches (Decru et al. 2017).

Platyclarias machadoi, present in all of our study streams, but in particularly large numbers in Bambou, needs a special comment as it is not recorded in the studies compiled in Table 5. Due to the small amount of information on its distribution, it is stated as DD-species (data deficient) in the IUCN Red List (IUCN 2021). There are also two more species *Marcusenius dundoensis* and *Ctenopoma multispine* which were found in our streams that were not recorded in the other river investigations listed in Table 5. Both species have, however, been reported previously from the nearby Kasai River basin (Froese and Pauly 2021). As many of the Congo River tributaries are poorly sampled it would not be surprising to find the presence of species new to the region after (more) intensive sampling.

A species caught in all three streams although in a smaller number as well as in several other rivers of lower and middle Congo is *Hepsetus microlepis*. In the investigations of the Salonga area and N'sele region it is named *Hepsetus odoe* as it precedes the revision of the genus and the revalidation of *Hepsetus microlepis* (see Monsembula Iyaba and Stiassny 2013; Stiassny et al.

* See footnote on page 196.

2021). The fish names in our study follow those of Decru et al. (2015). *Hepsetus microlepis* is reported from large parts of the lower and middle Congo basin in rivers as well as in large lakes (Decru et al. 2015). The species *Myomyrus macrodon* was the only one caught only during the night. Mormyridae, the family of *Myomyrus macrodon* and all the other species caught at night in this study, are nocturnally active and noted for large cerebellums as well as for use of electricity and sound that are beneficial when searching for food at night (Froese and Pauly 2021).

Fish size. Headwater streams are usually environmentally impoverished in relation to downstream watercourses as suggested by the river continuum concept (Welcomme 1974; Doretto et al. 2020). A smaller diversity of habitats and limited food resources probably affect the growth and occurrence of fish in our acid headwater streams. Information on fish size distribution is not commonly available but information on maximum TL can be used as a comparison. The common fish *Parauchenoglanis balayi* (Sauvage, 1879) is such an example. Its maximum TL noted in FishBase (Froese and Pauly 2021) is 39 cm but the longest single specimen in our study was 32 cm, with all others reaching lengths < 20 cm. *Clupeocharax schoutedeni* is another abundant species with > 200 caught specimens with a maximum length of 20 cm in our study compared to the FishBase TL maximum of 25 cm.

Some of the common species, however, in the presently reported study, reached larger sizes than recorded in FishBase (Froese and Pauly 2021). *Clarias angolensis* and *Raiamas christyi* (Boulenger, 1920) are such cases where the longest individuals caught in our study exceeded the FishBase maximum values by 5 and 20 percentage points, respectively. The most frequent TL of *Clarias angolensis* varied between 16.5 and 23.5 cm with a median of 19.5 cm while the corresponding values for the *Raiamas christyi* were 11.5–19.0 with a median of 15.6 cm. *Pollimyrus tumifrons* (Boulenger, 1902) in Bongo had several specimens with TL larger than the max TL listed in FishBase. The large data set of this study is probably the reason for finding large specimens of species that were not usually so well studied.

Tolerance of acidity. The majority of fish thrive at a narrow range of a near neutral pH (Kwong et al. 2014). As fish are sensitive to low pH which affects their survival and reproduction (Kwong et al. 2014), it is remarkable that a majority of the captured species were found in water with a pH between 5.0 and 5.5 (Table 7). There are, however, other areas in the central Congo basin with fish studies in highly acid waters. In three rivers of Salonga National Park in the Equateur Province, pH values of 4.8 and 4.9 were recorded when fish were caught at 15 sites (Monsembula Iyaba and Stiassny 2013). Nineteen of the species found in our three streams were also present in the Salonga waters. Sometimes these fish were just found at single sites in Salonga, but *Bryconaethiops boulengeri*, *Mesoborus crocodilus* Pellegrin, 1900, *Schilbe marmoratus*, and *Hemichromis elongatus* had a wider regional occurrence. In recent studies of Lake Tumba, where the median pH of the water was 4.3, reported species that were also found in our study were *Mormyrops anguilloides* and *Clarias angolensis* (see Zanga et al. 2019). This indicates a high tolerance to the low pH of these species. Taken together with the findings in our study, we suggest that the minimum pH listed in FishBase (Froese and Pauly 2021) needs to be adjusted for some species from this region where brown, acid waters are so common.

Fish biomass aspects. Three earlier publications from Africa with areal fish biomass data were found (Loubens 1969, 1970; Kapetsky unpublished*). However, those dealt with relatively large rivers and seasonally flooded ones (Kafue River and a tributary to Lake Chad). Therefore, we compared our data with some tropical streams from South America. These originate from Brazil (two catchments), Venezuela, and Ecuador where the Ecuadorian streams are defined as headwaters (Angermeier and Karr 1983; Penczak and Lasso 1991; Agostinho and Penczak 1995; Bojsen and Barriga 2002). These streams were situated in forested landscapes with stream widths and depths similar to those of the streams in our study. Biomass values in the South American streams varied from 0.5 to 1.9 $g \cdot m^{-2}$ in streams of central Panama, from 1.5 to 17.9 $g \cdot m^{-2}$ in Venezuela, 2.0–8.3 $g \cdot m^{-2}$ in small tributaries of the Paraná River, Brazil, 1–10 $g \cdot m^{-2}$ in the Ecuadorian Amazon, and 13.4–63 $g \cdot m^{-2}$ in a stream in Brazil. Median values for these studies varied between 1.5 and 25 $g \cdot m^{-2}$. The biomass values from the three investigated streams in our study (Table 9, median 0.14 $g \cdot m^{-2}$) were thus considerably lower than those from these South American streams.

One cause of lower biomass in our study is the lack of small specimens in the catch. Da Silva Gonçalves and de Souza Braga (2012) published a table relating the weight of caught species and SL. Based on this study we calculate that we may have missed 70% of fish biomass. That would raise the median biomass from 0.14 to 0.20 $g \cdot m^{-2}$. But this only explains a minor part of the difference. An important feature of all the South American streams, in addition to a different fish fauna, was a circumneutral pH and generally less colored water. Most likely the low pH values of our study streams affect the fish especially when it comes to species presence and physiological responses to a low pH. A secondary effect may be the brown-colored, nutrient-poor water (cf. Table 1). Such dark water affects the food chain and especially prevents the development of phytoplankton, periphyton, and submerged macrophytes, i.e., primary production in the water is reduced due to the

* Kapetsky JM (1974) Growth, mortality and production of five fish species of the Kafue River floodplain, Zambia. PhD dissertation, University of Michigan, 194 pp.

low light conditions (e.g., Sanches et al. 2011). Several of the dominant species, such as *Clarias angolensis* and *Enteromius holotaenia* caught in the study streams, feed on aquatic insects, shrimps, and fishes (Froese and Pauly 2021). As the streams in our study have low to very low pH and were often strongly colored, the constraints on fish biomass will be considerable, in comparison to the South American streams.

Only one previous study of the fish biomass for African headwaters has been found. Malaisse (1976) reported values of 1.3, 26.1, and 31.7 kg · km^{-1} (i.e., not per area) in the reaches of a tributary to the Kwa River (Welcomme and de Merona 1988). A comparable median value for the presently reported study would be 1.1 kg · km^{-1} based on all streams and years. This value is similar in magnitude to that from the most upstream stretch in Malaisse's study, 1.3 kg · km^{-1}. A biomass value for a stream distance is, of course, influenced by the stream width, which was not included in Welcomme and de Merona (1988). Since we have not found a study with a similar design as ours for African headwaters, it is, therefore, possible that the biomass data presented in our study are unique for African headwaters.

Overfishing risk. Overfishing could be a major threat to the sustainability of continued fishing of the fish populations (Brummett et al. 2011). This would result in reduced catches and changes in fish size and relative abundance. Over the course of our study, no sign of overfishing in the streams could be discerned since there were no statistically significant changes in fish size (TL) or relative abundance over time. If a fish gear discriminates on the basis of size, this could lead to a pronounced decrease in the abundance of some species. The fishing gear used by local people such as plaited basket dips (ecopage) and poisons are not likely to be size discriminating. Our study was, however, not designed to detect the effects of earlier overfishing, for example, species already lost.

Welcomme (1976) attempted to evaluate the importance of small rivers (first order streams) and estimated those with a mean length of 1.6 km to have a mean fish yield of 8 kg · $year^{-1}$. Recalculated for the stream's length in this study, the yield would be 9 kg · $year^{-1}$. Annual fish catches in our study were well below this value in Bambou and Lebomo (4.4 and 5.7 kg · $year^{-1}$, respectively), but slightly higher in Bongo (11.5 kg · $year^{-1}$). This result together with no signs of reductions in catches between the years indicates that the streams were not severely overfished during the study period. No information was available about the local people's fishery, but due to an increasing population, this risk is likely to increase. Any effect of the research fishing during the study period was most likely temporary. The finding of species with larger TL than previously reported also suggests that overfishing is not yet an issue.

Conclusions

This study presents a comprehensive investigation of the fish community composition for several years in three headwater streams in the Congo basin drainage area. Alestids, cyprinids, clariids, and mormyrids were the most common fish families and, in total, 50 species representing 15 families were found. The reason for the low richness compared to other tributaries is most probably because they are small headwater streams. Ten species were found in lower pH waters than those reported in FishBase (Froese and Pauly 2021), and for 18 species we provide the first information on the lowest tolerated pH found. For several species, the lowest end of the pH range should be revised to be as low as 5–5.5. From the LTL area, where ichthyological information has been limited, we now have the first estimates of fish biomass in headwater streams ranging from 0.05 to 0.7 g · m^{-2} with a median of 0.14 g · m^{-2}. This relatively low value is probably caused by the extremely acidic and humic water. We did not find evidence of overfishing despite the local residents having their main protein source from local fish. Fish were in some cases larger than previously reported which also suggests overfishing not to be as devastating (yet) as might have been feared. Fish monitoring is proposed as an integral part of effective fisheries management especially when local fish are an important food resource. To be successful, such a project should involve representatives from local communities for which sustainable fishing is important.

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