The diversity and dry season habitat associations of fish communities in the Kabompo River Basin, Upper Zambezi, Zambia

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Abstract

The Zambezian headwaters contain diverse fish communities which support thriving fisheries. This region and its fishes are under pressure from multiple anthropogenic threats, including overexploitation and large-scale developments with potential knock-on effects for the riparian communities. Previous studies have focused on known fisheries areas and the mainstem Zambezi River, neglecting large tributaries such as the Kabompo River. Consequently, little literature is available on the diversity and ecology of the fishes that inhabit these large tributaries, hindering the effective management and protection of biodiversity. This study aimed to fill the current knowledge gaps in the diversity and habitat associations of fish communities in the Upper Zambezi, using the Kabompo River as a case study. The first objective was to provide an updated checklist of the fishes of the Kabompo River basin using a compilation of historical data and field surveys. This study detailed the occurrence and distribution of 83 fish species within the Kabompo River basin. All these species have been recorded in the Upper Zambezi, with some of their ranges extending into the Middle (29 species) and Lower Zambezi (23 species) while others have more restricted distributions. The most diverse families were the Cyprinidae (26 species) and the Cichlidae (15 species). A number of potential undescribed species, whose taxonomic distinctiveness need further investigation were also collected. Taxonomic conflicts are also highlighted for some of the taxa that were previously considered to have broad geographic ranges or disjunct distributions. Consistent with findings from other studies within the region, the current taxonomy underestimates the diversity of fishes in the Kabompo River and Upper Zambezi. The second objective was to assess the habitat use of small-bodied fish communities during the low-flow period in 2019. Reconnaissance trips identified dominant mesohabitats along the middle Kabompo River around Jivundu. A total of 139 mesohabitats were sampled across the five dominant mesohabitats identified; *Phragmites mauritianus*, wood, rock, *Vallisneria aethiopica* and bare substrate. Catch per unit effort, species richness, Shannon diversity and Pielou's evenness differed significantly between these mesohabitats. Twenty-six species showed significant associations ($p < 0.05$) with a specific mesohabitat type or environmental variable (current velocity or depth). Eight species were associated with the woody habitat, with three of these, *E. radiatus*, *E. unitaeniatus*, and *P. ngamensis* being almost exclusively associated with this habitat. *Enteromius kerstenii, E. lineomaculatus* and *S. depressirostris* were almost exclusively associated with *P. mauritianus* and represent potential indicator species for this habitat. A number of species were also with both *P. mauritianus* and woody habitats. Nine species showed statistically significant associations with the rocky mesohabitat, with *Amphilius uranoscopus* and *Petrocephalus longicapitis*, being almost exclusive to rocky sections of the river. Therefore, species such as *A. uranoscopus* are potential indicators for monitoring the integrity of rocky habitats under threat from sedimentation. The strong associations indicate that this comprehensive baseline may be valuable indicators/ proxies for identifying anthropogenic induced change in the Kabompo basin. This would provide a basis to determine fish responses to regional environmental changes associated with human activities.

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Chapter 1: General introduction

Introduction

The Zambezi River system has a complex geomorphological history that has resulted in diverse fish faunas of distinctly separate origins occurring in different sections of the river system (Timberlake, 2000; Moore and Larkin, 2001; Moore *et al.*, 2007; Moore *et al.*, 2012). This system is divided into three regions (Upper, Middle and Lower) based on geomorphological characteristics and the existence of unique fish fauna (Wellington, 1955). The Victoria Falls mark the lower limit of the Upper Zambezi, the Middle Zambezi extends from the Victoria Falls to the lower end of Cahora Bassa Gorge, which marks the upper limit of the Lower Zambezi (Wellington, 1955) (Figure 1). The Middle Zambezi contains two large hydroelectric dams, Lake Kariba and Lake Cahora Bassa, which both support large-scale commercial fisheries (Tweddle, 2010).

Communities along the river's 2575 km course are directly dependent on this system for water, fishing, floodplain agriculture, and the river has important cultural significance. Small-scale fisheries significantly contribute to food and nutrition security for many vulnerable communities who exploit this resource through traditional and modern fishing methods (Tweddle *et al.,* 2004; Béné and Heck, 2005). Fish further provide an additional source of income, as they are sold in local markets or to neighbouring countries (Welcomme, 2011). There are, however, growing concerns because these resources are threatened by overexploitation and planned large-scale industrial developments, particularly in the Upper Zambezi (Tweddle, 2010; Weyl *et al.,* 2010). Studies have documented severe declines in catch rates and loss of larger and more vulnerable species due to a combination of factors, particularly increasing fishing effort, use of more efficient and destructive fishing gears, pollution, habitat destruction and excessive water abstraction (Peel *et al.,* 2014; Tweddle *et al.,* 2015). The process of fishing down the food chain and degradation in the system places biodiversity at significant risk, with profound cascading implications. Studies in other tropical systems have documented the role of diverse fish communities and rare species in maintaining ecosystem function through increasing functional diversity (Mouillot *et al.,* 2013; Leitão *et al.,* 2016). However, for many regions in southern Africa, and the Upper Zambezi in particular, effective management and biodiversity conservation is compromised by limited knowledge of the ecology of these systems.

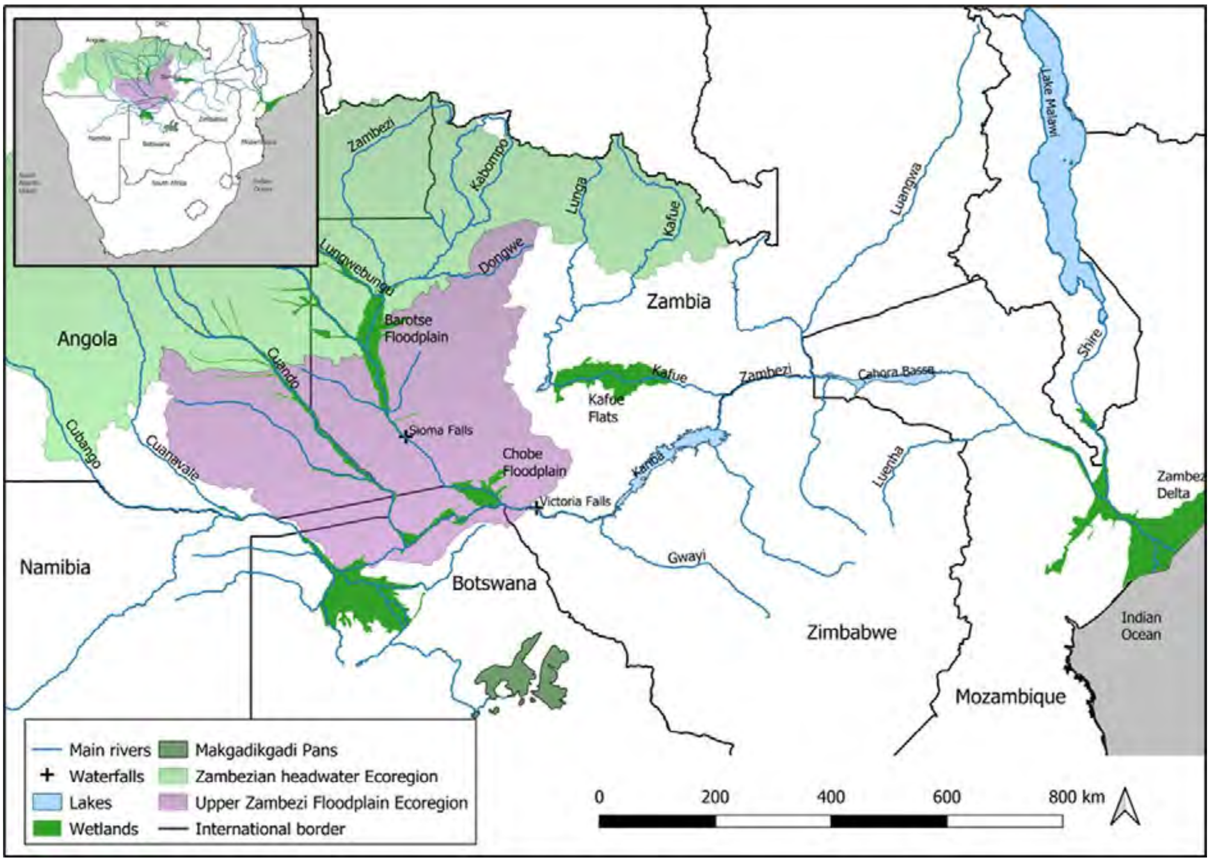

Figure 1: The Zambezi River and its major tributaries showing the location of prominent features that divide the system.

There are growing concerns on the potential impacts of ongoing and planned developments in the upper catchments of the Kabompo River, one of the most important headwater tributaries of the Upper Zambezi. The relative paucity of specific information to inform conservation and management of the Zambezi headwaters motivated the undertaking of this study. The aim was to document the diversity and provide preliminary insights into the ecology of the fishes of this river. There is a general increase in demand for natural resources by local communities accompanied by urbanisation and industrialisation that contribute to rapid deforestation in the Kabompo catchment (Vinya *et al.,* 2011). The current and future largescale mining and damming pose a threat to the Kabompo River (Maybeck, 2001; Vinya *et al.,* 2011). This study provides baseline information on the diversity of the fish communities in the Kabompo River basin and documents low flow habitat associations of species in selected wadeable habitats. This information will form the basis for future monitoring of biodiversity trends and identify fish responses to global environmental changes associated with human activities. This will help to inform evidence-based natural resource management practices used to manage and mitigate these threats.

Study area

With a catchment area of 72 140 km^2, the Kabompo River is one of the prominent tributaries of the Upper Zambezi River. The Kabompo River is fed from the Kalahari Sand formation, which is the primary regional aquifer in northwestern Zambia (Tweddle 2010). The river originates from a marsh on the watershed near the Zambian border with the Democratic Republic of the Congo (Cochran-Patrick, 1928) (Figure 2). The headwater sections of this river above Kabompo Gorge has fast-flowing waters and coarse substrates (Figure 3A). The riparian forests in this section are relatively intact (Fanshawe, 2010), and they contribute considerable amounts of organic matter input into the river. The Kabompo Gorge represents a potential barrier to the longitudinal migration of fish species. In sections, the Gorge comprises massive boulders, and during the dry season, it is completely dry in areas (Melland, 1919). A 35 km^2 hydroelectric dam is under construction in the Kabompo Gorge to generate electricity for remote communities. However, this project has been temporarily halted (Copperbelt Energy Corporation annual general meeting transcript, 2021).

Below the Gorge, the river gradually widens before flowing into the first large floodplain near Ntambu (Figure 3B). Wooded vegetation predominantly lines the river between the Gorge and the Ntambu Floodplains, however, it is less dense than in the upper reaches and is surrounded by seasonal inundated riverine grassland (Fanshawe, 2010). The Ntambu Floodplains begin to form near the confluence of the Chisola River with the Kabompo and stretch downstream for approximately 50 kilometres and reaching 2 kilometres wide in places.

These floodplains are grass-dominated with numerous dambos and pools. The Ntambu Floodplain represents an important area for local communities that use the plains for agricultural and fisheries activities. The integrity of the floodplains is threatened by these practices and mining operations located in the headwaters of the Musangezhi River. This mining operation involved the damming of the Musangezhi River and the adjacent Chisola River. These dams alter flows and trap sediment/nutrients (Winton *et al.*, 2019), while mining operations likely cause increased sediment loading and heavy metal pollution, as seen from similar mining operations in the Kafue catchment (Mbewe *et al.*, 2016).

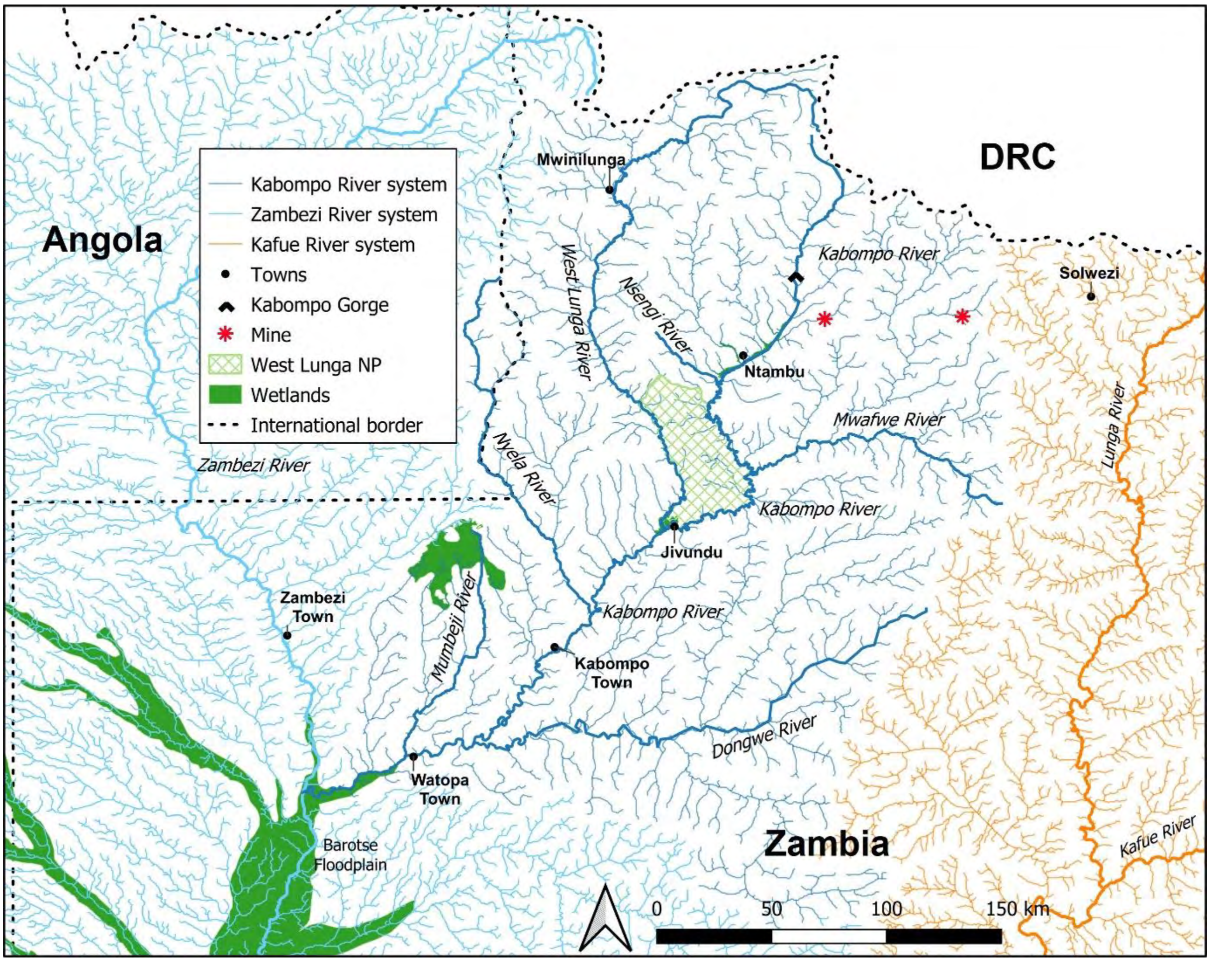

Figure 2: Overview of the Kabompo River in relation to neighbouring rivers indicating major tributaries and settlements.

By the time the Kabompo River forms the eastern boundary of the West Lunga National Park, it is 60 metres wide and starts to flow south-easterly (Figure 3C). The river is convoluted and characterised by deep, slow-flowing, Kalahari sand dominated stretches interrupted by shallow gravel patches and rocky outcrops (Figure 3D). Woody debris (e.g., logs and trees) deposited during the flood season and *Vallisneria aethiopica* beds provide instream structure for fishes in an otherwise featureless environment. The marginal vegetation in the middle sections consists of thin belts of riparian forest interrupted by *Phragmites* reeds (Fanshawe, 2010).

The West Lunga National Park represents the single area of direct protection for fishes, with fishing in and along the park side of the river prohibited and monitored by the Park authorities. The park's centre consists of extensive seasonal floodplains surrounded by Miombo and *Cryptosepalum* dry evergreen forests, representing the largest evergreen forest in Africa outside of the equatorial region (McIntyre, 2016) (Figure 3E). In the lower southwestern corner of the park adjacent to the settlement of Jivundu, extensive floodplain grassland with sections of floating vegetation extend to the north and west, towards the confluence of the West Lunga River. In the lower sections, the West Lunga River is more densely forested along the river than the Kabompo in the middle sections (Figure 3F). Numerous large tributaries join the Kabompo River below the West Lunga. These tributaries increase the river's flow and width, while the instream habitats are similar to those around Jivundu. In the lower river reaches, the wooded marginal zone decreases, with *Phragmites* reeds and other small macrophytes dominating the margins (Figure 3G and H). The floodplain sections such as those near Ntambu and in the West Lunga National Park are essential habitats for numerous species of fish during the high-water season. Once the floods recede, fish retreat to the marginal and instream habitats of the mainstem.

Kabompo and Manyinga town are two of the largest urban settlements along the river, but many small towns and villages are scattered throughout the landscape. These communities engage in various land use activities that include crop and livestock production, timber extraction, and harvesting of other natural resources for income and livelihoods. These activities are mainly concentrated along the main roads and in and around floodplain reaches.

Climate

This region has three distinct seasons, i) dry and cool (April to July), ii) dry and hot (August to October), and iii) wet and hot (November to March) (Gumindoga et al., 2020). The mean annual precipitation for the basin ranges from 900 to 1500 mm/year in a south to north gradient with a mean of 1200 mm/year (Gumindoga et al., 2020). The mean temperatures at a basin scale range from 14 °C in the dry and cool season, to 22 °C in the hot and wet season (Mwansa 2018).

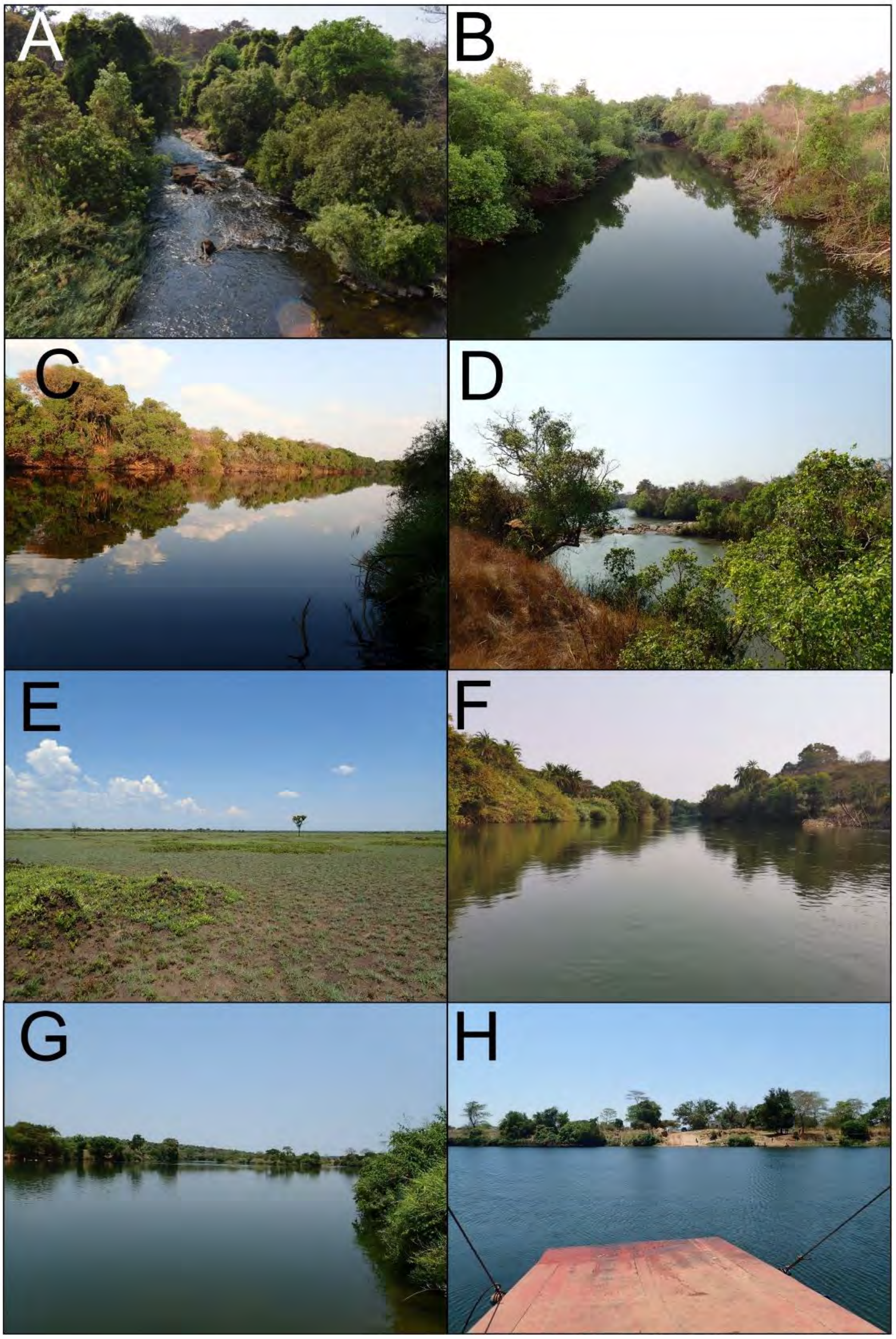

Figure 3: The diversity of habitats along the course of the Kabompo River: (A) forested headwater reaches with characteristic rocky substrates and high current velocity, (B) Kabompo River above the Ntambu floodplain showing the slow-flowing sections lined with riparian forest and grassland floodplains, (C) Kabompo River near Jivundu with riparian forest and Phragmites reeds, (D) rocky outcrops in the main channel interrupting the slow-flowing sections, (E) grass floodplains in the centre of the West Lunga National Park, (F) lower sections of the West Lunga lined with woody riparian vegetation, (G) wide slow flowing section of the river near Kabompo Town, (H) wide slow flowing section of the lower Kabompo near Watopa.

Threats to aquatic biodiversity

Overexploitation

Similar to many inland fisheries globally (Welcomme, 2011), the Zambezi fisheries are classified as overfished (Weyl *et al.*, 2010). Overexploitation has resulted in the Upper Zambezi fisheries experiencing a shift in target species as catch rates are declining and catch compositions are shifting from larger valuable species to smaller, less valuable species (Peel *et al.*, 2014; Tweddle *et al.*, 2015). Within the Kabompo River, harvesting is predominantly at subsistence level and less intense than in the Barotse Floodplain and Zambezi Region (former Caprivi Region) of the Upper Zambezi. However, more intense harvesting occurs around large settlements and extensive floodplains. The continued use of unsustainable practices (e.g., excessive gill netting, drift netting, and mosquito seine nets) exploiting all size classes and species indiscriminately with high efficiency will lead to further unsustainable harvest and local species decline (Pelicice *et al.*, 2017).

Habitat degradation and habitat loss

Habitat degradation is one of the major threats and causes of freshwater biodiversity loss globally (Arthington *et al.*, 2016). Destructive agricultural practices and resource use pose the greatest risk to the critical aquatic habitats of the Kabompo River. While the impacts of other threats are documented in the Upper Zambezi, the effects of habitat loss and degradation at a species level are not well known. In the Kabompo catchment, mining, logging of high-value timber species, and bush clearing for agriculture practices or charcoal production are causing extensive areas to be transformed. These land-use activities may lead to sedimentation and increased turbidity (Walling and Fang, 2003). Increased sediment loading can potentially lead to the smothering of rocky habitats, and thus represents a major threat to rheophilic and lithophilic species. Loss of the woody riparian vegetation affects the input of allochthonous material and could also alter the temperature regimes, particularly in the upper reaches (Pusey and Arthington, 2003). Degradation of floodplains alters the critical spawning and feeding habitat exploited by the fish during the high flow period (Welcomme, 2008). These impacts have significant implications for species and ecosystem functioning (Brejão *et al.*, 2018).

Impoundments and abstraction

The annual flood cycle is hypothesised to represent the driving force behind the ecological functioning of floodplain rivers like the Upper Zambezi and Kabompo (Junk *et al.*, 1989; Taylor *et al.*, 2017). Flow regime modification through intense water abstraction and dam construction represents a major threat to fish communities of large tropical floodplain rivers (Agostinho *et al.*, 2004; Dudgeon *et al.*, 2006). Several small impoundments have been constructed in the Kabompo River catchment along the upper and middle Kabompo, West Lunga and Dongwe rivers (Lehner *et al.*, 2021). Dams in the Musangezhi and Chisola rivers were constructed to provide water for the mining operations at the First Quantum Limited Trident Mining Project (AES, 2019). A small hydroelectric dam is under construction along the Kansanjiku River as part of the Rural Electrification Program by the Government of the Republic of Zambia (AES, 2019). Although there are no large impoundments on the mainstem Kabompo at present, construction of a 35 km^2 hydroelectric dam at Kabompo Gorge has started, although it has been temporarily halted (Copperbelt Energy Corporation annual general meeting transcript, 2021). These impoundments influence the flow regimes of these tributaries and may affect the fisheries in the Kabompo River. Impoundments reduce flow with the potential to cause downstream sections to flow intermittently. The ecological impacts for fishes that prefer the lotic environment will be adverse, with the transformation to a lentic environment altering the species assemblage and causing localised extinctions, as reported from elsewhere (Kenmuir, 1984; Agostinho *et al.*, 2016). Dams also fragment species and form impassable barriers for species that undertake seasonal spawning migrations (van der Waal, 1996). There is also a risk that non-native species may be introduced into these impoundments for fisheries benefits, as has been generally the case across the region. Artificial impoundments have allowed proliferation and have acted as refugia and stepping stones to spread non-native species across southern Africa (Johnson *et al.*, 2008; Havel *et al.*, 2008; Havel *et al.*, 2015).

Non-native species

Biological invasions are a significant driver of the global decline in biodiversity across many ecological systems and taxonomic groups (Panlasigui *et al.*, 2018). The introduction of non-native species into the Zambezi is of major conservation concern. Non-natives can out-compete native species or alter the ecological balance of an area (Ellender and Weyl, 2014). Introduced species of significant concern include the Nile tilapia (*Oreochromis niloticus*) and the Australian redclaw crayfish (*Cherax quadricarinatus*), both of which are established in the

Upper Zambezi. These species were both introduced into the Upper Zambezi through escapes from aquaculture facilities or deliberate introductions for fisheries benefits (Tweddle, 2010; Madzivanzira *et al.*, 2020; Madzivanzira *et al.*, 2021a). The impacts of Nile tilapia include competition and hybridisation with native cichlid species (e.g., *O. andersonii* and *O. macrochir*), decreasing biological diversity, and may result in the local extinction of these species (Canonico *et al.*, 2005; Deines *et al.*, 2014). Nile tilapia are present within the Kabompo River basin, where they were first reported in 2010 (Tweddle, 2010), and confirmed in the present study. At present, *C. quadricarinatus* has not been reported from the Kabompo River despite being prevalent in the Barotse Floodplain, but their invasion of the Kabompo is inevitable (Madzivanzira *et al.*, 2021a). The threats possessed by the Australian redclaw crayfish include direct and indirect predation on native species through polytrophic generalist feeding, habitat modification and the loss of macrophytes (Madzivanzira *et al.*, 2020; Madzivanzira *et al.*, 2021b). Additionally, they pose a significant risk to local fisheries as they feed on gillnet catches, reducing the catch's marketability (Madzivanzira *et al.,* 2021c).

Epizootic ulcerative syndrome

Epizootic ulcerative syndrome (EUS) is a fungal disease caused by *Aphanomyces invadans*. The disease is characterised by body lesions, skin ulcerations and bloody patches on the body, causing high mortality rates (Iberahim *et al.*, 2018). The disease infects a wide range of freshwater and estuarine fish globally (Oidtmann *et al.*, 2008). In the Upper Zambezi, the disease was first reported in 2006 from fish caught in the Chobe and Zambezi rivers near the Chobe Game Reserve (Andrew *et al.*, 2008). Since then, the disease has been detected elsewhere across the region, including the Barotse Floodplains and in the Kabompo River (Choongo et al., 2009; Huchzermeyer and van der Waal, 2012). Epizootic ulcerative syndrome is known to infect at least 24 species from 15 genera in the Upper Zambezi (Huchzermeyer and van der Waal, 2012).

Thesis outline

As this thesis aims to contribute to the understanding of ichthyological biodiversity and the dry season habitat use of fish species in the Kabompo River basin, an initial step was to conduct a comprehensive literature review (Chapter 2). The review synthesised scientific and grey literature for the Kabompo River available in online repositories. The compilation of these data provided an updated checklist of fish species based on historical museum specimens catalogued in the NRF-South African Institute for Aquatic Biodiversity National Fish Collection and supplemented by new sampling in 2019. Species distributions and taxonomic groups of interest are comprehensively discussed across several families and genera. A low water mesohabitat use assessment was undertaken to contribute towards closing the knowledge gap of species ecology in the region (Chapter 3). Shallow water sections were surveyed in the middle Kabompo, focusing on five dominant mesohabitat types and identifying important habitats and potential indicator species of anthropogenic change. The main findings of these studies are synthesised in Chapter 4, and suggestions for future research are outlined.

Chapter 2: Diversity and distribution of freshwater fishes in the Kabompo catchment, Upper Zambezi

Introduction

Freshwater biodiversity is under significant threat (Tickner *et al.*, 2020), with freshwater fishes having the highest extinction rate among vertebrates (WWF, 2018). The Living Planet Index (LPI) shows an average decline of 84% (range 77% to 89%) for freshwater vertebrates since 1970 (Deinet *et al.*, 2020). During this period, freshwater fishes have experienced declines at twice the rate of marine and terrestrial vertebrates (WWF, 2018). In Southern Africa, an estimated 11.2% of freshwater fishes were classified as either Vulnerable, Endangered, or Critically Endangered in 2009 under the IUCN Red List of endangered species, with an additional 19.6% classified as data deficient (Tweddle *et al.*, 2009; IUCN, 2021). However, this represents an aggregation of evaluations from both well and poorly surveyed areas, potentially distorting the proportion of threat status for our region's fishes. Within southern Africa, a high proportion (70%) of fishes in the Cape Fold Ecoregion (CFE) are listed under highly threatened categories of the IUCN (i.e., Vulnerable, Endangered or Critically Endangered) (Tweddle et al., 2009; Weyl *et al.*, 2014; Chakona *et al.*, 2018b, IUCN, 2021). The CFE represents one of the most extensively surveyed areas in southern Africa (Ellender *et al.*, 2017). This sampling bias has uncovered unique assemblages of endemic stream fishes in the CFE (Ellender *et al.*, 2017). In contrast, many fishes in south-central Africa's tropical and sub-tropical river systems remain poorly explored. For example, fishes of the Upper Zambezi are predominantly (97%) listed as either Least Concern or Data Deficient (IUCN, 2021). This primarily reflects the poor systematic knowledge in the region, which hampers accurate mapping of the distribution ranges of fishes in tropical and sub-tropical river systems (Abell *et al.*, 2008; Tweddle *et al.*, 2009; Chakona *et al.*, 2018a).

Growing evidence, resulting from increased sampling effort and implementation of genetic techniques, is showing the existence of high levels of undocumented diversity within almost all the fishes studied thus far across many families and genera from southern Africa (Kramer *et al.*, 2003; Kramer and Van der Bank, 2011; Goodier *et al.*, 2011; Eccles *et al.*, 2011; Kramer *et al.*, 2012; Chakona and Swartz, 2013; Morris *et al.*, 2016; Riddin *et al.*, 2016; Chakona and Skelton, 2017; Chakona *et al.*, 2018; Chakona *et al.*, 2018b; Chakona *et al.*, 2020; Bragança *et al.*, 2020a; Bragança *et al.*, 2020b; Mazungula and Chakona, 2021; Bragança *et* *al.*, 2021; Mutizwa *et al.*, 2021; Kambikambi *et al.*, 2021). The discovery of narrow range endemic lineages and candidate species previously included under a single widespread species has considerable implications for conservation status assessments and the determination of appropriate management strategies to prevent biodiversity loss (Bickford *et al.*, 2007; Maldonado-Ocampo *et al.*, 2008). The development of species checklists based on the synthesis of all available information supplemented by targeted biodiversity surveys is a critical initial step towards addressing aspects of evolutionary biology, biodiversity research, management and conservation as it allows researchers to determine essential research needs for a region (Clemann *et al.*, 2014; Spier *et al.*, 2018; Reyserhove *et al.*, 2020).

Gap analysis for the Zambezi has identified ichthyological knowledge gaps for the large tributaries of this river. The Zambezi River system has a long history of ichthyological exploration that dates back more than 150 years beginning with Peters (1868,), but the 1960s to mid-1970s was the period of most active collections and surveys (Jackson, 1961a; Bell-Cross, 1965; Jubb and Gaigher, 1971; Bell-Cross, 1972). These collections formed the foundation of review articles and books for this region, notably Jackson (1986); Bell-Cross and Minshull (1988); Skelton (1993, 2001); Marshall (2000, 2011); Bills and Marshall (2004). Since the late 1990s, there has been a resurgence in biodiversity and ecological exploration in the Zambezi system, mainly driven by the need to improve ecological and taxonomic knowledge and fisheries management practices, with the main focal area targeting the Upper Zambezi and its major tributaries as well as the interlinking Okavango system (Tweddle *et al.*, 2003; Tweddle *et al.*, 2004; Bills *et al.*, 2012; Bills *et al.*, 2013). The increased interest was strongly supported by the development of genetic and molecular analyses, the technological development which rejuvenated systematic biology and turned even once thought well-studied regions from a biodiversity perspective into areas of new discovery (Skelton, 2016).

Historical collection records for specimens catalogued in the NRF-SAIAB National Fish Collection highlights the extent of previous sampling expeditions within the Upper Zambezi (Figure 4). Extensive work has been conducted in the Upper Zambezi, however, these surveys focussed on targeted regions depending on the specific focus of the researchers. Collections and studies have focused on the large floodplain reaches (e.g., the Barotse Floodplains and Chobe Floodplains) and the Zambezi Region (former Caprivi Region) in Namibia, while more broadscale studies incorporated collections or analyses from multiple sections of the Upper Zambezi (Figure 4). The focus of these surveys in target areas has left sampling gaps in the large tributaries like the Kabompo and Luanginga rivers. From an ichthyological perspective, sampling gaps such as those on large tributaries of the Upper Zambezi occur throughout the Zambezi basin, with scientific literature for some of the largest tributaries isolated to a few locations. The most notable contribution for sampling large tributaries in the Upper Zambezi was during the African Wildlife Foundation (AWF) Four Corners Project (Tweddle *et al.*, 2004), which surveyed a broad area, including the Kabompo and some tributaries of the Middle Zambezi.

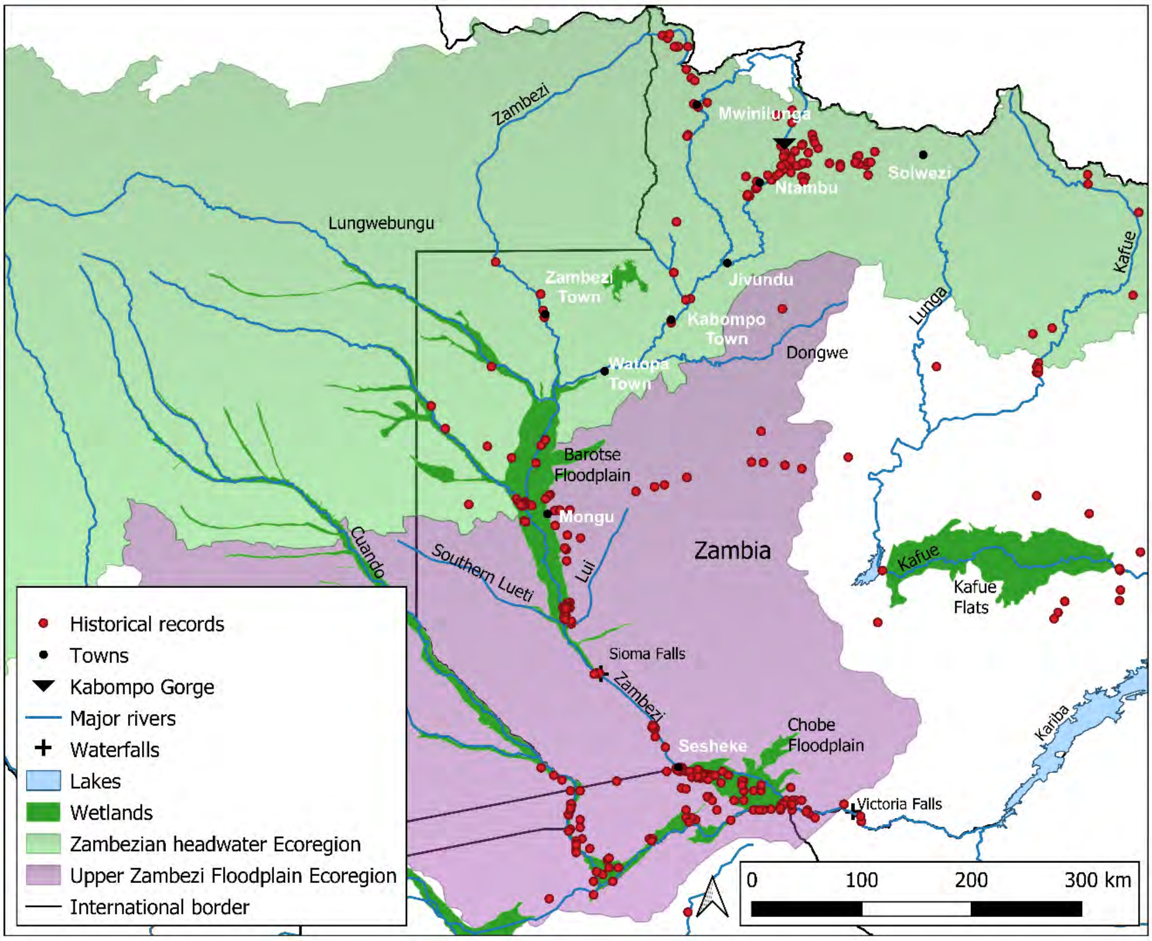

Figure 4: Location of historical sample localities in the Upper Zambezi for specimens catalogued at the NRF-SAIAB National Fish Collection.

Attempting to fill information gaps for a large geographic area is difficult due to financial, logistical and travel constraints associated with sampling vast, remote areas. The present study represents the first phase of a more coordinated approach to document the diversity and distribution patterns of fishes of the Zambezi. This chapter aims to synthesise the available information for the Upper Zambezi, with emphasis on the Kabompo River. Based on previous surveys and targeted sampling to fill sampling gaps in the middle Kabompo and West Lunga, an updated checklist of the fishes of this river is provided, and species distributions in the Kabompo are discussed. Potential taxonomic discrepancies and anomalies are highlighted based on colour patterns, distribution patterns of some species and outcomes of current literature in the region.

Methods

Literature analysis

The review of current literature for the Upper Zambezi was conducted following the guidelines for Preferred Reporting Items for Systematic reviews and Meta-Analyses (Moher *et al.*, 2009). The search protocol was undertaken using both the SCOPUS database and the Institute of Scientific Information (ISI; Thomson Reuters) Web of Science online database. The search criteria "Zambezi River"* AND "Fish"* was used to search these databases for English literature containing relevant information on the biodiversity and ecology of freshwater fishes and fisheries of the Upper Zambezi River. The literature search for the Kabompo River used the initial search criteria "Kabompo River"* AND "Fish"*, but due to the lack of literature, an additional search of "Kabompo" was conducted for specific literature regarding the Kabompo River. Each publication returned in the searches was assessed to determine its contribution of information to the review. Publications not obviously related to the topic of the study were rejected based on their title, abstract or after reading the text. Once the article selected by the inclusion criteria were examined, the reference lists of these articles were inspected to check for any additional relevant published articles and grey literature. Additional, grey literature was accessed by emailing the respective authors or targeted searches on Google Scholar and organisations websites. Masters and Doctoral theses were sourced from the South East Academic Libraries System (SEALS) Digital Commons (http://vital.seals.ac.za). The dominant grey literature examined were project reports and environmental impact assessments (EIA's). All included articles were classified by their geographical area and research focus under the following headings: i) fisheries, ii) biodiversity, iii) ecology, iv) threats/impacts and v) conservation. Numerous articles addressed several of these topics, and a single article may be categorised under more than one topic. A schematic diagram of the article selection process and the relevant research classified under the broader topics is presented below (Figure 5).

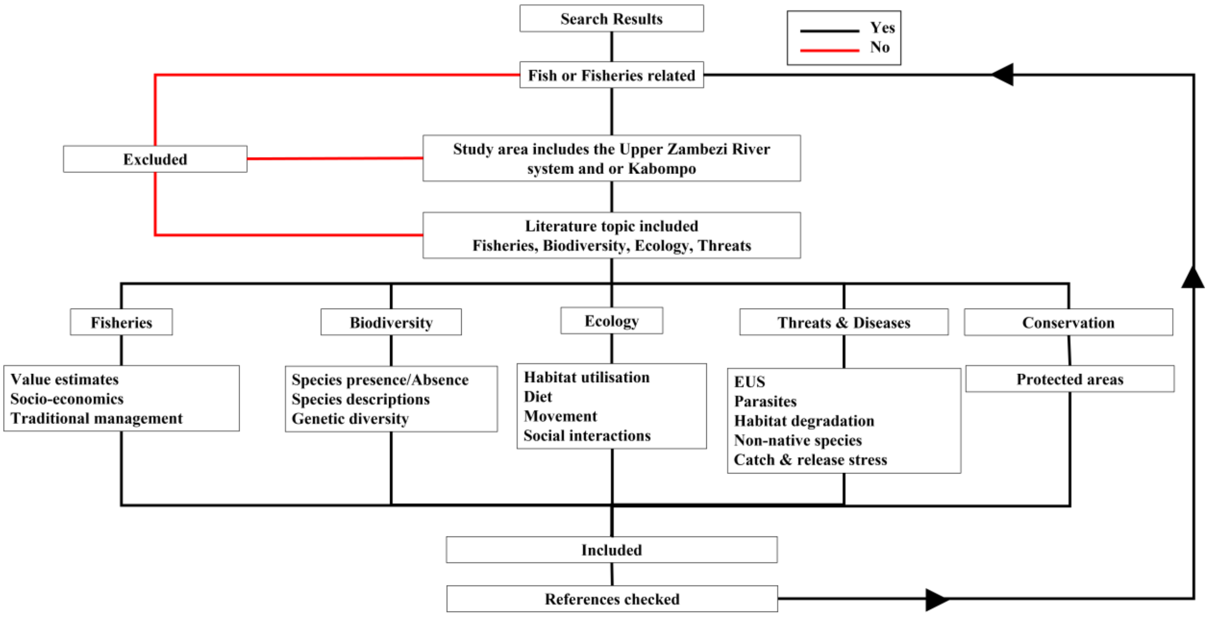

Figure 5: Schematic of the literature assessment process based on the PRISMA by (Moher *et al.,* 2009).

Data collection

As the Kabompo River was the target area for the present research, historical sampling records and species accounts for specimens accessioned in the National Research Foundation-South African Institute for Aquatic Biodiversity (NRF-SAIAB) National Fish Collection database occurring in the Kabompo River were obtained from the records available on GBIF (https://www.gbif.org). The National Fish Collection at NRF-SAIAB represents the largest fish collection in Africa and a key repository. There are 908 historical fish records in the NRF-SAIAB repository for the Kabompo River basin. These records are from 107 sampling sites and they date from 1983 to 2013. Species names listed in the NRF-SAIAB database were updated based on valid species names listed in Eschmeyer's Catalogue of Fishes (Fricke *et al.*, 2020) and the most recent available literature.

To supplement historical records and begin to fill in knowledge gaps, the present study sampled the Kabompo River in three sections (upper, middle, lower) during the dry season (September to November) of 2019. The upper section was located above Kabompo Gorge at the T5 road bridge (one site), the middle section was sampled at Ntambu and Jivundu (five and seven sites respectively). The lower section of the Kabompo comprised largely of deep, slow-flowing sections and therefore, the lower section was only sampled at a set of rapids upstream from Watopa pontoon (one site). In the West Lunga River, sampling occurred in the upper section near Mwinilunga Town. The lower section consisted of three shallow sections upstream from the confluence with the Kabompo River. The location and the description of sample sites are available in Appendix 1 Table A1. Ethical approval was granted by the Rhodes University Ethics committee (2019-0270-2016), and research permits were obtained from the Zambian Department of Fisheries.

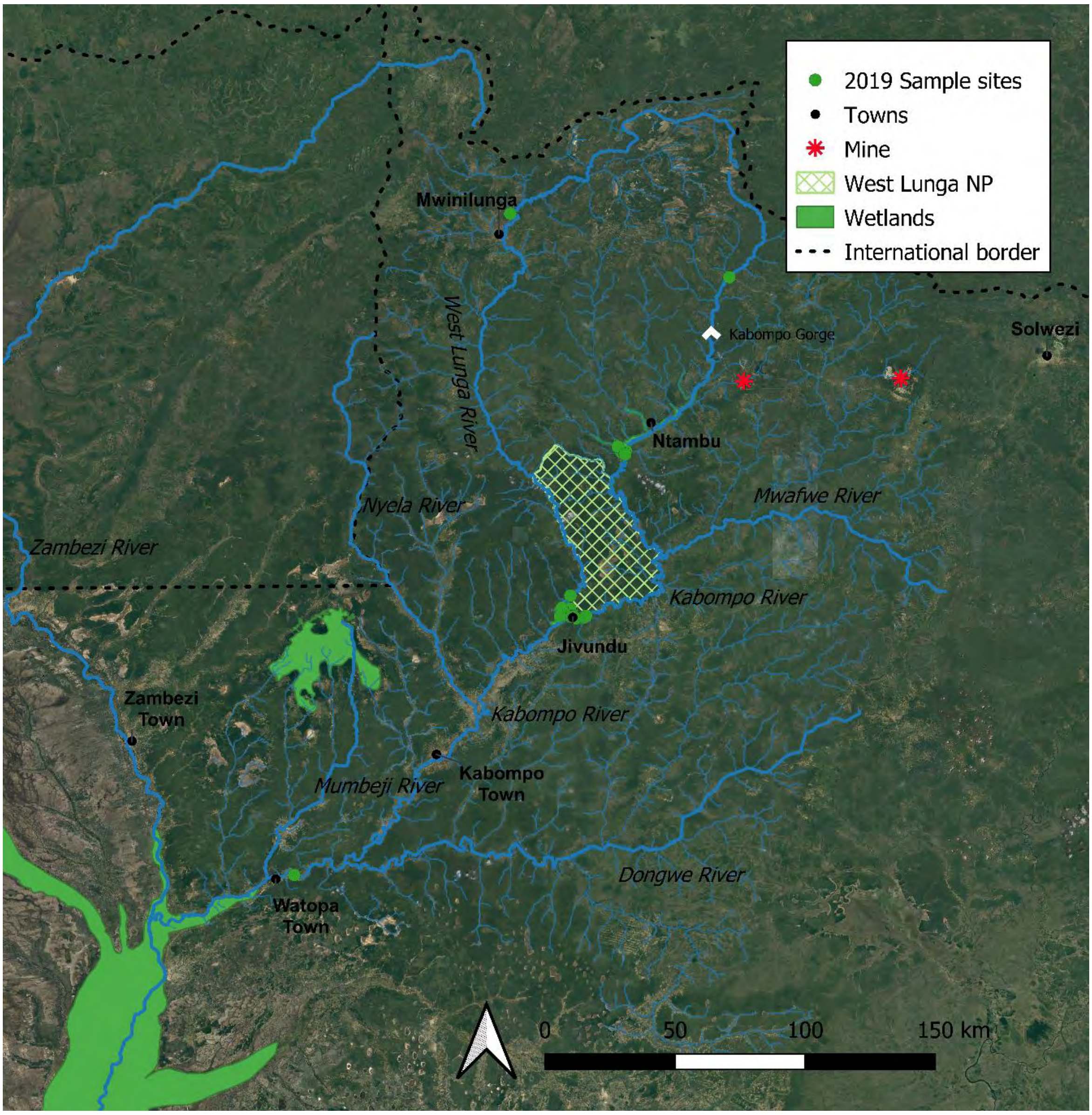

Figure 6: Distribution of the 2019 low water sample sites in the Kabompo and its tributaries.

Reconnaissance trips were made by boat along the Kabompo and West Lunga rivers to identify shallow areas (< 1 metre deep) that were wadeable and accessible for electrofishing and netting with a D-frame net. Due to the abundance of large Nile crocodiles (*Crocodylus niloticus*) and hippopotamus (*Hippopotamus amphibius*) safety concerns restricted sampling to safely wadable sections. Sites were selected to represent a variety of habitats present during the low water period. The predominant habitats during this period were riffles, backwaters, shallow main channel margins and side channels.

Four main sampling methods were used based on the habitat type. Electrofishing was the best-suited method and was conducted in a two-person team. One person operated a SAMIS 725M 12V DC backpack electrofisher (Frequency: 50-80 Hz; Duration: 30- 300 microseconds), and the secondary catcher downstream of the sampling area with a large D-framed net (70 cm x 80cm) to collect any stunned fish not collected in the electrofishing net. Electrofishing was conducted in a wide range of habitats, but area and time fished were not recorded, as the objective was to sample as many species as possible. A D-framed net (70 cm x 80cm) was used to sample areas with thick vegetation (e.g., lilypad beds) and was thrust into the sample area 3 to 5 times. Angling was used for sampling the deeper mainstem sections, targeting the larger predatory fish species such a tigerfish (*Hydrocynus vittatus*) and large catfish (*Clarias* spp.) using artificial lures or chicken liver as bait. Additional samples were bought from local fishers if they represented species not collected using the methods above.

Specimen collection, care and curation

Fish collected were placed into 20-litre buckets that contained fresh river water and were kept in the shade. The water in the buckets was replaced with clean river water at regular intervals to keep it fresh. The samples were immediately processed on-site. A subsample of specimens representing all the species sampled at each site was selected and retained as voucher specimens, and for genetic collections, the rest of the fishes were released alive. Fish were identified to species level based on the available keys and best available literature (Skelton, 2001; Bruwer and van der Bank, 2003; Tweddle et al., 2004; Tweddle et al., 2012).

Fish retained as voucher specimens and for genetic collections were euthanised with an overdose of clove oil and photographed to document the live colour pattern. A small piece of muscle tissue was then dissected from the right side of each specimen, and the tissue sample was immediately stored in an Eppendorf tube containing 95% ethanol (Chakona and Skelton, 2017). Tissue samples were stored in a freezer in the field and deposited in the National Biomaterials Bank at the South African Institute for Aquatic Biodiversity (SAIAB). Voucher specimens were fixed in 10% formalin in the field, and once in the laboratory, specimens were transferred through an alcohol gradient of 10% and 50% (to wash out the formalin) and then transferred to 70% for long-term storage (Chakona and Skelton, 2017).

Data analysis

Species occurrence data were summarised based on historical occurrence records from NRF-SAIAB and collections from the present study to indicate species presence in the Kabompo River basin. For each species, the distribution range within the Kabompo River was mapped and listed as occurring above or below the Kabompo Gorge. Species distributions were further noted whether they occurred within the three sections (upper, middle, lower) of the Zambezi system. Wide-ranging taxa that occur in neighbouring systems to the Zambezi and other river systems in Africa were noted. Only species presence within the mainstem Kabompo River are listed as above or below the Kabompo Gorge in the table. Species present in tributaries but not recorded in the mainstem Kabompo are noted and discussed where relevant. Historical collection sites were classified by stream order according to the Strahler stream order methods to identify which stream orders were priorities during historical surveys. Sites were classified by stream order to identify sampling gaps. Sampling sites were categorised based on the streams order classification available in the Hydrosheds database (https://hydrosheds.org) (Linke *et al.*, 2019).

Results

Literature analysis

The search results presented below are based on the total number of articles found in the ISI Web of Science and Scopus databases that match the inclusion criteria and additional publications obtained from the selected publications' reference lists. The search results for "Zambezi River"* AND "Fish"* on the Web of Science database yielded 102 articles, of which 73 matched the inclusion criteria. The exact search on the SCOPUS databases retrieved 162 results, most of which were recovered from the Web of Science search. An evaluation of these articles yielded an additional 26 papers. The reference list of initial search articles contributed an additional 66 articles, and grey literature contributed a further 17 articles. Related articles retrieved through Google Scholar not recovered from the initial search or reference lists contributed 17 publications. Fifteen articles were retrieved directly from authors while three theses were retrieved from SEALS. In total, 200 fish or fisheries-related articles that matched the inclusion criteria were retrieved for the Zambezi basin. One hundred and forty-nine articles (75%) are directly related to the Upper Zambezi or part of a broadscale study that included the Middle and/or Lower Zambezi or neighbouring systems (Figure 7). These broadscale studies accounted for 29% of the available literature for the Upper Zambezi, with these broad articles focusing on species biodiversity and ecology. Historical publication records remained steady from 1960 to 1990 before picking up steeply from 1991 to 2020.

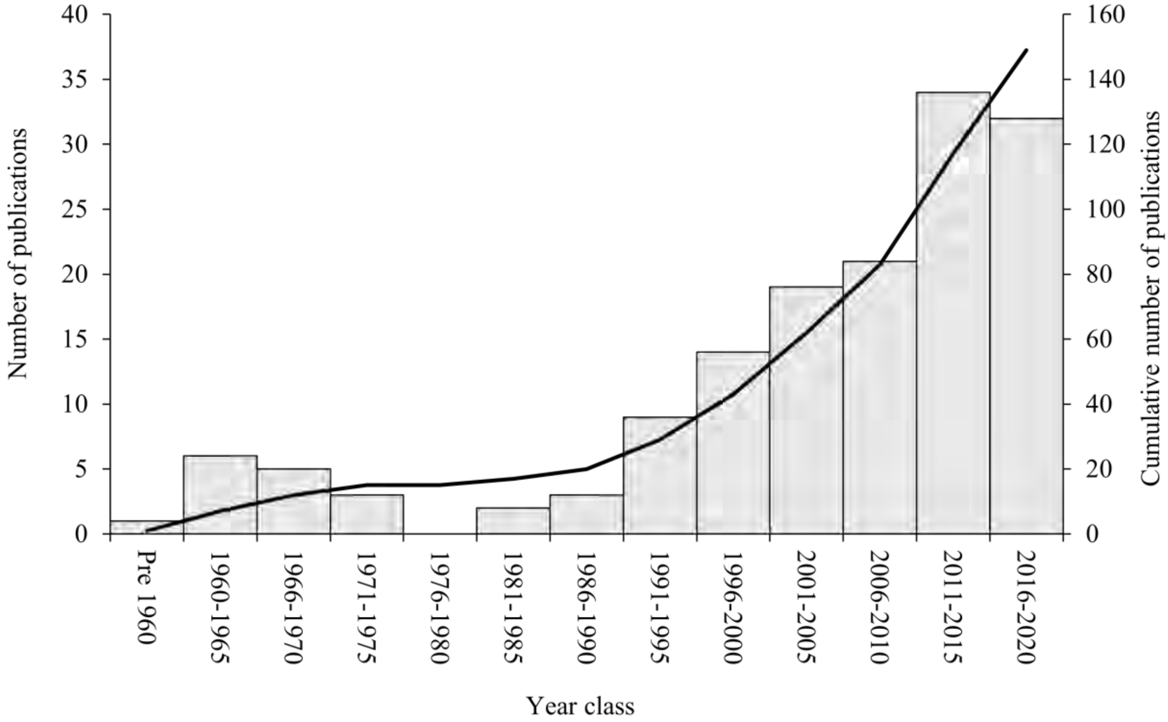

Figure 7: Number of papers per year class and the cumulative number of papers (black line) found in English that refers to fish or fisheries in the Upper Zambezi from pre-1960 to 2020.

A total of 106 publications focused strictly within the Upper Zambezi, of which 70% were peer-reviewed journal articles. The focus area for the literature available on the Upper Zambezi was in and around the large floodplain reaches (e.g., Barotse Floodplain, Chobe and Zambezi region), accounting for 70% of studies (Figure 8A-B). The studies focused on the fisheries, catch composition, estimated value, and market/trade-related aspects in these floodplain reaches. In the three floodplain reaches which are fisheries dominant regions, ecological studies concentrated on economically important species recording seasonal movement patterns, age and growth and diet composition. Biodiversity studies were undertaken on broader areas across the Upper Zambezi, with one-third of them focussing on species of commercial importance associated with large floodplain fisheries. As a result, many sections of the Upper Zambezi, particularly tributaries, remain poorly sampled. For example, only 16 of the 107 studies (15%) encompassed riverine habitats in large tributaries. The dominant source of the literature for these large tributaries are reports by non-governmental organisations, conservation groups and private consulting firms. The geographical scope of these studies is limited, as most of them focussed on the Cuando, Luanginga, Lungwebungu and Kabompo rivers. Literature for the Luanginga and Lungwebungu are all from a single project in and around the Liuwa Plains National Park conducted in 2012 and 2013, representing a minor section of these large rivers.

Literature searches for "Kabompo River"* AND "Fish"* yielded only a single article by Winemiller (1991) on Scopus and the Web of Science. To find additional literature on the Kabompo River, a general search of "Kabompo"* was undertaken. The general search on Scopus resulted in 26 articles and 11 articles on the Web of Science, all of which were retrieved in the Scopus search. However, these 26 articles primarily focus on economic activities relating to geology and forestry in the Kabompo catchment. The single fish-related article by Winemiller (1991) was once again retrieved in the general search. This article related to the ecology of *Serranochromis* species and sampled multiple reaches and tributaries in the Upper Zambezi, fitting the focus area of Upper Zambezi rather than confined to the Kabompo River. The Kabompo River *Serranochromis* species were a minor component of the study, only incorporating two immature individuals of *Serranochromis thumbergi*. The reference list of the 26 articles yielded no additional results. One article retrieved from the reference list of articles for the Upper Zambezi was the species description of *Enteromius neefi* from the Kabompo River. Besides these two articles, the dominant ichthyological literature for the Kabompo River is confined to grey literature of consultant reports. These fish faunal reports are confined to small and targeted surveys for environmental impact assessments (EIA's) relating to mining projects in the headwaters of the Mwafwe tributary and upstream from the Ntambu Floodplains and surrounding tributaries. An ichthyological assessment for the hydroelectric dam development at Kabompo Gorge covered a broad area from above the Gorge to the lower reaches of the Ntambu floodplains sampling sentinel sites on an annual or biannual basis. The AWF Four Corners project sampled a broad area within the Kabompo River targeting small and large tributaries predominantly in the upper sections but did conduct collections in the lower section.

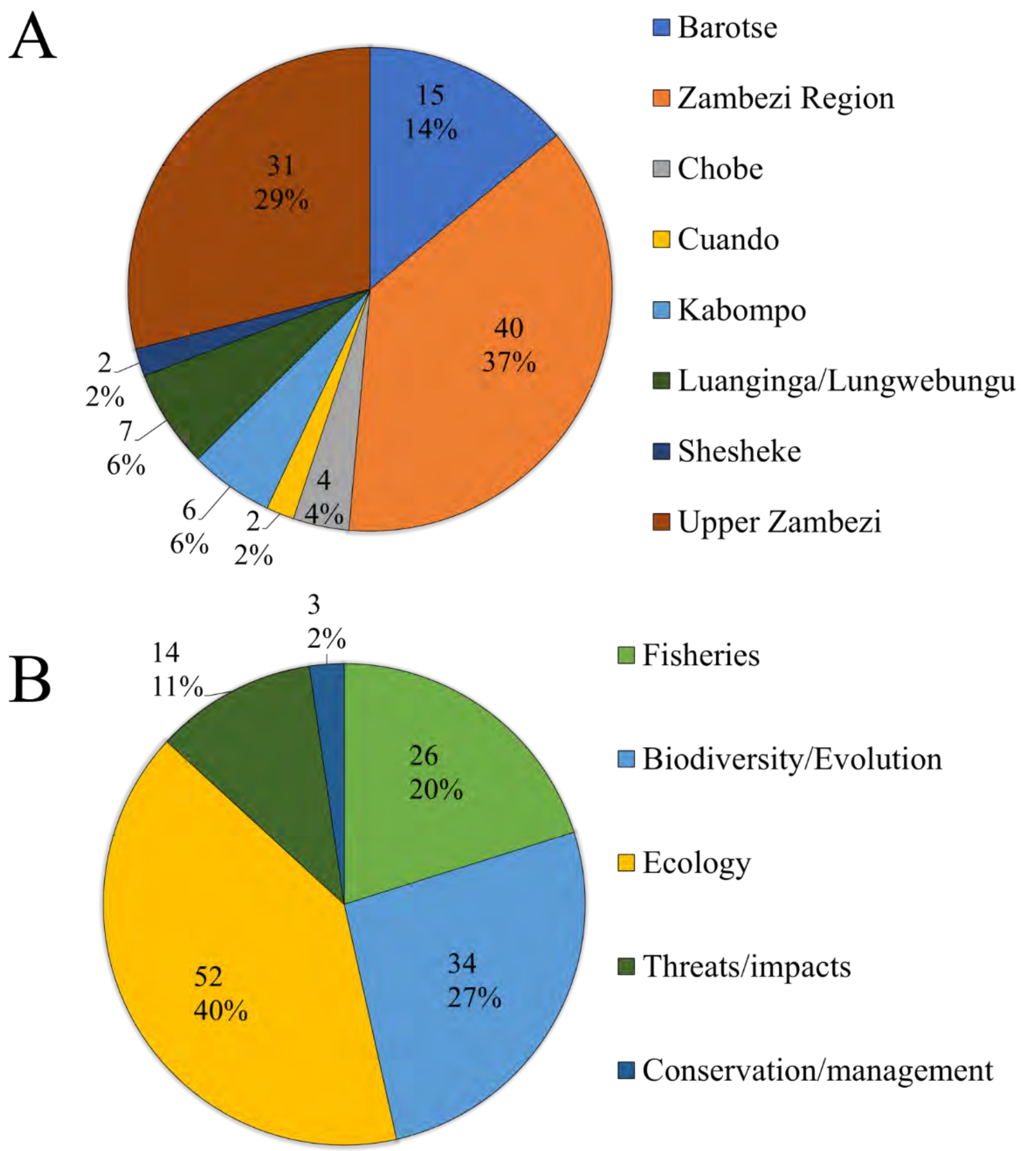

Figure 8: The proportion of publications within the Upper Zambezi. (A) Location of the 107 studies undertaken within the Upper Zambezi, (B) broad subject of the upper Zambezi publications, as publication could be classified into more than one topic the total is greater than 107 publications. The top number indicates the number of publications, while the bottom percentage is the proportional contribution.

Geographical coverage

The NRF-SAIAB National Fish Collection database indicate that 107 sites were sampled in the Kabompo River between 1983 and 2013. The main sources for these collections are EIAs undertaken in the upper parts of the catchment near Ntambu and the headwaters of the Mwafwe River (Figure 9). Historical collections focused in a small area with 78% of sampling sites in and around the two large copper mines (Figure 9). The AWF Four Corners projected conducted more widespread surveys, sampling the West Lunga, Nyela and lower reaches of the mainstem Kabompo providing valuable geographical spread. An additional 17 sites distributed between the upper, middle and lower reaches of the Kabompo were added to the sampling effort during the present study. Sampling was centred in the middle reaches of the Kabompo River with 12 sites sampled at the Ntambu Floodplains and Jivundu near the southern edge of the West Lunga National Park. The area around Jivundu allowed access to the lower section of the West Lunga river.

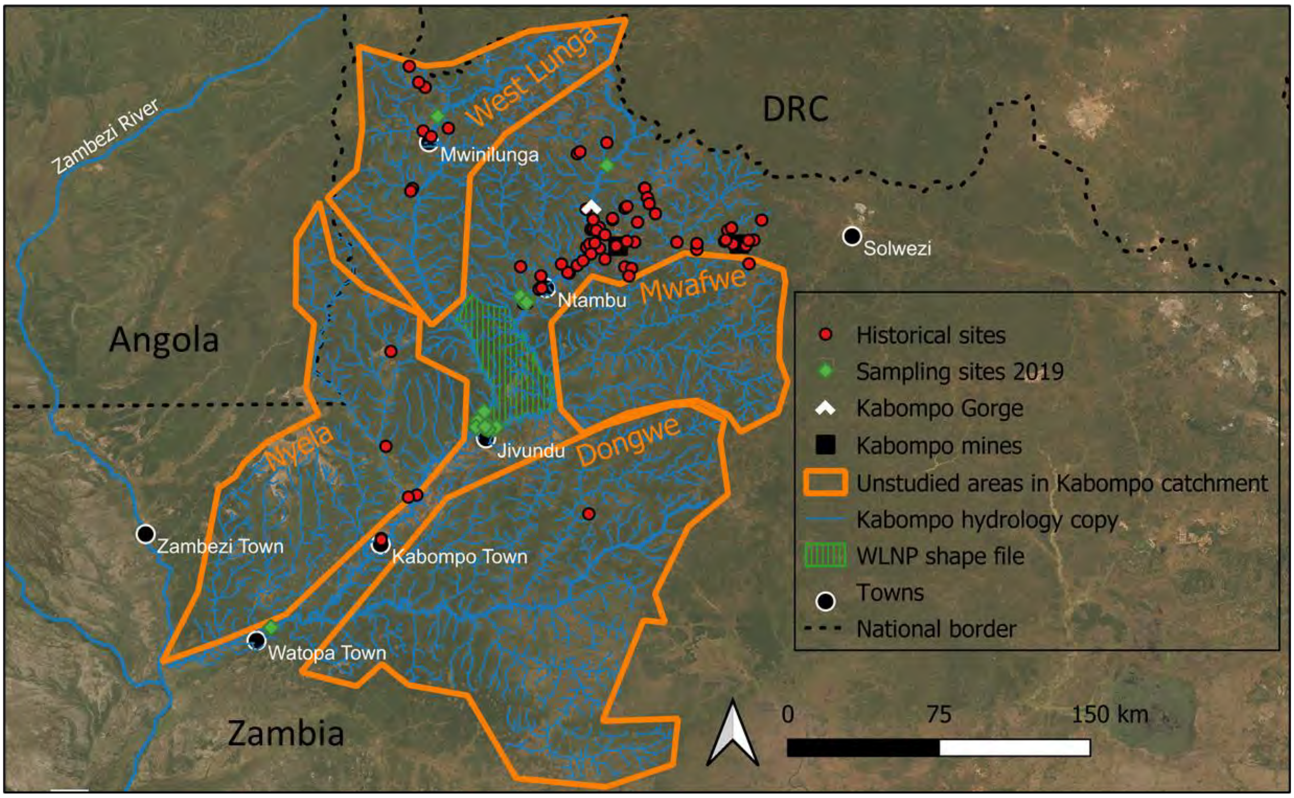

Figure 9: The historical and newly added sample localities in the Kabompo River basin. The regions with few studies are highlighted within the orange polygons.

The West Lunga River, relative to the other tributaries, was the most sampled with 12 (8 historic and 4 new) sample localities. The geographical spread of these localities is poor, with sites concentrated in the upper reaches near Mwinilunga Town, and from the present study, the lower reaches near the confluence with the Kabompo River. Consequently, the upper most headwater sections near the Democratic Republic of the Congo, consisting of intermittent marshland-type habitats, are unsampled. Additionally, most of the middle and lower sections of the West Lunga have not been sampled, leaving a major sampling gap in this tributary. The

Nyela River contains four localities, and the Dongwe River only has a single locality. Numerous westbank tributaries originating from extensive floodplains near the Angolan border are unstudied, including the western sections of the Nyela River (Figure 9). The Dongwe River, southern portion of the Mwafwe River and several eastern draining affluents of the Kabompo remain undersampled. Therefore, from the analyses, four large, regions with few studies are identified i) middle and lower Mwafwe, ii) West Lunga, iii) Nyela River and adjacent west bank Kabompo tributaries, and iv) Dongwe River.

An assessment of collection sites by river order indicates that historical collections have focused on lower-order streams and tributaries of the Kabompo (Figure 10A-B). First to third-order streams account for 66.4% of all the sites sampled to date in the Kabompo River, with third-order streams accounting for 35.8% of these sites (Figure 10B). Higher-order sections (4th to 6th) represented in collections are few and centred around floodplains or riffle habitats. The system's lower reach is poorly sampled, with only three sample localities occurring in the mainstem Kabompo River at or below Kabompo Town. Similarly, historical sampling localities are focused on first to third order tributaries in the West Lunga, with five of the 12 collections occurring in the 5th order mainstem sections of the West Lunga (Figure 10).

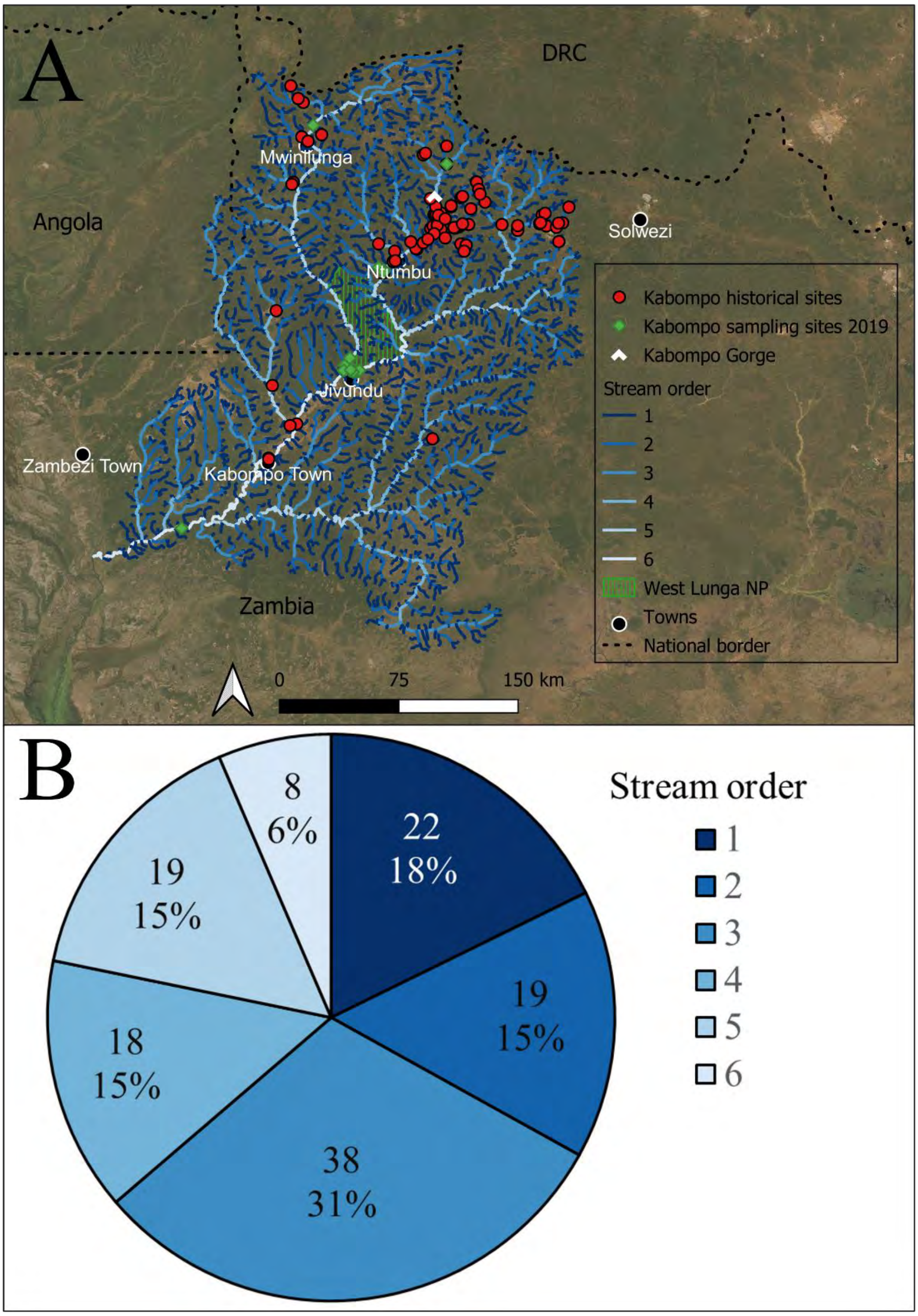

Figure 10: A) The historical and newly added sample localities in the Kabompo River in relation to Strahler stream order. B) The proportion of sample sites in the Kabompo River basin classified by stream order.

Fish fauna

A total of 88 fish species in 41 genera and 16 families were recorded from surveys undertaken in the Kabompo River and its tributaries over the past three decades (Table 1). Only one introduced species, Nile tilapia *Oreochromis niloticus,* has been recorded from the Kabompo River basin. The Cyprinidae, Cichlidae and Mormyridae dominate diversity accounting for 55% of the species (Figure 11).

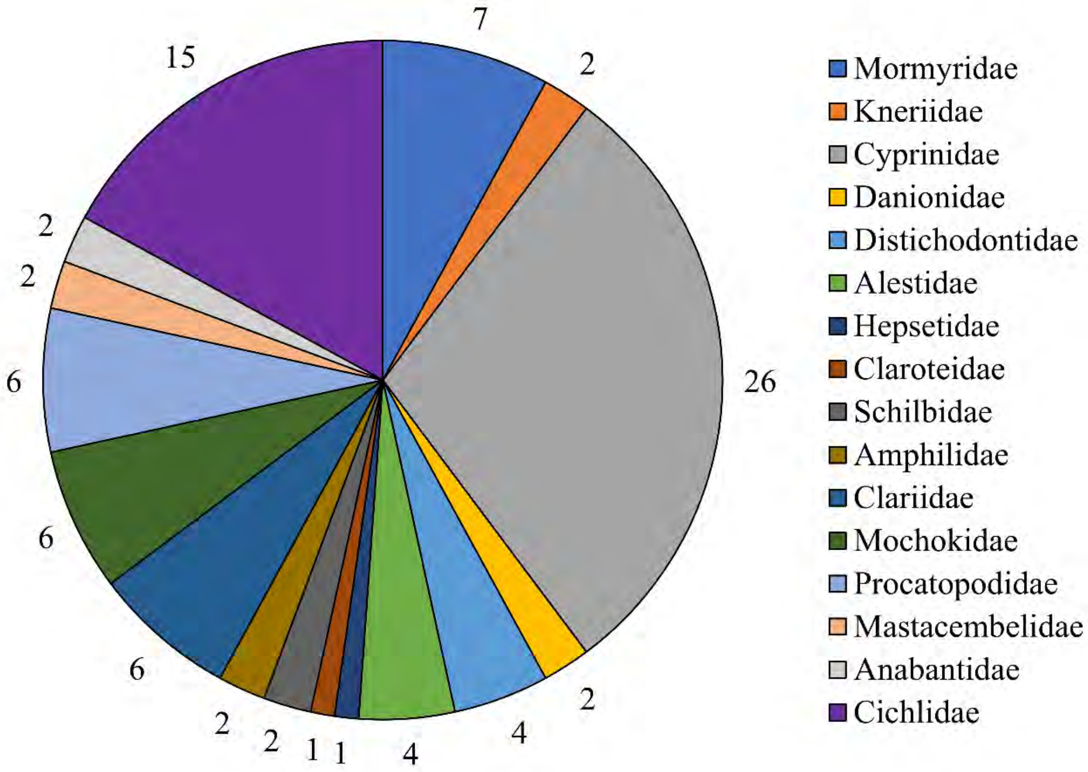

Figure 11: The relative contribution of each family present in the Kabompo River. Families are listed in taxonomic order, and only formally described species were considered The number outside the circle indicate the number of species for each family.

All the species recorded in the Kabompo are widely distributed throughout the Upper Zambezi. Thirty-one species occur above the Kabompo River Gorge, and all except '*Lacustricola' hutereaui* occur below the gorge. Interestingly, the typical floodplain species (e.g., *M. altisambesi*, *E. afrovernayi*, *E. paludinosus* and *C. gariepinus*) are largely absent from the section above the gorge. In the river below the gorge 83 species are present, all of which are known from the Upper Zambezi, with some having ranges extending into the Middle (29 species) and Lower Zambezi (23 species). There are 49 wide-ranging species that have distributions extending beyond the Zambezi system, into the Congo, Kwanza, Cunene and

Limpopo river systems. Previous studies have highlighted once widespread species to consist of complexes which is likely similar for many of these species. In contrast, five species (*C. wittei, E. brevianalis, N. machadoi, C. neumanni and T. ruweti*) show restricted distributions within the Kabompo despite being widely distributed in the Upper Zambezi or southern Africa. The recent surveys added new locality records in the Kabompo River for seven species. Thirteen potential undescribed species have been collected during sampling expeditions whose taxonomic distinctiveness need further investigation (Table 1). These 13 potentially undescribed species were excluded from the calculations above. The full plate of species distribution maps is available in Appendix 2, Plate 1-23.

Table 1: List of fish species present in the Kabompo River and Upper Zambezi and their distributions in the Zambezi River system. Widespread species that occur in neighbouring river systems, excluding the Okavango, are specified. The species conservation status is given according to the IUCN Red List DD - Data Deficient; EN - Endangered; LC - Least concern; NA- Not assessed, and VU – Vulnerable. Putative species thus far sampled in the system are listed separately.

	Kabompo River		Zambezi River			Widespread	IUCN
Species name	Above Gorge	Below Gorge	Upper	Middle	Lower		
Mormyridae							
Mormyrus lacerda		X	X			X	LC
Hippopotamyrus szaboi	X	X	X				LC
Cyphomyrus cubangoensis		X	X				LC
Marcusenius altisambesi		X	X				LC
Marcusenius angolensis			X			X	LC
Petrocephalus longicapitis	X	X	X				LC
Petrocephalus okavangoensis		X	X				LC
Pollimyrus castelnaui			X				DD
Pollimyrus cuandoensis			X				DD
Pollimyrus marianne		X	X				LC
Paramormyrops jacksoni			X				DD
Kneriidae							
Kneria polli	X	X	X			X	LC
Parakneria fortuita		X	X			X	LC
Cyprinidae							
Enteromius afrovernayi		X	X	X			LC
Enteromius bifrenatus	X	X	X			X	LC
Enteromius brevidorsalis	X	X	X			X	LC
Enteromius eutaenia	X	X	X	X	X	X	LC
Enteromius fasciolatus		X	X	X	X	X	LC
Enteromius kerstenii		X	X	X	X	X	LC

	Kabompo River		Zambezi River			Widespread	IUCN
Species name	Above Gorge	Below Gorge	Upper	Middle	Lower		
Enteromius lineomaculatus	X	X	X	X	X	X	LC
Enteromius multilineatus		X	X	X			LC
Enteromius neefi	X	X	X				LC
Enteromius greenwoodi		X					DD
Enteromius paludinosus		X	X	X	X	X	LC
Enteromius poechii		X	X	X			LC
Enteromius radiatus		X	X	X	X	X	LC
Enteromius thamalakanensis		X	X				LC
Enteromius trimaculatus		X	X	X	X	X	LC
Enteromius unitaeniatus	X	X	X	X	X	X	LC
Enteromius barnardi		X	X	X			LC
Enteromius barotseensis		X	X			X	LC
Enteromius haasianus	X	X	X	X	X	X	LC
Enteromius miolepis	X	X	X				LC
Enteromius kessleri			X			X	LC
Enteromius lujae			X			X	LC
Enteromius viviparus			X			X	LC
Coptostomabarbus wittei		X	X			X	LC
Clypeobarbus bellcrossi	X	X	X				DD
Labeo cylindricus	X	X	X	X	X	X	LC
Labeo lunatus		X	X				LC
Labeobarbus codringtonii	X	X	X				LC
Danionidae							
Engraulicypris brevianalis			X			X	LC
Opsaridium zambezense		X	X	X	X	X	LC
Distichodontidae							

	Kabompo River		Zambezi River			Widespread	IUCN
Species name	Above Gorge	Below Gorge	Upper	Middle	Lower		
Nannocharax machadoi		X	X	X		X	LC
Nannocharax multifasciatus		X	X			X	LC
Nannocharax dageti	X	X	X			X	LC
Nannocharax lineostriatus			X				DD
Nannocharax minutus			X				LC
Neolebias lozii			X				
Alestidae							
Brycinus lateralis		X	X	X	X	X	LC
Hydrocynus vittatus		X	X	X	X	X	LC
Micralestes acutidens		X	X	X	X	X	LC
Rhabdalestes maunensis	X	X	X				LC
Hepsetidae							
Hepsetus cuvieri		X	X			X	LC
Claroteidae							
Parauchenoglanis ngamensis		X	X			X	LC
Schilbidae							
Schilbe depressirostris	X	X	X	X		X	LC
Schilbe yangambianus	X		X			X	LC
Amphiliidae							
Amphilius cubangoensis			X				
Amphilius uranoscopus	X	X	X	X	X	X	LC
Zaireichthys pallidus		X	X				DD
Zaireichthys conspicuus			X				DD
Clariidae							
Clariallabes platyprosopos		X	X				LC
Clarias gariepinus		X	X	X	X	X	LC

	Kabompo River		Zambezi River			Widespread	IUCN
Species name	Above Gorge	Below Gorge	Upper	Middle	Lower		
Clarias ngamensis		X	X			X	LC
Clarias stappersii	X	X	X			X	LC
Clarias theodorae	X	X	X		X	X	LC
Clarias liocephalus	X	X	X			X	LC
Mochokidae							
Chiloglanis fasciatus	X	X	X				LC
Chiloglanis neumanni	X	X	X	X	X	X	LC
Synodontis nigromaculatus		X	X			X	LC
Synodontis woosnami		X	X			X	LC
Synodontis macrostigma		X	X			X	LC
Synodontis macrostoma	X	X	X			X	LC
Synodontis leopardinus			X			X	LC
Synodontis thamalakanensis			X			X	LC
Synodontis vanderwaali			X			X	LC
Procatopodidae							
‘Lacustricola’ johnstoni		X	X	X	X	X	LC
‘Lacustricola’ katangae	X	X	X		X	X	LC
‘Lacustricola’ jubbi		X					LC
‘Lacustricola’ hutereaui	X	X	X			X	LC
‘Lacustricola’ chobensis		X	X				NA
‘Lacustricola’ pygmaeus		X	X				NA
Mastacembelidae							
Mastacembelus frenatus	X	X	X				LC
Mastacembelus vanderwaali	X	X	X				LC
Anabantidae							
Ctenopoma multispine		X	X				LC

	Kabompo River		Zambezi River			Widespread	IUCN
Species name	Above Gorge	Below Gorge	Upper	Middle	Lower		
Microctenopoma intermedium		X	X				LC
Cichlidae							
Hemichromis elongatus			X			X	LC
Coptodon rendalli		X	X				LC
Oreochromis macrochir		X	X				V
Oreochromis andersonii		X	X				V
Oreochromis niloticus (NN)		X	X	X	X		LC
Pharyngochromis acuticeps		X	X	X	X	X	LC
Pseudocrenilabrus philander	X	X	X	X	X	X	LC
Sargochromis carlottae		X	X	X			LC
Sargochromis codringtonii			X	X		X	LC
Sargochromis giardi		X	X	X		X	LC
Serranochromis altus			X				LC
Serranochromis angusticeps			X	X		X	LC
Serranochromis jallae		X	X			X	LC
Serranochromis macrocephalus	X	X	X	X	X		LC
Serranochromis thumbergi		X	X			X	LC
Serranochromis longimanus			X				LC
Tilapia ruweti		X	X				LC
Tilapia sparrmanii		X	X				LC
Nothobranchiidae							
Nothobranchius capriviensis			X				EN
Nothobranchius kafuensis			X	X			LC
Total	**31**	**81**	**104**	**32**	**23**	**58**	

	Kabompo River		Zambezi River			Widespread	IUCN
Species name	Above Gorge	Below Gorge	Upper	Middle	Lower		
Putative species							
Enteromius eutaenia ‘red-eye’		X					
Enteromius sp. ‘dark-eutaenia’							
Enteromius ‘purple stripe’		X					
Enteromius ‘Manyinga spot’		X					
Enteromius ‘chubby head’		X					
Enteromius ‘Kabompo twin stripe’		X					
Zaireichthys sp. ‘brown north’		X					
Zaireichthys sp. ‘north blotch’							
Zaireichthys sp. broad bar’		X					
Zaireichthys sp. ‘pallid, fine spotted’		X					
Zaireichthys n. sp. ’granular pattern’		X					
Chiloglanis sp. ' plain, small eye'	X						

Species accounts and distributions

Mormyridae

The Kabompo has seven mormyrid species belonging to six genera and they all have ranges extending into the Upper Zambezi. Six of these species are widespread and in the Kabompo are common where they occur, with the exception of *Mormyrus lacerda* which is represented by few specimens in the collections and was rarely sampled during the recent surveys. This species has only been recorded at localities just below the Ntambu Floodplain in the Kabompo River (Appendix 2, , Plate 1). Only two species, *Hippopotamyrus szaboi* and *Petrocephalus longicapitis* have been recorded above the Kabompo Gorge. Both species also occur in river sections below the gorge. The present study extended the range of *Cyphomyrus cubangoensis* into the Kabompo River. This species was previously only known from the Upper Zambezi, Kwando and Okavango rivers. *Pollimyrus marianne* was common in the Kabompo, Mwafwe and West Lunga rivers. Within the Kabompo River, its distribution is limited to sections below the gorge.

Kneriidae

This family is represented by two species, *Kneria polli* and *Parakneria fortuita*, in the Kabompo River. Both species have ranges extending beyond the Kabompo River as they have been recorded in the Upper Zambezi and Okavango systems. Interestingly, within the Kabompo River, *K. polli* was only recorded from fast-flowing riffle sections at or above the gorge. It has also been recorded from headwater sections of the Mwafwe, West Lunga and Nyela rivers. Specimens of *K. polli* were also generally associated with unidentified ectoparasites that were usually attached to the fins as shown in Figure 12 . *Parakneria fortuita* was less common, but ad hoc observations suggest that *Parakneria* species are more effectively sampled at night (R. Bills, pers. communication).

Figure 12: Presence of an ectoparasite on the pectoral fin of *Kneria polli* sampled from the upper Kabompo. Photo credit: Dr A Chakona ©NRF-SAIAB

Cyprinidae

The Cyprinidae is represented by 27 species in five genera, making it the most diverse family in the Kabompo River (Table 1). *Enteromius* was the dominant genus, being represented by 21 species. Of these species, only eight occur above and below the gorge, with the other 13 occurring exclusively below the gorge. The typical floodplain species, for example, *E. afrovernayi*, *E. fasciolatus*, *E. multilineatus*, *E. paludinosus* and *E. thamalakanensis* were not recorded from above the gorge where fast-flowing riffles are the dominant habitat but rather *E. eutaenia*, *E. unitaeniatus* and *E. lineomaculatus* were more common above the gorge. Most of the *Enteromius* species are widely distributed throughout the Zambezi and adjacent river systems, although growing evidence from ongoing studies suggest that a number of them may harbour several undescribed species (see below). The present study also extended the range of *E. greenwoodi* (Figure 13), a species that was previously only known from the upper sections of the Cuanza and Okavango rivers. There is a need for further investigation to determine whether these newly collected specimens are conspecific with *E. greenwoodi,* or they may potentially represent an undescribed species. Specimens of *E. paludinosus* collected from the floodplains near Jivundu appeared to be stubby and much deeper bodied compared to the "typical" *E. paludinosus* from other systems in southern Africa (Figure 14). Their status will be determined as part of an ongoing investigation of the diversity of *Enteromius* species in southern Africa. *Coptostomabarbus wittei,* a broadly distributed species that occurs in the Kafue and Congo system, was only reported from a single locality in the east bank tributary of the Nyela River, a tributary of the Kabompo River (Appendix 2, Plate 8). *Clypeobarbus bellcrossi* also has a limited distribution range in the Kabompo, as it was only recorded from two localities, one above Kabompo Gorge and another one in the mainstem Kabompo River below.

Figure 13: *Enteromius greenwoodi* from the Kabompo River. Photo credit: Dr Albert Chakona ©NRF-SAIAB.

Figure 14: Comparison of A) *Enteromius paludinosus* collected near Jivundu and B) “typical” *Enteromius paludinosus*. Photo credit A) Dr A Chakona ©NRF-SAIAB, B) D Tweddle ©NRF-SAIAB.

The two *Labeo* species *L. cylindricus* and *L. lunatus* show vastly different occurrence records, with the latter recorded for the first time in the Kabompo River during sampling in 2019. *Labeo lunatus* is at present only reported from a rocky outcrop in the main channel of the lower West Lunga, likely an aspect of the lack of sampling effort in the deeper mainstem rock sections. However*,* *L. cylindricus* is widespread in the Kabompo, West Lunga and Mwafwe rivers in various hard structured habitats. The largest cyprinid known to occur in the system *Labeobarbus codringtonii* appears to be widespread, although sampling records are scattered, potentially due to its preference for deeper rapid type habitats. Local fishermen report catching large specimens of *L. codringtonii* in the deep rocky sections near Jivundu. However, large specimens were not observed, and a more targeted effort is needed to sample this species.

Danionidae

Two genera with a single species each occur in the Kabompo River. *Opsaridium zambezense* is abundant and widespread throughout the Kabompo River in small and large fast-flowing river channels. Although being considered a wide and disjunctly distributed species across southern Africa, *Engraulicypris brevianalis* appeared to be uncommon in the Kabompo River basin as it was only recorded from a single locality in the Lumwana River (Appendix 2, Plate 9).

Distichodontidae

Within the Kabompo River, only two distichodontid species, *Nannocharax multifasciatus* and *Nannocharax dageti* are common in this river. Both species are also widely distributed across the Upper Zambezi and Okavango River, including the adjacent Congo basin for *N. dageti*. The distribution of *N. multifasciatus* is restricted to below the gorge while *N. dageti* is present above. Interestingly, two distichodontid species that are present in other sections of the Upper Zambezi, *N. lineostriatus* and *N. minutus*, have not yet been recorded from the Kabompo River. In addition, *N. machadoi* appears to be less common in the Kabompo basin, as it was only recorded from a single locality in the Mwombezhi River, a tributary of the Mwafwe River (Appendix 2, Plate 9).

Alestidae

Four genera containing one species each occurs within the Kabompo River. Few records are available for *Brycinus lateralis,* likely an aspect of the lack of sampling effort in larger mainstem sections. The other three species are widespread and occur within the main channels of the Kabompo and its tributaries. The present study added new locality records in the Kabompo River for *Hydrocynus vittatus.* Although the species has long been reported from the system, no locality records were documented in the Kabompo. At present, only a single

Alestidae species *Rhabdalestes maunensis* is documented from above the Kabompo Gorge and occurs in the section below. Local fishermen state that *H. vittatus* does not occur above the Gorge.

Hepsetidae

The family is represented by a single species, *Hepsetus cuvieri,* which is common in slow-flowing and vegetated sections of the Middle Kabompo River. The species has not been recorded above the gorge. It is also widely distributed in the Upper Zambezi, Quanza, Cunene, Okavango and Kafue rivers. Despite being common in the Kabompo River, the African pike is rather rarely caught by local fishers.

Claroteidae

Parauchenoglanis ngamensis is a species complex that contains populations distributed across multiple river systems in southern and central Africa, including the Zambezi, Okavango, Congo and Cunene. The species is broadly distributed in the Kabompo River occurring sporadically in a diversity of habitats, including rocky riffles and woody structures below the gorge.

Schilbidae

The Schilbidae is represented by two species in the Kabompo. *Schilbe depressirostris* is widespread occurring above and below the gorge. The second species *Schilbe yangambianus* prefers headwater streams and is reported from a single locality above Kabompo Gorge and four headwater localities in the Mwafwe.

Amphiliidae

The family is represented by two genera, *Amphilius* and *Zaireichthys*. Although findings from previous and ongoing studies indicate that what is currently referred to as *A. uranoscopus* in southern Africa is a complex of several species, for this study this name is maintained until the taxonomic revision of this group has been finalised. Within the Kabompo

River, *A. uranoscopus* is broadly distributed above and below the gorge. The Kabompo is currently represented by only one formally described species of *Zaireichthys*, *Z. pallidus*. This species has only been recorded in river sections below the gorge. The distribution range of this species is considered to encompass many rivers in the Upper Zambezi as we as the Okavango River. Recent surveys have also collected specimens that could not be attributed to *Z. pallidus*, and possibly represent an undescribed species (Figure 15). These specimens have been tentatively named, *Zaireichthys* sp. 'brown north', pending further taxonomic work. *Zaireichthys* sp. 'brown north' is confined to sections below the gorge.

Figure 15: *Zaireichthys* present in the Upper Zambezi and Kabompo. A) *Zaireichthys conspicuus.* B) *Zaireichthys pallidus.* C) *Zaireichthys* sp. 'brown north'. Photo credits A and B: D. Tweddle ©NRF-SAIAB.

Clariidae

The Clariidae is one of the most diverse catfish families within the system, represented by six species in two genera. All the species are broadly distributed below the gorge. Two species *Clarias ngamensis* and *Clarias gariepinus* do not occur above the gorge like the other four species. The present study extended the range of *C. ngamensis* a species widely distributed in southern Africa into the Kabompo. The larger *Clarias* species, especially *C. gariepinus* and *C. ngamensis* are essential in the subsistence fishery. An interesting observation made at a

Jivundu floodplain pool was the presence of a large leech attached to a *C. ngamensis* caught by a local fisherman (Figure 16).

Figure 16: Large leech attached to a *Clarias ngamensis* specimen from a pool near Jivundu.

Mochokidae

The family is represented by two genera, *Chiloglanis* and *Synodontis*. *Chiloglanis fasciatus* is widespread occurring above and below the gorge. *Chiloglanis neumanni* has a more restricted distribution occurring above and below the gorge but is not present below Ntambu. Recent surveys have also collected *Chiloglanis* specimens that could not be attributed to *C. fasciatus* or *C. neumanni*, and possibly represent an undescribed species (Figure 17). These specimens have been tentatively named, *Chiloglanis* sp. 'plain, small eye', pending further taxonomic work. *Chiloglanis* sp. 'plain, small eye' is confined to sections above the gorge and a locality in the Mwafwe. The Kabompo is currently represented by four formally described species of *Synodontis.* The most common *Synodontis macrostoma* is distributed throughout the Kabompo and is the only species known to occur above the gorge. The other three species (*Synodontis nigromaculatus, Synodontis macrostigma* and *Synodontis woosnami*) are less common and only known from few localities in the Kabompo. The present study extended the range of *S. nigromaculatus* and *S. woosnami* into the Kabompo River. These species were previously only known from the Upper Zambezi, Kwando and Okavango rivers.

Figure 17: *Chiloglanis* sp. 'plain, small eye from the Kabompo River. Photo credit: Dr Albert Chakona ©NRF-SAIAB.

Procatopodidae

Six species of topminnow, all in the genus '*Lacustricola*' occur in the Kabompo system. *Lacustricola johnstoni* and *Lacustricola jubbi* are broadly distributed in sections below the gorge. Interestingly, *'Lacustricola' katangae* is widely distributed in the sections below the gorge and occurs in the section above to. The second species that occurs above the gorge *'Lacustricola' hutereaui* is confined to this section of the Kabompo. Similarly, the redescribed '*Lacustricola*' *chobensis* is only know from two locations on the mainstem Kabompo near Ntambu, and the newly described '*Lacustricola*' *pygmaeus* is only known from two localities in the Nyela River, despite both occurring broadly in the Upper Zambezi and Okavango systems Appendix 2, Plate 17 and 18). '*Lacustricola' katangae* and '*Lacustricola' johnstoni* are the two most broadly distributed species commonly encountered in the Kabompo system and its large tributaries. *Lacustricola hutereaui* appears uncommon with distribution records from the middle and lower Kabompo, upper Mwafwe, upper West Lunga and upper Nyela.

Mastacembelidae

Mastacembelus eels are represented by two species in the Kabompo system, both of which are broadly distributed in the Upper Zambezi. *Mastacembelus frenatus* is more widespread and abundant, occurring in various habitats in both large and small rivers in the Kabompo. *Mastacembelus vanderwaali*, a rocky habitat specialist, is less common, but does occur in various reaches of the Kabompo. Neither of these species likely form part of the fishery as local onlookers regularly mistook them for snakes during sampling, and they were not present in local markets.

Anabantidae

The family of labyrinth fishes in the Upper Zambezi are represented by two genera *Microctenopoma* and *Ctenopoma* with a single species each. *Ctenopoma multispine* and *Microctenopoma intermedium* are widespread species throughout much of the Kabompo, but presently are not known to occur above Kabompo Gorge.

Cichlidae

Fifteen cichlid species from seven genera have been recorded from the Kabompo. Records for almost all *Sargochromis* and *Serranochromis* species are confined to a single locality. The present study extended the distribution range of *Oreochromis andersonii*, *Oreochromis macrochir, Serranochromis altus* and *Serranochromis angusticeps* into the Kabompo. All these species are known from the Upper Zambezi and Okavango. *Serranochromis macrocephalus* and *Serranochromis jallae* are widespread with the former also occurring above the gorge. Two small species, *Pseudocrenilabrus philander* and *Tilapia sparrmanii* are widely distributed occurring above and below the gorge. *Tilapia ruweti* has a distribution presently limited to the Nyela river in the Kabompo River basin (Appendix 2, Plate 22). *Coptodon rendalli* a popular fisheries species is widespread in the sections below the gorge. Cichlids form an essential component of the subsistence and commercial fishery due to their high-quality flesh. The non-native *Oreochromis niloticus* occurs in the Kabompo, Mwafwe and West Lunga rivers.

Discussion

The long history of ichthyological studies within the Upper Zambezi basin has generated valuable literature for the region. However, because most of the previous studies mainly focused on species of economic importance and floodplain habitats, riverine habitats and their associated species have remained poorly explored. Despite the limited availability of scientific literature for the Kabompo River, the synthesis of this information in conjunction with museum collections, supplemented by additional field sampling from the present study, has facilitated the compilation of a species checklist and identification of important sampling gaps within this river.

The Kabompo River hosts a diversity of species of mixed origins, containing species with distribution ranges from the Congo River system in the north to the Limpopo River system in the south (Skelton, 2001; Tweddle *et al.*, 2004). The fish fauna of the Kabompo River, like the Upper Zambezi, reflect the river's complex geological history. Poll (1967) recorded many species common to both the Zambezi and the Congo River system headwater tributaries, many of which occur in the Kabompo. The distribution of these species resembles recent probable river capture events between the Zambezi and the north-flowing Kasai River (Congo system) (Bell-Cross, 1965). The separation of species that occur above and below the gorge provides a valuable opportunity to study historical drainage arrangements and species evolution patterns. Detailed sampling of the section above Kabompo Gorge will be a critical first step for assessing these patterns.

Until the present study, the most recent relevant published checklist for comparison was generated for the Upper Zambezi and detailed the presence of approximately 120 species, of which 25 appeared to be undescribed (Tweddle *et al.*, 2004). Species lists from consultant reports document 69 fish species in 16 families from above Kabompo Gorge to the Ntambu floodplains (AES, 2019), while the EIAs undertaken in 2009, 2011 and 2018 around the mining facilities mainly sampling the Kabompo, Musangezhi and Chisola Rivers with several of their tributaries detailed the presence of 38 to 58 species across 16 families (Bok and Bills, 2011; Bok and Bills, 2012; EOH- Coastal and Environmental Services, 2019). The synthesis of these checklists supplemented by additional sampling efforts resulted in a detailed checklist of 83 formally described species and 13 putative species present in the Kabompo River. The families that contribute greatest to fish faunal diversity in this river are the Cyprinidae (mainly the genus *Enteromius*), Cichlidae, Mormyridae and Mochokidae. These families all contain species distributed throughout the Upper Zambezi and neighbouring systems. Their relative contributions towards overall diversity are comparable to reports from the Okavango, Cuito and Kwanado systems (Bills *et al.*, 2013) and adjacent ecoregions (Huchzermeyer, 2013; Van Steenberge *et al.*, 2014).

The focus of sampling within the Kabompo River basin, mainly targeting low order streams, has resulted in sampling bias towards smaller-bodied fish species. This, in conjunction with general sampling methods (e.g., backpack electrofishing and D-nets), explains the dominance of smaller-bodied species in historical records and the general absence of the larger clariid and cichlid species. A major limitation to sampling larger species is the inability to use gill nets effectively. The numerous crocodiles that damage the nets and safety risks restricting alternative methods such as a seine net in deeper sections means other methods are required to represent the larger species better in sampling records. A possible solution may be drift boat-based electrofishing, an effective method for sampling large species in deeper large sections of the river (Temple and Pearsons, 2007). Alternatively, non-destructive methods, such as environmental DNA (e-DNA), represent a novel approach to document biodiversity in this species-rich system (Cilleros *et al.*, 2019; Doble *et al.*, 2020). However, e-DNA requires reference samples for comparison, so initial DNA barcoding is required to generate the reference library. The absence of a reference library is thus a major limitation to the use of this method at present. An alternative is needed as taxonomic identification is only as good as the reference database (Thomsen and Sigsgaard, 2019). A baited remote underwater stereo-video station (stereo-BRUVs) is a freestanding video recording device capable of measuring fish lengths (Langlois *et al.*, 2020). Stereo-BRUVs offer another potential alternative as this approach has proved effective for documenting the diversity in other larger rivers, for example, in Australia (Ebner and Morgan, 2013; Ebner *et al.*, 2015) and South America (Schmid *et al.*, 2017). Given the generally clear waters of the Kabompo River, BRUVs may provide valuable species distribution data and a better understanding of species diversity and ecology in various habitats that include the main channel, backwaters, and floodplain environments that are not accessible with the more conventional methods. However, the lack of a specific sampling protocol for bait type, soak time and replication, pose potential bias for this method and could reduce the comparability of the data, as reported by Gladstone *et al.* (2012). The use of complementary sampling approaches which include the conventional fish traps, electrofishing, gill-netting and seine netting, depending on habitat type, supplemented with more modern techniques such as eDNA and BRUVs should be adopted to advance the documentation of the diversity of fishes in the Kabompo River, as well as other larger rivers in the region.

Potential taxonomic conflicts

Even though sampling efforts in the Kabompo River have been restricted to a relatively small area, a number of potential taxonomic conflicts have been identified across many families of freshwater fishes, highlighting that the ichthyofaunal diversity in this region has not been fully documented. Examples of the cases where hidden diversity and potential candidate species have been identified within some of the species in the Kabompo and adjacent rivers are given below.

Cyprinidae

Recent studies have indicated that the current taxonomy underestimates the taxonomic diversity in this family (Tweddle and Skelton, 2008; Van Ginneken *et al.*, 2017; Skelton *et al.*, 2018; Kambikambi *et al.*, 2021). Several new species and genetically distinct lineages have been identified within species in the genus *Enteromius* (Englmaier *et al.*, 2020; Kambikambi *et al.*, 2021). Many of these species' complexes were previously considered to have wide geographic ranges (Kambikambi *et al.*, 2021) or had disjunct distributions (Chakona *et al.*, 2015; Martin and Chakona, 2019). A similar scenario is expected for *Enteromius neefi*, a species with an unusual disjunct distribution divided into two populations, one in the Limpopo River system in South Africa and another one in the Upper Zambezi and Kafue rivers (Skelton, 2001). The type locality of *E. neefi* is the Kabompo River. Considering the wide geographic separation and the fact that this species has not been recorded in intervening systems between these two populations, it is likely that the Limpopo population may represent an undescribed species. *Enteromius pallidus* was once considered to have a disjunct distribution with a population in the coastal rivers of the Eastern Cape and an inland population from the Limpopo River system. Genetic analysis revealed these two populations not to be closely related with species-level genetic difference between them (Chakona *et al.*, 2015). *Enteromius kerstenii*, another disjunctly distributed species in southern and eastern Africa (Skelton, 2001), could also potentially harbour hidden diversity. This is based on genetic analysis (Schmidt *et al.*, 2017a), and the distribution of *E. kerstenii* in southern Africa closely mirrors that of *Hippopotamyrus*, a genus that has been recently found to contain multiple genetically distinct and allopatrically distributed lineages (Mutizwa *et al.*, 2021). Indeed, studies of other disjunctly distributed species in the region have found a similar pattern, for example, a study of *Amphilius natalensis* led to the discovery and description of four new species (Mazungula and Chakona, 2021).

Studies of other widely distributed species of *Enteromius*, for example, *E. paludinosus*, *E. anoplus,* and *E. eutaenia* have revealed existence of extreme levels of hidden diversity (De Graaf *et al.*, 2007; Schmidt *et al.*, 2017; Englmaier *et al.*, 2020; Kambikambi *et al.*, 2021) The present study collected comprehensive tissue samples for genetic analysis and voucher specimens that represent an important resource for examining the potential existence of undocumented diversity within some of the wide-ranging species that occur in the Kabompo River and adjacent basins, for example *E. eutaenia, E. paludinosus and E. kerstenii*. Tweddle *et al*. (2004) recorded seven morphotypes within *E. eutaenia* that were provisionally designated as *E. eutaenia*, *E. '*sharp eutaenia', *E.* 'redeye eutaenia', *E*. miolepis, *E*. 'short stripe eutaenia', *E.* 'purple stripe' and *E.* 'dark eutaenia'. There are ongoing studies to determine the taxonomic integrity of these morphospecies (Chakona *et al.,* in prep). An understanding of the taxonomy of closely related species that have little morphological variation from one another may help understand ecological drivers of speciation in the Zambezi River system.

Amphiliidae

Amphilius uranoscopus

Based on recent studies that showed that *Amphilius uranoscopus* is confined to the Wami River system in Tanzania, the species that is currently called *A. uranoscopus* in southern Africa clearly represents a distinct species from those in east Africa (Thomson and Page, 2010; Chakona *et al.*, 2018). Revision of this species in southern Africa is likely to result in the revalidation of at least one of the synonyms of *A. uranoscopus*. Four species were previously described, *A. cubangoensis* described from the Okavango River, *A. hargeri* described from the Ruo River, *A. brevidorsalis* described from the Revue River and *A. leroyi* described from the Ruvu River basin. A recent study by Chakona *et al*. (2018) uncovered genetic and geographic structuring within *A. uranoscopus*, suggesting that there could be more species that will require formal description. There is ongoing work evaluating the taxonomic statues of *A. uranoscopus* in southern Africa incorporating an integrative taxonomic approach.

Zaireichthys species

The Kabompo River currently contains a single species of this genus, Z. *pallidus*. However, during the present survey, specimens that were collected form the middle sections of the Kabompo were morphologically distinct and could not be ascribed to any of the currently known species from this region. They therefore, likely represent a new species to science. Indeed, a study by Chakona *et al.* (2018) revealed that *Z. monomotapa* is a complex of at least four lineages. Similarly, Tweddle *et al.* (2004) identified 6-8 morphospecies in the Upper Zambezi, of which only *Z. conspicuus* and *Z. pallidus* are formally described while statues of *Z.* 'north blotch', *Z.* 'brown north', *Z.* 'brown Luampa', *Z.* 'pale Luampa' and *Z.* 'north spotted' are under evaluation. Additionally, at least three more morphospecies *Z.* 'broad bar', *Z.* 'pallid, fine spot' and *Z.* 'granular' are documented in the EIA reports from the Kabompo River (Bok and Bills, 2012). A more comprehensive analysis of the genera is required on a large scale as *Zaireichthys* appears not to be a monophyletic group (Thomson, 2013) The revision of these sand catlets is likely to uncover more hidden diversity. This group is also of interest as its distribution will help to shed some light on the drainage evolution and historical connections across east and southern Africa, to understand the mechanisms that shaped the biogeographic patterns of the fishes of this region.

Mochokidae

Chiloglanis

Two *Chiloglanis* species *C. fasciatus* and *C. neumanni* occur in the Kabompo and upper Zambezi. *Chiloglanis fasciatus* is confined to the Upper Zambezi and Okavango River systems while *C. neumanni* has a disjunct distribution that includes the Zambezi basin and the Cunene River systems (Skelton, 2001; Marshall, 2011). Recent studies of *Chiloglanis* species across Africa have highlighted the underestimation of diversity and deep genetic divergence within once widely distributed species (Ng and Bailey, 2006; Friel and Vigliotta, 2011; Schmidt *et al.*, 2015; Schmidt *et al.*, 2016; Schmidt *et al.*, 2017b; Chakona *et al.*, 2018; Schmidt and Barrientos, 2019). *Chiloglanis neumanni* is likely to be confined to drainages in east Africa. Indeed, consistent with Marshall's (2011) assertion that what is currently regarded as *C. neumanni* in southern Africa could be a complex of species, a genetic study by Chakona *et al.* (2018) discovered six lineages, two of which are currently being described as new species to science. There is additional diversity that remains to be discovered and described within this genus in the region. For example, in the Kabompo River, specimens collected from above the gorge were uniform brown in colour, and morphologically distinct, and they could not be ascribed to any of the species within the region. Ultimately, the species diversity of *Chiloglanis* within southern Africa is underestimated, but current and planned studies will address this hidden diversity.

Conclusion

As species is the basic unit of communication for all fields of biological research, there is need for expediting the pace at which species descriptions are generated. The use of integrative taxonomic approaches has stimulated renewed interest in taxonomic revisions of freshwater fishes of southern Africa. Recently, one genus was resurrected *Cheilobarbus* and three new genera have been erected, *Amatolacypris*, *Sedercypris*, *Namaquacypris* for polyploid cyprinids endemic to the CFE and adjacent ecoregions in South Africa (Skelton *et al.*, 2018). Comprehensive revisions of *P. afer, E. anoplus* and *A. natalensis* have led to the description of 6 new species and revalidation of 3 species (Chakona and Skelton, 2017; Mazungula and

Chakona, 2021; Kambikambi *et al.*, 2021). Similar patterns such as those mentioned above are expected for other groups, e.g., *Mormyrus*, *Kneria*, *Nannocharax*, '*Lacustricola*', *Synodontis* *Pharyngochromis* and *Pseudocrenilabrus*. There is growing taxonomic capacity through training of postgraduate students through initiatives at the NRF-SAIAB. It is envisioned that these initiatives and the training of students will continue to advance our knowledge and help to address the taxonomic impediment.

Chapter 3: Habitat use of small-sized fish communities in the Kabompo River

Introduction

Despite encompassing only 0.8% of the Earth's surface and being under immense pressure, freshwater ecosystems provide several services that are essential to human livelihoods (Geist, 2011). One of the most recognised services is inland fisheries, which contributes towards livelihoods both directly (food security and micronutrients) and indirectly (boat building) (Welcomme, 2011; McIntyre *et al.*, 2016), especially for riparian communities. In tropical and subtropical systems, the high diversity of freshwater fish (Lévêque *et al.*, 2008), plays a significant role in driving multispecies fisheries like those in the Zambezi basin. The Zambezi River basin spans a large portion of southern tropical Africa (Timberlake, 2000), and represents one of the main inland fisheries in the region. Riparian communities and surrounding areas within the Upper Zambezi utilise at least 50 of the 102 fish species present (Purvis, 2002; Peel *et al.*, 2012; Peel *et al.*, 2014). The annual flood pulse, which is hypothesised to drive ecosystem functioning in floodplain ecosystems like the Upper Zambezi (Junk *et al.*, 1989; Taylor *et al.*, 2017), also has significance for the subsistence fishery. Fishers take advantage of the predictable migration of fish species on and off the floodplains (Bell-Cross, 1974; Tweddle *et al.*, 2004). Once floodwaters recede and floodplains start to desiccate, adult and juvenile fish retreat to the mainstem channel (Abbott *et al.*, 2007). During the low water season, the main river channel and its habitats provide essential refugia for the fishes. However, the available low water habitats and resources become increasingly limited as waters subside to the minimum flow levels. Species exploit these habitats with a degree of species-specific association as the risk of predation increases and competition intensifies (Winemiller, 1996).

Changes in habitat quality and quantity are primary drivers of the reduction in distribution ranges and decline in population sizes of freshwater fishes across several regions (Branigan *et al.*, 2018; Deinet *et al.*, 2020; WWF, 2020), and is considered one of the greatest threats to biodiversity loss in southern Africa (Darwall *et al.*, 2009). Many river systems in southern Africa have been modified in various ways, and their management is quite complex. This is particularly the case for the larger transboundary systems such as the Zambezi River that is under pressure from multiple anthropogenic stressors including invasion by and spread of non-native species (Andrew *et al.*, 2008; Chifamba and Videler, 2014; Deines *et al.*, 2014;

Nunes *et al.*, 2016; Madzivanzira *et al.*, 2021), habitat loss (Timberlake, 2000), flow modification (Bills and Marshall, 2004; Siwila *et al.*, 2013; Kling *et al.*, 2014), and pollution (Feresu and Van Sickle, 1990; Mbewe et al., 2016). These threats all compromise the integrity of the Upper Zambezi and its habitats. The continued expansion of current agricultural developments, the harvest of high-value timber species, and present and planned mining activities will likely increase the demand for water resources and increase sedimentation, ultimately affecting instream habitats. The alteration and loss of critical instream habitats can potentially have major knock-on effects on system productivity and function, with likely impacts on subsistence fisheries, which are already under threat from unsustainable harvesting practices (Tweddle, 2010; Tweddle *et al.*, 2015). Therefore, quantifying system change is critical for identifying, managing and reducing the impacts of economic developments.

The close association of riverine and stream fishes with specific habitats means that they can provide valuable insights into predicting or quantifying potential responses to anthropogenic impacts (Fausch *et al.*, 1990). Assessments of these associations at a large scale (e.g., catchment scale), similar to the surveys carried out in Chapter Two, are valuable for determining biodiversity and broad-scale ecological patterns. However, environmental variables can appear homogeneous over stream or catchment scales, explaining broad habitat specificity but making it difficult to identify relationships between environmental variables and species (Rice *et al.*, 2020). More fine scale assessments (e.g., mesohabitat 1-100 m) better explain the presence or abundances of a species or species assemblages as environmental features are more variable (Rice *et al.*, 2020). Variations in physical habitat characteristics, namely water depth and velocity (Crook and Robertson, 1999; Love *et al.*, 2017), substrate composition (Meulenbroek *et al.*, 2019), submerged and emergent vegetation (Hutchison *et al.*, 2020), wood and root masses (Pusey and Arthington, 2003; Kalogianni *et al.*, 2020), have been reported as important factors that influence habitat use by fishes. Information on species presence, abundance and associations are informative when collected from least impacted systems as this closely represents the near-natural baseline state for comparison with altered environments (Gullison *et al.*, 2015; Gatti *et al.*, 2015).

As already highlighted in the preceding chapters, there is currently very limited knowledge on the ecology and habitat use of small fish species in the Kabompo River, and indeed the Upper Zambezi River system in general, which hinders effective conservation and management to reduce the impacts of human activities in the region. Seasonal habitat movements of both small and large species onto the floodplains is well documented in the Upper Zambezi (Kelley, 1968; Purvis, 2002), but at present targeted low water movement and habitat use studies mainly focused on large cichlid species and tigerfish *Hydrocynus vittatus* using radio telemetry tags (Thorstad *et al.*, 2001; Thorstad *et al.*, 2004; Thorstad *et al.*, 2005; Økland *et al.*, 2005; Økland *et al.*, 2007). Therefore, knowledge of low water habitat associations for small-bodied fishes is limited or rather anecdotal. The development of baseline data on species abundance, diversity, habitat associations and identification of potential indicator species provides a benchmark for monitoring the influence and impacts of future developments within the Kabompo River basin. The aim of the present study was to document, for the first time, habitat associations of freshwater fishes in the Kabompo River through targeted sampling of five dominant mesohabitats during the low flow period. It was hypothesised that (i) heterogeneous and complex mesohabitats will host higher species diversity and abundance than homogenous and less complex mesohabitats, (ii) species will show consistent association with specific mesohabitat features, for example rocky habitats, vegetated river margins and woody habitats, and (iii) stenotopic species will be the more promising to use as surrogates or indicators of ecological change that affect specific habitats. The implications of the research findings are discussed regarding the management of important small fish communities and the long-term sustainability of subsistence and small-scale fisheries in the region.

Methods

Sampling was conducted during the dry season (September – November) of 2019 in the middle reaches of the Kabompo River (Figure 18). The Kabompo is a large perennial eastern headwater tributary of the Upper Zambezi River located in Zambia's Northwestern Province. Sampling focussed on shallow (< 1 m deep) wadable sections of the river due to safety risks associated with the presence of crocodiles and hippopotamus. Reconnaissance trips were made by boat along a 25 km stretch of the river near Jivundu, 450km downstream from its source and 300 km upstream from the confluence with the Zambezi River, to identify suitable sites (Figure 18). Within each sampling site (20 – 178 m length), fish were sampled from available and accessible (< 1 m deep) distinct mesohabitats (Table 2; Figure 19) using a backpack electrofisher (SAMUS 750MP, frequency 50-80 Hz, duration 30- 300 microseconds with a D-shaped net 30cm L x 15cm W and 1 mm mesh size). A total of 139 mesohabitats were sampled across the 14 sites (labelled CRK001 to CRK014) and five mesohabitat types, utilising a two-step method, i) mesohabitat identification and fish collection, ii) measuring mesohabitat variables and environmental parameters. This two-step method ensured each mesohabitat was disturbed as little as possible before sampling. Site CRK002 was excluded from the analyses due to the absence of one of the dominant habitat types. The location of all 14 sites is available in Appendix 1, Table A1.

Table 2: General description of mesohabitat types that were sampled during low flow period in the Kabompo River in 2019. The number of mesohabitats sampled for each habitat type is also indicated.

Habitat	Code	Definition	No. mesohabitats
Bare substrate	Bare	Sections of gravel and sand bottoms isolated from structured habitats, with filamentous algae occasionally present.	16
P. mauritianus	Phrag	A section of riverbank or island dominated by emergent *Phragmites mauritianus* (acute reed).	29
Rock	Rock	An area dominated by cobble, boulders or bedrock in still or flowing waters.	33
V. aethiopica	Vall	Patches of *Vallisneria aethiopica* over sand and gravel substrate	30
Woody debris	Wood	Partially or completely submerged log, tree roots or tree branches along the bank or in the main channel	31

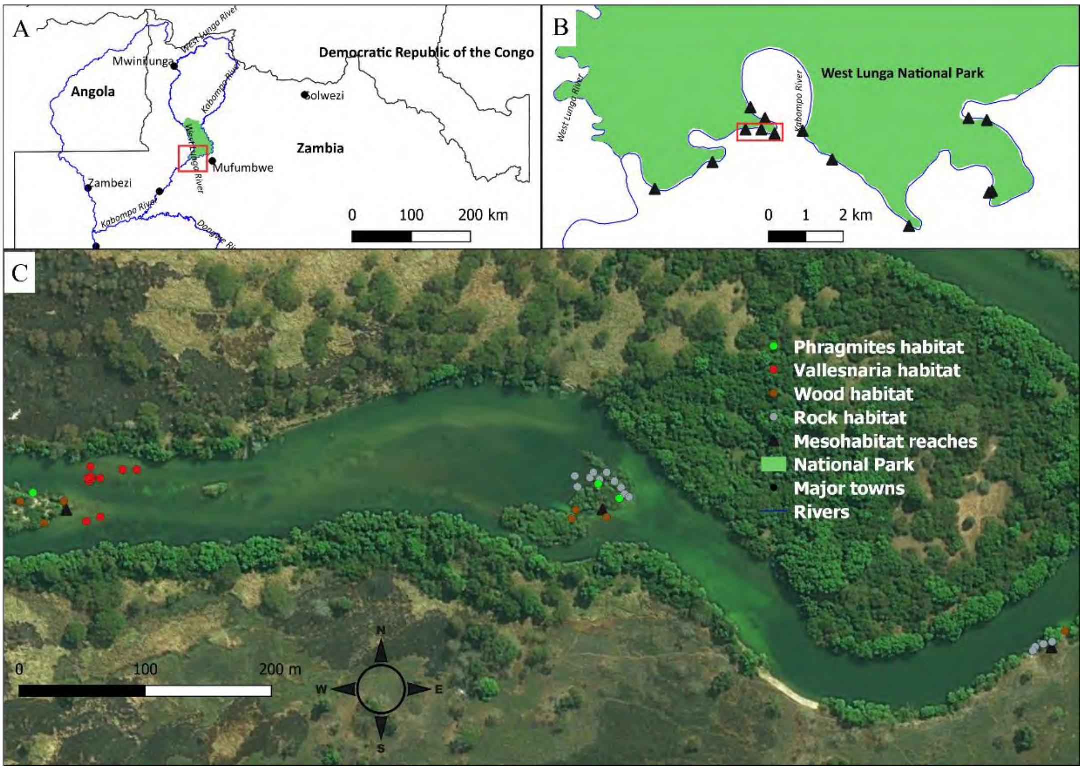

Figure 18: A) Locality of mesohabitat sites sampled in the Kabompo River. B) Distribution of the 14 sites where the mesohabitats were sampled. C) Example of the distribution of mesohabitats sampled at a site.

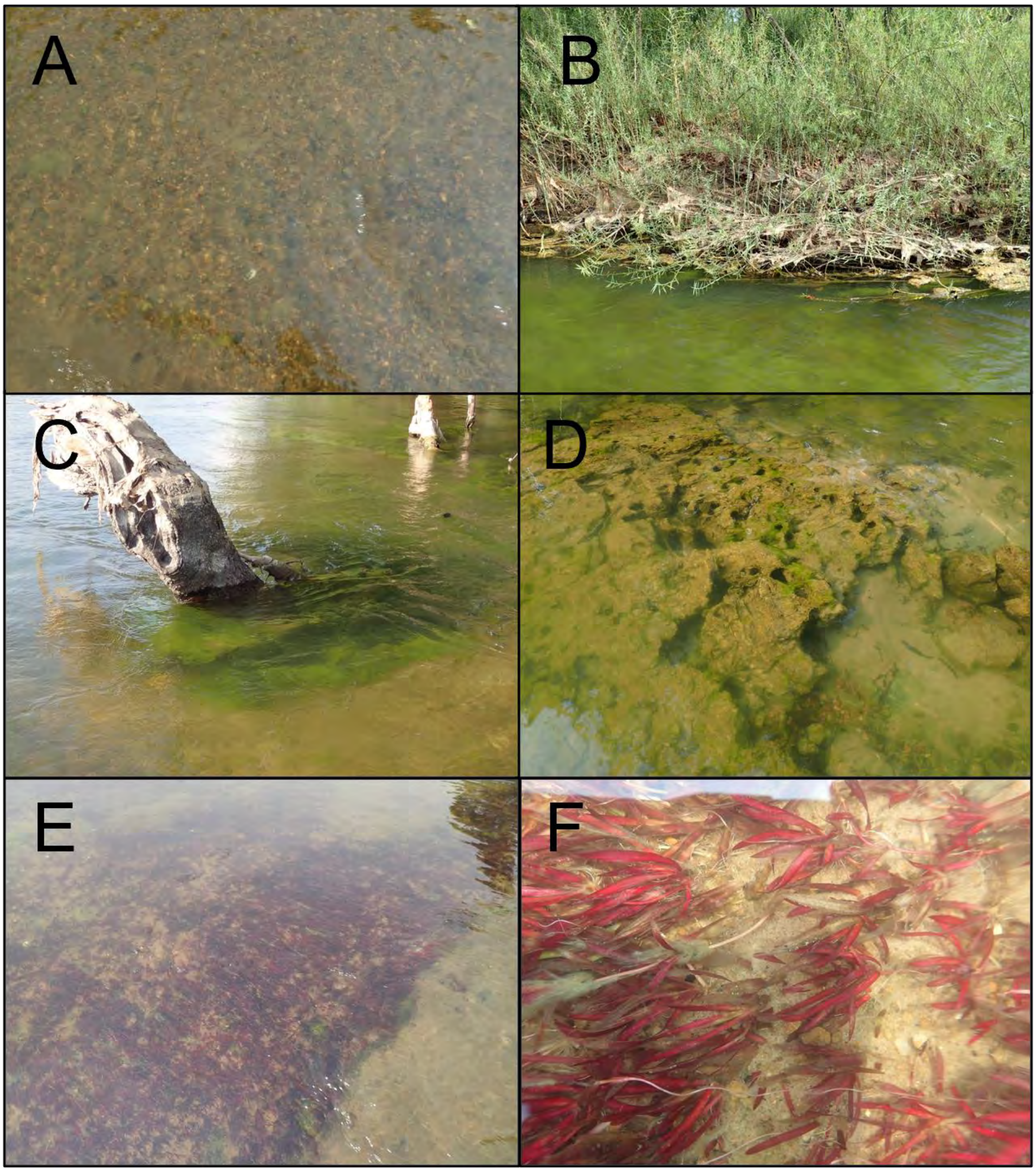

Figure 19: Photographs of the five main habitats sampled during the habitat use survey in the middle Kabompo. A) gravel; B) marginal *Phragmites mauritianus*; C) example of a partially submerged log; D) Rock habitat with bedrock and cobble present; E) *Vallisneria aethiopica*; F) Close up image of the short *Vallisneria aethiopica*

Site identification and fish collection

All mesohabitats in a shallow river reach were identified before sampling to ensure there were at least 3 metres between sampled mesohabitats and limited overlap in habitat type. Sites were electrofished in an upstream direction to reduce the chance of recapturing individuals. The same person fished each mesohabitat to avoid sampling bias between operators. Block nets were not used in the present study, contrary to standard practice (Temple and Pearsons, 2007), due to safety risks and the suitability to use block nets in all five mesohabitat types consistently. The sampling duration was timed at each mesohabitat using a stopwatch, and a mesohabitat was considered sampled once no more stunned fish were caught. Sampled fish were put into a 20-litre bucket containing river water and allowed to recover. Fish were identified to species level using Skelton (2001), Bruwer and van der Bank (2003), and Tweddle *et al.* (2012), and their total length was recorded to the nearest millimetre using a wetted measuring board. Total length was selected due to the variations in tail forms amongst the species sampled, varying from pointed to forked. Once fish were identified and measured, they were returned to the river alive. Any non-fish bycatch was noted and immediately released.

Characterising habitat and environmental variables

A total of six habitat variables (length, width, mean depth, substrate type, mean current velocity, and estimated abundance of filamentous algae) were documented for each discrete mesohabitat. The sampled mesohabitat area was assessed by measuring the length parallel to the river channel, and three width measurements were taken at 25, 50, and 75% of the length perpendicular to the river channel. The mean depth and substrate type were measured and visually assessed at 25, 50 and 75% of the mesohabitat length using a replicate of three measurements along each width measurement, for a total of nine substrate and depth measurements per mesohabitat. Measurements of mesohabitat length and width were taken using a 100-metre tape measure. Depth was measured using a 1-metre ruler with the reading taken downstream of the current direction to prevent the current from pushing water up against the ruler and overestimating the depth. The substrate composition was evaluated by visually estimating the substrate type at each point, and the nine estimates were used to approximate the average overall substrate composition. Substratum was classified based on a modified

Wentworth scale (Bovee, 1986), classified as silt/sand (0.5-1 mm), gravel (10-60 mm), cobble (60-250 mm), boulder (250-1000 mm), and bedrock (> 1000 mm). Leaf litter and small woody debris were also noted as substratum types. Surface current velocity at each mesohabitat was measured using a foam float, timed to travel one metre using a stopwatch. Three current measurements taken at each mesohabitat were then converted into velocity ($cm.s^{-1}$) and averaged. The abundance of filamentous algae was visually estimated at each mesohabitat using the categories 0-25%, 25-50%, 50-75% and >75% coverage and given a score from 1-4, corresponding to the different categories of cover.

Statistical analysis

Relative abundance, species richness and diversity

The importance of different mesohabitat types for the small fish communities in the Kabompo River were assessed through differences in catch per unit effort (CPUE) (fish/ minute), sample species richness (S), Shannon-Weiner diversity (H′) (Shannon, 1948), and Pielou's evenness (J′) (Pielou, 1966). All statistical analyses were performed in R studio (RStudio Team, 2021) using the “vegan” (Oksanen *et al.*, 2019) and “car” packages (Fox *et al.*, 2019). Analyses were first performed on untransformed data. Untransformed data were tested for homogeneity of variance using a levene’s test (Fox et al., 2019). Untransformed catch per unit effort, sample species richness (S), Shannon-Weiner diversity (H′) and Pielou's evenness (J′) data was heterogeneous, and therefore, non-parametric Kruskal-Wallis tests were performed to test for significant differences in the indices calculated. Where significant difference were found a Wilcoxon rank sum test was performed using the conservative Bonferroni adjusted p-values. Statistical significance was set at a = 0.05 for all statistical test.

Habitat assemblage structure

Differences in fish species assemblage structure between mesohabitat types were described using individual species abundance. Only species with a frequency of occurrence ≥10% within one or more of the five mesohabitat types were incorporated in the analyses. Non-metric multidimensional scaling (nMDS) was used to describe patterns in fish assemblage structure between mesohabitats, as nMDS is a robust ordination technique commonly used to investigate fish assemblage structure (Ruetz *et al.*, 2007; Rowe *et al.*, 2009). Under the metaMDS function, data were autotransformed using Wisconsin double standardisation and square root transformed. Both transformations were found to improve results (Oksanen *et al.*, 2019). The nMDS was run on the autotransformed data using the Bray-Curtis dissimilarity indices with three dimensions ($k = 3$) and a maximum number of 100 iterations starting from the previous best. The overall performance of the nMDS was assessed using the stress coefficient (Clarke and Warwick, 1994). The difference in the composition of fish assemblages among habitats was further explored with a PERMANOVA, based on the Wisconsin double standardisation and square root transformed data and Bray-Curtis dissimilarity indices with 999 permutations (Clarke, 1993). Pairwise Adonis comparisons were performed to identify where the significant differences were present, using the conservative Bonferroni adjusted p-values (Arbizu, 2020). The mean between and within mesohabitat dissimilarities was calculated using the meandist function in “vegan”. To identify the species that most contributed to the total disparity between mesohabitats, similarity percentage analysis (SIMPER) was performed on the Wisconsin double standardisation, and square root transformed data using a cut-off of 70% (Clarke and Warwick, 1994).

Species-specific habitat use

Interactions between species-specific habitat uses were investigated using individual species log-transformed abundance data. Data were log transformed to reduce the influence of highly abundant species. Associations were investigated by canonical correspondence analysis (CCA). Only species that had a frequency of occurrence ≥10% in one or more mesohabitat types were included in the CCA analyses to reduce the influence of rare species. Before the CCA, the gradient length of species composition was tested using detrended correspondence analysis (DCA) (ter Braak, 1995; ter Braak and Smilauer, 2012). The gradient lengths were greater than 4 SD units, indicating a high beta diversity (ter Braak, 1995). Therefore, a unimodal model (CCA) was used as it is better suited for the data (ter Braak and Smilauer, 2012). The recorded mesohabitat variables were tested for collinearity using Pearson's correlations with a cut of off ($R = 0.7$) (Dormann *et al.*, 2013). Collinear variables were removed, and stepwise forward selection model building was performed to find the most parsimonious CCA model suggested by Borcard *et al.*, (2018). This process reduces the number of environmental variables by removing strong linear dependencies and keeping significant environmental variables (Borcard *et al.*, 2018). The results of the CCA were tested by permutations assessing the significance of each constrained axis and the significance of each environmental variable (Borcard *et al.*, 2018). All multivariate analyses were performed in Rstudio (RStudio Team, 2021) using the "vegan" package (Oksanen *et al.*, 2019). Additionally, the significance of species associations with the environmental variables and mesohabitats they clustered towards in the CCA was assessed using the signassoc function and 999 permutations and Sidak's corrected p-values for multiple testing available in the "indicspecies" package (De Cáceres and Jansen, 2020; De Cáceres, 2020).

Results

A total of 139 mesohabitats were sampled across the five main mesohabitat types in 13 sites from September to November 2019. Seven of these mesohabitats had no fish recorded (4 gravel, 1 *P. mauritianus*, 1 rock and 2 wood). A total of 2343 fish were collected across 13 families, 26 genera and 49 species, representing 53% of the species known to occur in the system (Table 3). Across the five main sampled mesohabitats, the most widespread and abundant species were *Enteromius greenwoodi* (FO = 64.03%) and *Chiloglanis fasciatus* (FO = 35.25%) (Figure 20) and three other species (*'Lacustricola' johnstoni, Pharyngochromis acuticeps, Tilapia sparrmanii*) and juvenile cichlids were also sampled across all the mesohabitat types. These juvenile cichlids were small (4-27 mm) and extremely difficult to identify in the field and were left with this description. Eleven *Enteromius* species were collected, with only *E. greenwoodi* found in all the five habitats and *E. lineomaculatus* was present in all except the bare habitat. *Enteromius unitaeniatus* occurred in *Phragmites* and woody habitats, whilst the remaining eight *Enteromius* species were present in all except the *Vallisneria* and bare habitats. Nine incidental species with an overall FO = 0.72% were recorded at a single mesohabitat site. *Oreochromis andersonii, O. macrochir and O. niloticus* were only found in *Phragmites* while *R. maunensis, S. nigromaculatus* and juvenile *Serranochromis* were only collected from rocky habitat and *C. rendalli, M. altisambesi* and *S. thamalakanensis* were only collected from the woody mesohabitat (Table 3). Bycatch was minimal and consisted of potamonautid crabs (*Potamonautes* spp) and unidentified tadpoles.

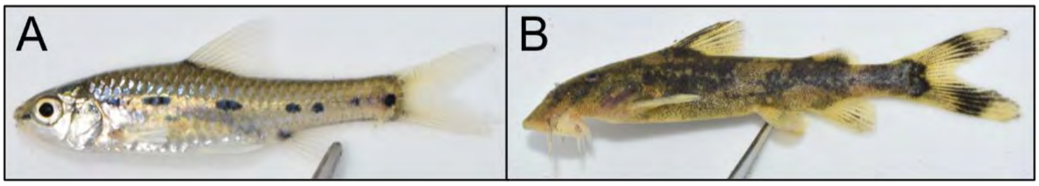

Figure 20: Dominant species in the middle Kabompo river. A) *Enteromius greenwoodi*; B) *Chiloglanis fasciatus*.

Table 3: The frequency of occurrence (FO), relative abundance in percentage (RA), the total number of individuals (n), and mean total length (max-min) of fish and two bycatch species caught in five microhabitats in the Kabompo River from September to November 2019.

		Frequency of occurrence						Relative abundance							Total length (mm)	
Species	Code	Overall	Phrag	Rock	Vall	Wood	Bare	Overall	Phrag	Rock	Vall	Wood	Bare	n	Mean	Range
Enteromius greenwoodi	EGRE	64.75	75.86	36.36	96.67	58.06	56.25	27.83	36.46	9.40	55.96	10.59	64.86	652	35.22	(61-25)
Chiloglanis fasciatus	CFAS	35.25	6.90	63.64	50.00	25.81	18.75	20.66	1.71	40.13	26.90	4.28	4.05	484	38.48	(59-22)
Nannocharax multifasciatus	NMUL	26.62	55.17	9.09	10.00	48.39	0.00	3.80	7.68	1.19	2.71	5.91	0.00	89	38.88	(49-32)
Tilapia sparrmanii	TSPA	25.18	48.28	15.15	3.33	45.16	6.25	4.18	7.46	1.85	0.18	9.57	1.35	98	59.65	(120-33)
Pharyngochromis acuticeps	PACU	25.18	13.79	57.58	20.00	16.13	6.25	4.82	0.85	7.28	8.48	1.02	2.70	113	26.62	(110-8)
Enteromius kerstenii	EKER	20.86	58.62	9.09	0.00	29.03	0.00	4.91	13.86	1.19	0.00	8.35	0.00	115	40.45	(65-10)
Synodontis macrostoma	SYOMA	20.14	6.90	48.48	3.33	29.03	0.00	3.84	0.43	6.75	0.18	7.33	0.00	90	82.10	(133-41)
Lacustricola johnstoni	LJOH	17.27	31.03	9.09	6.67	29.03	6.25	4.35	2.77	2.25	0.36	13.24	6.76	102	33.07	(44-25)
Enteromius eutaenia	EEUT	17.27	34.48	9.09	0.00	35.48	0.00	2.09	4.69	0.66	0.00	4.48	0.00	49	55.45	(80-35)
Enteromius fasciolatus	EFAS	16.55	44.83	6.06	0.00	25.81	0.00	3.46	4.48	0.53	0.00	11.41	0.00	81	39.46	(57-28)
Labeo cylindricus	LCYL	16.55	3.45	51.52	10.00	6.45	0.00	1.79	0.21	4.64	0.54	0.61	0.00	42	89.86	(184-43)
Hippopotamyrus szaboi	HANS	15.83	13.79	27.27	0.00	29.03	0.00	1.37	1.07	2.38	0.00	1.83	0.00	32	84.22	(149-47)
Enteromius lineomaculatus	ELIN	15.83	41.38	6.06	6.67	19.35	0.00	2.09	5.54	0.26	0.36	3.87	0.00	49	44.23	(60-31)
Cichlidae juvenile	CJUV	10.07	10.34	3.03	10.00	6.45	31.25	1.20	0.85	0.13	2.17	0.41	12.16	28	12.54	(27-4)
Enteromius radiatus	ERAD	10.07	17.24	6.06	0.00	22.58	0.00	1.62	1.49	0.26	0.00	5.91	0.00	38	50.26	(77-35)
Nannocharax dageti	NDAG	10.07	6.90	3.03	16.67	19.35	0.00	0.73	0.64	0.13	0.90	1.63	0.00	17	41.41	(49-35)
Pseudocrenilabrus philander	PPHI	8.63	17.24	6.06	0.00	12.90	6.25	0.81	1.49	0.79	0.00	1.02	1.35	19	44.84	(72-22)
Parauchenoglanis ngamensis	PNGA	7.91	6.90	9.09	0.00	19.35	0.00	0.47	0.43	0.40	0.00	1.22	0.00	11	87.00	(157-42)
Enteromius unitaeniatus	EUNI	6.47	10.34	0.00	0.00	19.35	0.00	0.55	0.64	0.00	0.00	2.04	0.00	13	71.08	(85-57)
Enteromius afrovernayi	EAFR	6.47	17.24	3.03	0.00	9.68	0.00	0.73	2.13	0.53	0.00	0.61	0.00	17	34.65	(47-27)
Mastacembelus frenatus	MFRE	5.76	0.00	9.09	6.67	6.45	6.25	0.34	0.00	0.40	0.36	0.41	1.35	8	137.75	(195-90)
Petrocephalus longicapitis	PLON	5.76	0.00	24.24	0.00	0.00	0.00	0.85	0.00	2.65	0.00	0.00	0.00	20	68.20	(83-43)
Enteromius poechii	EPOE	5.04	10.34	3.03	0.00	9.68	0.00	0.47	1.28	0.13	0.00	0.81	0.00	11	67.82	(99-57)
Enteromius paludinosus	EPAL	5.04	13.79	3.03	0.00	6.45	0.00	0.38	1.07	0.13	0.00	0.61	0.00	9	49.11	(57-38)
Schilbe depressirostris	SDEP	5.04	17.24	0.00	0.00	6.45	0.00	0.30	1.07	0.00	0.00	0.41	0.00	7	103.14	(131-71)

Micralestes acutidens	MACU	5.04	3.45	12.12	6.67	0.00	0.00	3.16	0.21	9.40	0.36	0.00	0.00	74	26.55	(62-17)
Opsaridium zambezense	OZAM	4.32	3.45	15.15	0.00	0.00	0.00	0.68	0.21	1.99	0.00	0.00	0.00	16	52.40	(95-17)
Zaireichthys sp. 'brown north'	ZNOR	3.60	0.00	6.06	6.67	0.00	6.25	0.21	0.00	0.26	0.36	0.00	1.35	5	31.60	(38-20)
Enteromius bifrenatus	EBIF	3.60	6.90	3.03	0.00	6.45	0.00	0.30	0.64	0.26	0.00	0.41	0.00	7	41.00	(47-34)
Amphilius uranoscopus	AURA	3.60	0.00	12.12	0.00	3.23	0.00	0.38	0.00	1.06	0.00	0.20	0.00	9	71.44	(102-45)
Petrocephalus okavangoensis	POKA	2.88	0.00	3.03	0.00	9.68	0.00	0.21	0.00	0.26	0.00	0.61	0.00	5	65.60	(88-43)
Alestidae juvenile	AJUV	1.44	0.00	3.03	0.00	0.00	6.25	0.47	0.00	1.06	0.00	0.00	4.05	11	21.14	(22-15)
Pollimyrus marianne	PMAR	1.44	0.00	0.00	0.00	6.45	0.00	0.09	0.00	0.00	0.00	0.41	0.00	2	66.00	(69-63)
Clarias theodorae	CTHE	1.44	0.00	3.03	0.00	3.23	0.00	0.09	0.00	0.13	0.00	0.20	0.00	2	78.50	(83-74)
Synodontis sp.	-	1.44	0.00	3.03	3.33	0.00	0.00	0.09	0.00	0.13	0.18	0.00	0.00	2	63.5	(64-63)
Clarias stappersii	CSTA	1.44	0.00	6.06	0.00	0.00	0.00	0.09	0.00	0.26	0.00	0.00	0.00	2	181.50	(261-102)
Cyphomyrus cubangoensis	CCUB	1.44	0.00	6.06	0.00	0.00	0.00	0.13	0.00	0.40	0.00	0.00	0.00	3	69.00	(83-60)
Serranochromis macrocephalus	SMAC	1.44	0.00	6.06	0.00	0.00	0.00	0.09	0.00	0.26	0.00	0.00	0.00	2	213.50	(274-153)
Coptodon rendalli	CREN	0.72	0.00	0.00	0.00	3.23	0.00	0.04	0.00	0.00	0.00	0.20	0.00	1	82.00	-
Marcusenius altisambesi	MALT	0.72	0.00	0.00	0.00	3.23	0.00	0.04	0.00	0.00	0.00	0.20	0.00	1	96.00	-
Synodontis thamalakanensis	STHA	0.72	0.00	0.00	0.00	3.23	0.00	0.04	0.00	0.00	0.00	0.20	0.00	1	87.00	-
Rhabdalestes maunensis	RMAU	0.72	0.00	3.03	0.00	0.00	0.00	0.04	0.00	0.13	0.00	0.00	0.00	1	22.00	-
Serranochromis juvenile	SJUV	0.72	0.00	3.03	0.00	0.00	0.00	0.04	0.00	0.13	0.00	0.00	0.00	1	33.00	-
Synodontis nigromaculatus	SNIG	0.72	0.00	3.03	0.00	0.00	0.00	0.04	0.00	0.13	0.00	0.00	0.00	1	136.00	-
Oreochromis andersonii	OAND	0.72	3.45	0.00	0.00	0.00	0.00	0.04	0.21	0.00	0.00	0.00	0.00	1	109.00	-
Oreochromis macrochir	OMAC	0.72	3.45	0.00	0.00	0.00	0.00	0.04	0.21	0.00	0.00	0.00	0.00	1	96.00	-
Oreochromis niloticus	ONIL	0.72	3.45	0.00	0.00	0.00	0.00	0.04	0.21	0.00	0.00	0.00	0.00	1	81.00	-
Crab (*Potamonautes* spp)	CRAB	28.06	34.48	33.33	33.33	25.81	0.00							55	24.75	(92-4)
Tadpole	TADP	7.19	6.90	0.00	20.00	3.23	6.25							12	52.00	(67-10)

Abundance, species richness and diversity

The Catch per unit effort (fish/ minute), species richness (S), Shannon-Weiner diversity (H′) and Pielou's evenness (J′) data were heterogeneous. Catch per unit effort was highest in the *Vallisneria* habitat (Figure 21) and differed significantly between the five mesohabitats types ($p < 0.05$). Catch per unit effort in the bare mesohabitat were significantly less than the rock, *P. mauritianus*, wood and *V. aethiopica* mesohabitats (Supplementary 1, Table S1). The CPUE in the *Vallisneria* was significantly different from the rocky and the woody habitats. Species richness was highest in *P. mauritianus* and woody habitats (Figure 21) and differed significantly ($p < 0.001$) among the five mesohabitats (Table 4). Bare and *V. aethiopica* mesohabitats hosted significantly lower species richness than the other three mesohabitat types (Supplementary 1, Table S2). The species richness in the *Vallisneria* was also significantly higher than in the bare substrate. The highest Shannon diversity and Pielou's evenness were observed in woody and *P. mauritianus* mesohabitats (Figure 21). The Shannon diversity differed significantly between the five mesohabitat types (Table 4). Shannon diversity in woody, *P. mauritianus* and rocky habitats was significantly different than in bare and *V. aethiopica* habitats ($p < 0.01$) (Supplementary 1, Table S3). The woody and *P. mauritianus* were significantly different from the rocky habitat. Similarly, Pielou's evenness differed significantly ($p < 0.001$) between mesohabitat types (Table 4). Bare mesohabitats had significantly different and more uneven species assemblage than wooded and *P. mauritianus* mesohabitats (Supplementary 1, Table S4). Evenness was further identified to be significantly different ($p < 0.05$) between rocky habitats and the woody and marginal *P. mauritianus*. Species evenness also differed significantly between the *Vallisneria* and woody habitats.

Table 4: Summary of Kruskal-Wallis test results comparing measures of catch per unit effort (CPUE), Sample species richness(S), Shannon-Weiner diversity (H′) and Pielou's evenness (J′) for the five main low water habitats.

Habitat	χ^2	df	p-value
CPUE	24.250	4	**<0.001**
S	46.732	4	**<0.001**
H’	53.875	4	**<0.001**
J’	22.948	4	**<0.001**

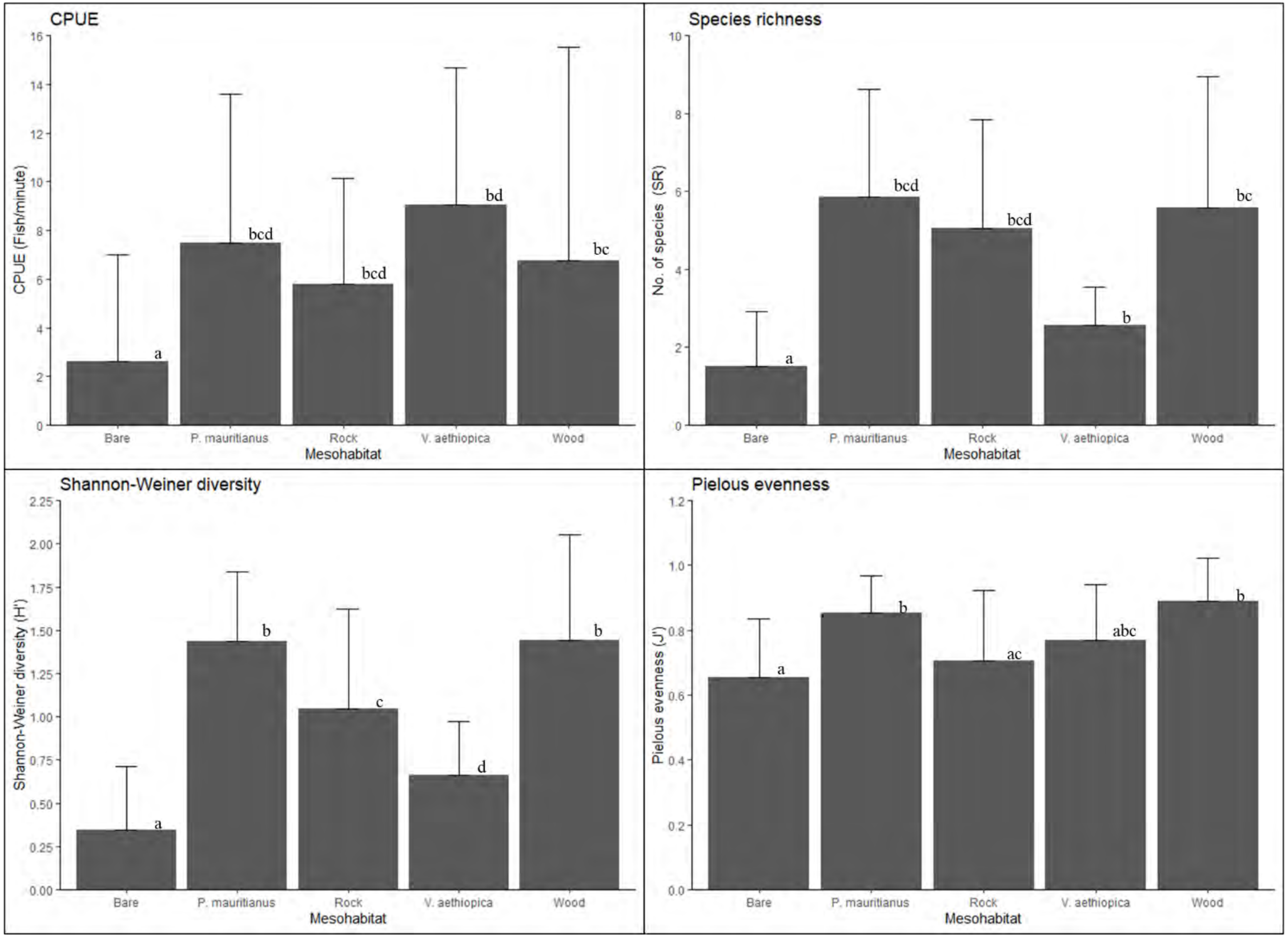

Figure 21: The mean and standard deviations for the fourth root transformed abundance, sample species diversity (S), Shannon-Weiner diversity (H′) and Pielou’s evenness (J′) between five dominant low water habitats in the middle Kabompo River

Mesohabitat species assemblage

The nMDS analysis showed overlap between species assemblages across mesohabitats (Figure 22). The nMDS stress level (stress = 0.198) represents an adequate configuration of the data in two dimensions. Differences in species assemblage between the five mesohabitat types were significant (ADONIS, $R^2 = 0.23$, p =0.001, Table 5), and habitat explained 23% of the variation in species assemblage. Species assemblages differed significantly ($p < 0.001$) between all habitats, except between bare and *V. aethiopica* mesohabitats (Supplementary 1, Table S5).

Table 5: Adonis2 performed on Wisconsin double standardisation and square root transformed species abundance for five low water mesohabitats in the Kabompo River. Using Bray-Curtis distance measure and 999 permutations.

	Df	SS	R2	F	Pr(>F)
Habitats	4	10.85	0.23	9.25	**0.001**
Residual	126	36.94	0.77		
Total	130	47.79	1.00		

The SIMPER analysis attributed the dissimilarity in species assemblages to fluctuations in shared species abundances and the presence/absence of species between the different mesohabitats (Table 6). The woody mesohabitat expressed the greatest within habitat dissimilarity (82%), while *V. aethiopica* habitat had the lowest within habitat dissimilarity (60.4%) (Table 7). The greatest between habitat dissimilarity was between the wooded and bare mesohabitats (92.0%) (Table 7). The dissimilarity between the wood and bare mesohabitats was caused by variations in common species abundance and the absence of *P. ngamensis*, *N. multifasciatus*, *E. eutaenia* and *N. dageti* in the bare mesohabitats (Table 6).

The *P. mauritianus* and woody mesohabitats showed considerable overlap in the nMDS, which is supported by the second lowest between mesohabitat dissimilarity in species abundance (79.9%, Table 7). Despite this, these assemblages are significantly different ($p < 0.05$, Supplementary 1, Table S5), attributed to differences in the abundance of 12 common species (Table 6). Species assemblages in bare mesohabitats was significantly different from all mesohabitats except the *V. aethiopica*, due to a combination of variability in species presence/absence and abundance (Table 6; Supplementary 1, Table S2-5). Generally, species presence and abundances were lower in the bare mesohabitats compared to the structured habitats.

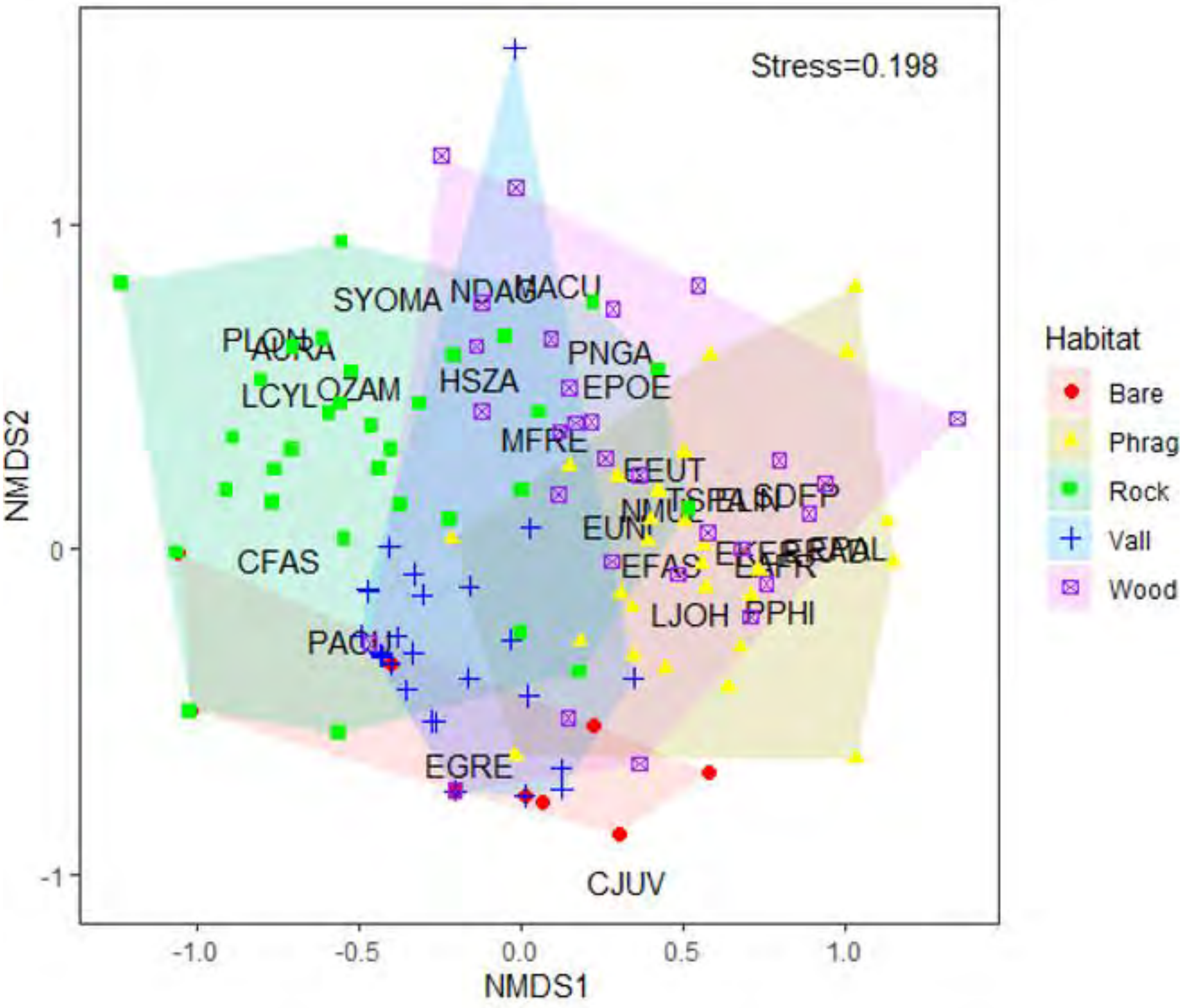

Figure 22: Non-metric multidimensional scaling (nMDS) ordination of 28 fish species abundance per sample among mesohabitats in the Kabompo River from September to November 2019; each point represents a sample (n = 123). Analysis performed using Bray-Curtis dissimilarity. Species codes are as per Table 3.

The heterogeneous or structured habitats had distinct species assemblages. Significant differences in species assemblage between the *P. mauritianus* and the rocky mesohabitats (p = 0.001, Supplementary 1, Table S5), were attributed to variations in the high abundance of *C. fasciatus, L. cylindricus* and *P. acuticeps* in rocky habitats and higher abundance of various *Enteromius* species in the *P. mauritianus*. The significant difference in assemblages between rocky and woody mesohabitats was largely influenced by variations in the abundance of *L. cylindricus* and *C. fasciatus* in these two habitats (p = 0.001, Supplementary 1, Table S5; Table 6). Lastly, the species assemblages of *V. aethiopica* mesohabitats were significantly different from the complex structured habitats. The mean dissimilarity between the *P. mauritianus* and *V. aethiopica* habitats was 86.9%, and species assemblages differed significantly (p = 0.001, Supplementary 1, Table S5). The high abundance of *E. greenwoodi* and the absence of *E. kerstenii, E. eutaenia* and *E. fasciolatus* in the *V. aethiopica* contributed the greatest to its dissimilarity. Similarly, species assemblages in wooded and *V. aethiopica* mesohabitats differed significantly ($p = 0.001$; Supplementary 1, Table S5), influenced by higher abundances of *E. greenwoodi* and *C. fasciatus* in the *V. aethiopica* compared to higher abundances of numerous *Enteromius* species in the woody habitats that were absent from the *V. aethiopica* (Table 6). Lastly, compared to the rocky mesohabitat, *V. aethiopica* had a higher abundance of *E. greenwoodi* while *L. cylindricus* and *P. acuticeps* were more abundant in rocky mesohabitats and contributed greatest to the dissimilarity. The full SIMPER analysis tables are available in supplementary 1 Table S6 to Table S15.

Table 6: Species identified by SIMPER analysis as responsible for greater than 70% of the total dissimilarity between five low water mesohabitat fish species assemblages in the Kabompo River. Percentages represent the proportion of dissimilarity and cumulative dissimilarity in brackets. Habitat and species codes as per Table 2 and Table 3 respectively.

Bare vs Phrag		Bare vs Rock		Bare vs Vall		Bare vs Wood		Phrag vs Rock	
EGRE	21% (21%)	EGRE	22% (22%)	EGRE	27% (27%)	EGRE	22% (22%)	LCYL	10% (10%)
CJUV	12% (33%)	CFAS	16% (38%)	CFAS	22% (49%)	CFAS	12% (34%)	CFAS	9% (19%)
CFAS	11% (44%)	CJUV	11% (49%)	CJUV	16% (65%)	CJUV	11% (45%)	PACU	7% (26%)
ELIN	6% (50%)	PACU	11% (60%)	PACU	11% (76%)	PACU	5% (50%)	ELIN	7% (33%)
EKER	6% (56%)	LCYL	10% (70%)			TSPA	5% (55%)	EKER	6% (39%)
PACU	5% (61%)	SYOMA	4% (74%)			PNGA	5% (60%)	EGRE	5% (44%)
NMUL	5% (66%)					NMUL	4% (64%)	EEUT	6% (50%)
EEUT	5% (71%)					EEUT	3% (67%)	NMUL	5% (55%)
						NDAG	4% (71%)	TSPA	4% (59%)
								SYOMA	4% (63%)
								HSZA	4% (67%)
								SDEP	3% (70%)

Phrag vs Vall		Phrag vs Wood		Rock vs Vall		Rock vs Wood		Vall vs Wood	
EGRE	19% (19%)	EGRE	8% (8%)	EGRE	23% (23%)	LCYL	10% (10%)	EGRE	21% (21%)
CFAS	11% (30%)	ELIN	8% (16%)	CFAS	13% (36%)	CFAS	10% (20%)	CFAS	12% (33%)
ELIN	8% (38%)	EEUT	7% (23%)	LCYL	12% (48%)	PACU	7% (27%)	NDAG	8% (41%)
NDAG	6% (44%)	EKER	7% (30%)	PACU	10% (58%)	TSPA	6% (33%)	NMUL	6% (47%)
NMUL	6% (50%)	TSPA	6% (36%)	NDAG	6% (64%)	EGRE	6% (39%)	TSPA	5% (52%)
EKER	6% (56%)	EUNI	6% (42%)	SYOMA	4% (68%)	PNGA	6% (45%)	PACU	5% (57%)
EEUT	5% (61%)	NMUL	6% (48%)	CJUV	3% (71%)	SYOMA	4% (49%)	PNGA	4% (61%)
PACU	5% (66%)	PNGA	6% (54%)			EEUT	5% (54%)	EEUT	4% (65%)
CJUV	4% (70%)	SDEP	5% (59%)			NMUL	5% (59%)	EUNI	4% (69%)
TSPA	4% (74%)	NDAG	5% (64%)			HSZA	4% (63%)	CJUV	3% (72%)
		HSZA	4% (68%)			NDAG	4% (67%)		
		EFAS	4% (72%)			EUNI	4% (71%)		

Table 7: Mean between and within habitat dissimilarity based on species relative abundance.

	Bare	*P. mauritianus*	Rock	*V. aethiopica*	Wood
Bare	73.2%				
P. mauritianus	90.4%	74.5%			
Rock	91.4%	91.4%	77.0%		
V. aethiopica	68.8%	86.9%	85.3%	60.4%	
Wood	92.0%	79.9%	89.1%	88.4%	82.0%
Mean within groups		73.4%			
Mean between groups		86.7%			
Overall between group		83.9%			

Fish habitat use

The relationship between log-transformed species abundance with environmental variables were assessed using canonical correspondence analysis (CCA). The test for collinearity incorporating the five mesohabitat types and eight other habitat characteristics, identified three variables (rocky substrate, woody debris substrate and gravel substrate) to have an $R > 0.7$ with their respective mesohabitat variable and were excluded (Supplementary 1, Table S16). The remaining analyses were performed on the five main mesohabitat types and five environmental factors. The DCA's performed on the log-transformed abundance data had gradient lengths greater than 4 SD units (Table 8). Therefore, a CCA (a unimodal model) is better suited for the data.

Table 8: Results of a DCA performed on log-transformed abundance data for 28 fish species from the middle Kabompo River in the 2019 low water season

Log-abundance	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.604	0.358	0.332	0.290
Decorana values	0.632	0.355	0.304	0.202
Axis lengths	4.317	4.477	4.230	3.510

The relationship between species abundance and environmental variables incorporated five environmental variables. These five variables were selected using a stepwise forward selection and 999 permutations (Supplementary 1, Table S17). The first two axes of the CCA ordination explained 65.6% of the variation between log-transformed species abundance and the five selected environmental variables (Table 9). The first four component axes were statistically significant ($p < 0.05$, Table 9). Species are separated along axis one by increased mean current velocity, while axis two separates species by mean habitat depth (Figure 23). Based on the CCA ordination and the permutation test, five variables, habitat type, mean surface current velocity, mean habitat depth, filamentous algae cover and leaf litter substrate had a significant effect on fish species abundance (Table 10).

Table 9: Summary of the CCA performed on the log abundance of 28 fish species from the Kabompo River and the anova.cca by axis performed with 999 permutations.

	Summary of the CCA			Anova.cca			
Axis	Eigenvalue	Proportion Explained	Cumulative Proportion	DF	ChiSquare	F value	Pr(>F)
CCA1	0.518	0.421	0.421	1	0.518	18.902	**0.001**
CCA2	0.288	0.234	0.656	1	0.288	10.518	**0.001**
CCA3	0.199	0.162	0.818	1	0.199	7.270	**0.001**
CCA4	0.074	0.060	0.878	1	0.074	2.703	**0.010**
CCA5	0.059	0.048	0.926	1	0.059	2.149	0.061
CCA6	0.043	0.035	0.961	1	0.043	1.583	0.327
CCA7	0.030	0.024	0.985	1	0.030	1.082	0.717
CCA8	0.018	0.015	1.000	1	0.018	0.668	0.869
Residual				122	3.345		

Table 10: Summary of anova.cca by term performed with 999 permutations for the CCA performed on species abundance.

Environmental variable	Df	ChiSquare	F value	Pr(>F)
Habitat	4	0.727	6.626	**0.001**
Current velocity	1	0.296	10.783	**0.001**
Mean depth	1	0.101	3.686	**0.001**
Algae	1	0.054	1.981	**0.007**
Leaf littler	1	0.053	1.919	**0.025**
Residual	122	3.345		

The analysis of species abundance data returned three distinct clusters, namely, i) a *P. mauritianus*/ wooded mesohabitat, ii) rock habitat/ habitat depth and iii) rheophilic cluster. Most of the species (15/28) were associated with the *P. mauritianus* and woody habitats while negatively associated with current velocity (Figure 23). The abundance of *E. eutenia*, *E. fasciolatus*, *E. radiatus*, *E. unitaeniatus*, *'L'. johnstoni* and *P. ngamensis* was significantly ($p < 0.05$) positively associated with wooded mesohabitats (Table 11). The abundance of six species (*E. eutaenia, E. kerstenii, E. lineomaculatus, N. multifasciatus, S. depressirostris* and *T. sparrmanii*) are significantly associated ($p < 0.02$) with *P. mauritianus*. Three species *E.*

eutaenia, N. multifasciatus and *T. sparrmanii* are significantly associated (p < 0.05) with *P. mauritianus* and woody mesohabitats. The six species (*H. szaboi, P. longicapitis*, *L. cylindricus*, *O. zambezense*, *A. uranoscopus* and *S. macrostoma)* that clustered with the rocky mesohabitat were all significantly associated (p ≤ 0.02) with this mesohabitat type (Table 11). The abundance of *H. szaboi* was further significantly associated (p < 0.01) with habitat depths greater than 56 cm (Table 11). Additionally, *C. fasciatus*, and *P. acuticeps* that clustered with increased current velocity showed a strong significant association (p < 0.005) with the rocky mesohabitat (Table 11). Based on species abundance, *M. acutidens* clustered towards increased mean habitat depth and rocky habitat and were significantly associated (p < 0.05) with both these environmental factors (Table 11). Three species (*C. fasciatus*. *N. dageti,* and *P. acuticeps*) were associated with increased mean current velocity indicating a more rheophilic response. Analyses of the significance of the relationship indicated that only *C. fasciatus* had a significant association (p < 0.01) with strong current velocities. In contrast, 13 species showed significant positive associations with very weak to weak current velocities (Table 11). The abundance of *E. greenwoodi* and juvenile cichlids were associated with increased algae density (Figure 23). *Enteromius greenwoodi* abundance was significantly associated (p = 0.005) with *V. aethiopica* and juvenile cichlids associated (p = 0.025) with the bare mesohabitat (Table 11). Five species (*E. afrovernayi*, *E. paludinosus*, *Enteromius poechii*, *N. dageti* and *P. philander*) showed no significant positive association with any of the five mesohabitat types but were associated with current velocity or depth based on Sidak's corrected p-values. *Mastacembelus frenatus* showed no significant any of the environmental variables incorporated in the present analysis.

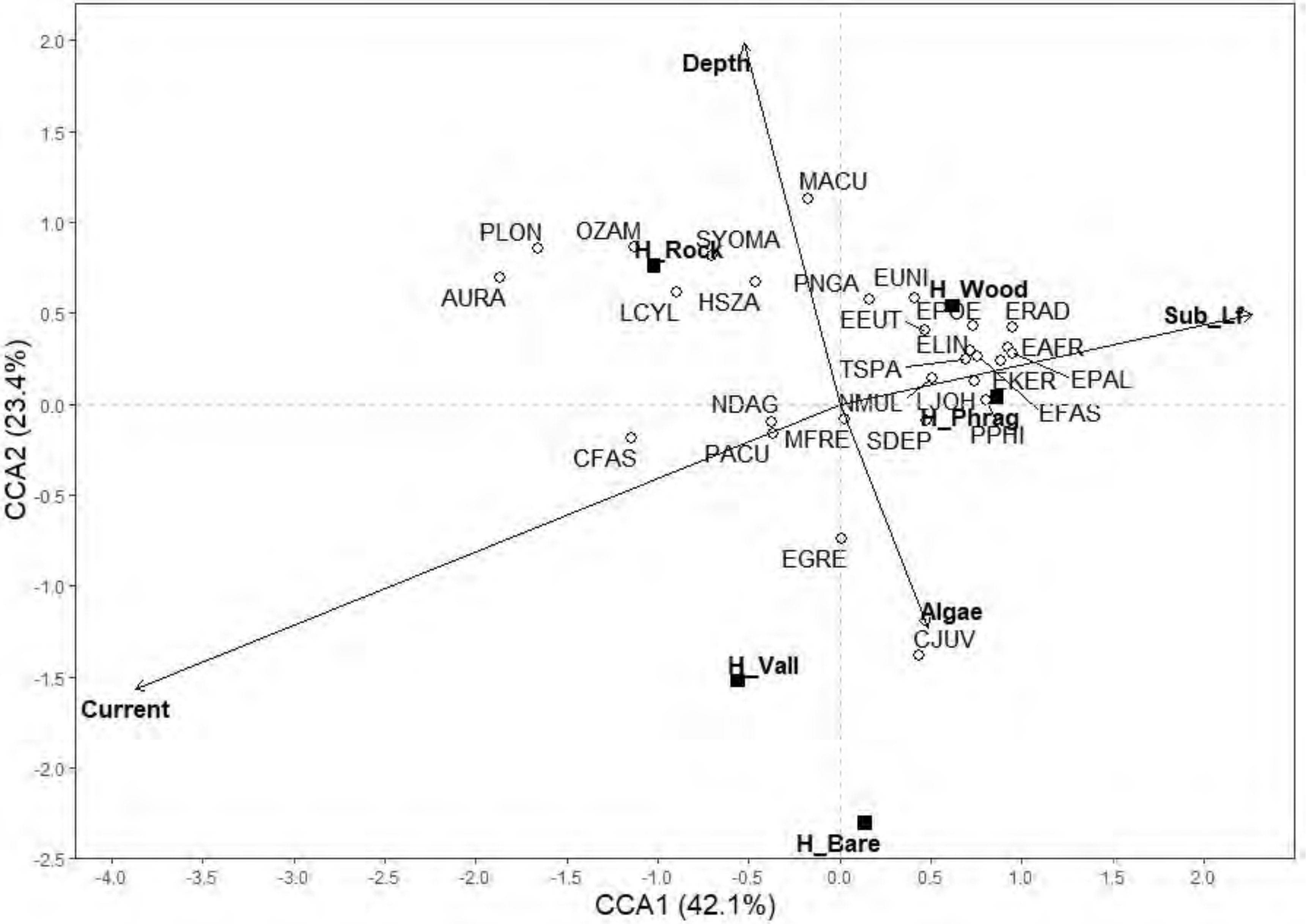

Figure 23: Canonical correspondence analysis (CCA) tri-plot of associations between fish community structure and various environmental variables based on log-transformed abundance data for 28 small fish from the Kabompo River. Scaling type two. Species are abbreviated by the first letter of their genus and the first three letter of their species name as per Table 3. , H_bare: bare habitat, H_Vall: *Vallisneria* mesohabitat, H_Phrag: *Phragmites* mesohabitat, H_wood: wooded mesohabitat, H_rock: rocky mesohabitat, sub_Lf: leaf litter substrate.

Table 11: Association between species abundance and three environmental variables for 28 fish species from the Kabompo based on Sidak's corrected p-values for the 2019 low water season. Species abbreviations are the same as for the CCA above. Number in bold indicate p-values < 0.05. Number below the current categories indicate the flow range in cm/s and the numbers below the depth catagories indicate the depth range in cm.

	Mesohabitat type					Current					Habitat depth			
Species	Bare	Phrag	Rock	Vall	Wood	Still	Weak	Medium	Strong	Very strong	Shallow	medium	Deep	Very deep
						0-20	20.1-40	40.1-60	60.1-80	>80	0-23	24-40	41-55	>55
AURA	1.000	1.000	**0.015**	1.000	1.000	1.000	1.000	1.000	1.000	0.07	1.000	1.000	1.000	0.34
CFAS	1.000	1.000	**0.005**	0.06	1.000	1.000	1.000	1.000	**0.005**	0.155	0.285	1.000	1.000	1.000
CJUV	**0.025**	1.000	1.000	1.000	1.000	0.26	1.000	1.000	1.000	1.000	0.34	1.000	1.000	1.000
EAFR	1.000	0.09	1.000	1.000	1.000	**0.005**	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EEUT	1.000	**0.005**	1.000	1.000	**0.02**	**0.005**	0.55	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EFAS	1.000	0.05	1.000	1.000	**0.02**	**0.005**	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.77
EKER	1.000	**0.005**	1.000	1.000	0.21	**0.005**	1.000	1.000	1.000	1.000	0.29	0.485	1.000	1.000
ELIN	1.000	**0.005**	1.000	1.000	0.25	**0.005**	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EGRE	1.000	0.43	1.000	**0.005**	1.000	1.000	1.000	1.000	0.46	1.000	**0.01**	0.58	1.000	1.000
EPAL	1.000	0.125	1.000	1.000	1.000	**0.03**	1.000	1.000	1.000	1.000	1.000	1.000	0.575	1.000
EPOE	1.000	0.27	1.000	1.000	0.665	**0.005**	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ERAD	1.000	1.000	1.000	1.000	**0.005**	**0.005**	1.000	1.000	1.000	1.000	1.000	0.08	1.000	1.000
EUNI	1.000	1.000	1.000	1.000	**0.025**	0.635	0.305	1.000	1.000	1.000	1.000	1.000	0.365	1.000
HSZA	1.000	1.000	**0.02**	1.000	0.26	1.000	1.000	0.19	1.000	1.000	1.000	1.000	1.000	0.05
LCYL	1.000	1.000	**0.005**	1.000	1.000	1.000	1.000	1.000	0.225	1.000	1.000	1.000	1.000	0.365
MFRE	0.965	1.000	1.000	1.000	1.000	0.97	1.000	0.865	1.000	1.000	1.000	1.000	1.000	0.155
MACU	1.000	1.000	**0.005**	1.000	1.000	**0.035**	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**0.01**
LJOH	1.000	1.000	1.000	1.000	**0.045**	**0.005**	1.000	1.000	1.000	1.000	1.000	0.065	1.000	1.000
NDAG	1.000	1.000	1.000	0.72	0.1	1.000	1.000	0.205	1.000	1.000	1.000	1.000	0.78	1.000
NMUL	1.000	**0.01**	1.000	1.000	**0.02**	**0.005**	0.155	1.000	1.000	1.000	1.000	0.105	1.000	1.000
OZAM	1.000	1.000	**0.005**	1.000	1.000	1.000	1.000	1.000	0.09	1.000	1.000	1.000	1.000	1.000
PNGA	1.000	1.000	1.000	1.000	**0.025**	0.27	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.25
PLON	1.000	1.000	**0.005**	1.000	1.000	1.000	1.000	0.475	1.000	1.000	1.000	0.19	1.000	1.000
PACU	1.000	1.000	**0.005**	0.455	1.000	1.000	1.000	0.34	1.000	1.000	1.000	1.000	1.000	1.000
PPHI	1.000	0.42	1.000	1.000	1.000	**0.005**	1.000	1.000	1.000	1.000	0.135	1.000	1.000	1.000
SDEP	1.000	**0.015**	1.000	1.000	1.000	0.99	0.555	1.000	1.000	1.000	1.000	0.885	1.000	1.000
SYOMA	1.000	1.000	**0.005**	1.000	0.255	1.000	1.000	0.435	1.000	1.000	1.000	1.000	1.000	0.355
TSPA	1.000	**0.04**	1.000	1.000	**0.01**	**0.005**	1.000	1.000	1.000	1.000	0.54	1.000	1.000	1.000

Discussion

Freshwater fish communities are structured through an intricate interaction of abiotic and biotic factors at various spatial scales (Galacatos *et al.*, 2004; Watkins *et al.*, 2015; Spurgeon *et al.*, 2018). Five environmental factors (current velocity, habitat type, depth, leaf litter and algae density) investigated in this study were all relevant to the spatial distribution of small fish species in the Kabompo River at a mesohabitat scale. The first two component axes explained 66% of the variability in fish community structure. The 'variation explained' is notable and likely due to the study occurring on a mesohabitat scale, as processes explaining species abundance and assemblage patterns become more challenging to identify at larger scales (Ims, 2005). The proportion of unexplained variation is attributed to the lack of fit of the data to the response model (Økland, 1999), spatial structuring itself (Borcard and Legendre, 1994), and other factors not assessed (Dray *et al.*, 2012).

All the environmental factors incorporated in the present study affect species abundance and distribution in river systems elsewhere (Crook *et al.*, 2001; Love *et al.*, 2017). Physical habitat structure has long been recognised as one of the primary features driving fish assemblages and composition (Gorman and Karr, 1978; Schlosser, 1982; Johnson *et al.*, 2007), and is an important focus for ecologists, fisheries scientists and restoration programs (Rosenfeld, 2003; Rosenfeld and Hatfield, 2006; Santos *et al.*, 2018). In freshwater systems, natural habitat structure is provided by woody debris, macrophytes and rocky structure (Everett and Ruiz, 1993; Matthews, 1998). In the Kabompo River, mesohabitat type significantly affected the relative abundance and diversity of small fish species, with more complex/heterogeneous habitats (*P. mauritianus*, rock, *V. aethiopica* and wood) hosting greater species diversity and CPUE than less complex mesohabitats (bare). Habitat heterogeneity influences the structure and composition of fish communities both directly and indirectly by regulating inter and intra-specific interactions of biotic and abiotic factors (Moniruzzaman *et al.*, 2021).

Two factors likely contribute towards driving higher diversity within more complex/heterogenous mesohabitats, i) refugia and ii) resources. In the main channel, wooded and rocky mesohabitats offer species protection from environmental factors (current velocity) and mediate predator-prey interactions (Barrios-O'Neill *et al.*, 2015), while *P. mauritianus* growing on the margins of the channel, disrupt flow along the shallow river's edge (van Ginkel and Cilliers, 2020). These refuge areas provide fish with an opportunity to conserve resources and limit metabolic activity (Crook and Robertson, 1999; Cook and Coughlin, 2010), while decreasing predation risks. The small fish communities in the Zambezi River have evolved with an assortment of fish, bird and mammalian piscivorous predators. The tigerfish *H. vittatus*, African pike *H. cuvieri*, large catfishes (*Clarias* spp) and the largemouth breams (*Serranochromis* spp.) are the dominant piscivorous fish predators in the Upper Zambezi, actively feeding on small mormyrid, cyprinids and synodontids (Jackson, 1961b; Winemiller, 1991). Predation structures species assemblages both directly and indirectly (Jackson *et al.*, 2001). Gorman (1988) proposed that a portion of this structuring can be attributed to prey species common avoidance of predators. During the low water season as protective habitats become more limited, species cluster in and around the remaining marginal or instream structures (Galacatos *et al.*, 2004; da Silva *et al.*, 2010), that provide physical and visual barriers to predators, reducing encounter rates and predator-prey interactions (Savino and Stein, 1982; Eklöv and Persson, 1995). However, the influence of these physical habitats on predator-prey interactions is species-specific (DeBoom and Wahl, 2013). For example, *H. vittatus* are active visual hunters that swallow prey fish whole, restricting their diet to small species (< 40% of the predators length) in open waters and the river margins near vegetation (Jackson, 1961; Økland *et al.*, 2005). In comparison, the *Serranochromis* species are more ambush and epibenthic predators (Winemiller, 1991), of the deeper marginal and backwater habitats (Thorstad *et al.*, 2001; Thorstad *et al.*, 2004). While increased habitat complexity can favour ambush predators (Martin *et al.*, 2010), small species use these shallow, complex habitats to avoid larger ambush predators, as larger species are more prone to terrestrial predation if the venture into shallow waters (Power, 1984). However, for the small fish species this is a trade off between predation by larger fish in deep water or birds in shallow water.

Although predation may play a role in structuring communities in the Kabompo River, habitat use is strongly linked to species resource requirements and ecomorphology. Structures in riverine habitats (e.g., macrophytes and woody structures and rocks) provide habitat for algae and invertebrates (Crook and Robertson, 1999; Benke and Wallace, 2003; Thomaz *et al.*, 2008) which provide a food source for small fishes. Woody structures play an essential role in streams and rivers as they create more heterogeneous habitats by increasing water depth and reducing current velocity (Kalogianni *et al.*, 2020). Sections with the reduced flow provide more appropriate conditions for phytoplankton and zooplankton production and the deposition of organic matter that provide a food source to invertebrates and small fish (Crook and Robertson, 1999). The *P. mauritianus* provide similar resource benefits as woody structures by creating a habitat for the aggregation of benthic invertebrates, zooplankton and detritus (Okun and Mehner, 2005; Okun *et al.*, 2005). A similar pattern likely occurs in the rocky habitat. The clustering of several *Enteromius* and other small fish species with wood, *P. mauritianus* and rock in still, or slow-flowing patches support findings for literature regarding their diet and ecology of feeding on aufwuchs, small invertebrates and zooplankton (Cambray, 1983; Skelton, 2001). These aggregations of resources are likely a significant contributor to the increased species diversity within these habitats.

Contrastingly, within the homogenous mesohabitats short *Vallisneria* and bare substrate do not provide similar benefits. Current velocity and depth were identified as two environmental variables that affected species presence and abundance. The *V. aethiopica* mesohabitats sampled in the present study were predominantly in shallow, fast-flowing sections and patches comprised of *V. aethiopica* plants with short ribbon-like leaves less than 10cm in length (CLR pers. obs.). These short *V. aethiopica* provide little refuge from the current velocity or predation, potentially evident by species within this habitat being sampled from the undercut sections behind the *V. aethiopica* patches (CLR pers. obs.). The lack of structure provides unfavourable conditions for some fish, invertebrates and algae species as macrophyte density mediates predator-prey interactions between fish species, fish-invertebrate predation and influences species diversity and abundance in freshwater systems (Valley and Bremigan, 2002; Pelicice *et al.*, 2008; Phiri *et al.*, 2012; Khosa *et al.*, 2021). Despite this, relative abundance in *V. aethiopica* was not different from the three structured habitats, due to the high abundance of *E. greenwoodi* and *C. fasciatus* that occurred in these small patches. The bare mesohabitat offers little protection and resources. The limited protection offered by the interstitial spaces of the bare substrate protects smaller species (e.g., *C. fasciatus* and *Z. pallidus*) that can use the available interstitial spaces or bury themselves in the substrate.(Camp *et al.*, 2012) Therefore, a combination of habitat simplicity and potentially unfavourable environmental variables are likely responsible for low species diversity in homogenous mesohabitats. Heterogenous/ complex habitats in low current velocity appear to be important refuges for small native fish species. Similar observations highlighting the importance of habitats in low flow for small-bodied fishes have been noted both in the field (e.g., the Kootenai River in Idaho (Branigan *et al.*, 2018), and laboratory experiments (Hockley *et al.*, 2014).

Throughout a species' life-history, a suite of complementary habitats are used at different stages to meet their requirements for optimal survival, growth and reproduction (Rosenberger and Angermeier, 2003). In the Kabompo River, this is evident in the large portion of small fish species that use the flooded vegetation during the annual flood cycle before being forced back to the mainstem habitats once waters subside (Kelley, 1968; Purvis, 2002). During the assessment of five dominant low flow mesohabitats species showed associations with one or more specific mesohabitat type. The intermittent rocky mesohabitat had the most significantly associated species, which are rocky habitat specialists (*H. szaboi* and *A. uranoscopus*) and habitat generalists (*L. cylindricus*, *C. fasciatus* and *Synodontis* species). The association of *H. szaboi, P. longicapitis, O. zambezense* and *A. uranoscopus* with the rocky habitat is congruent with current literature (Skelton, 2001; Bruton *et al.*, 2018). Although *L. cylindricus* and *C. fasciatus* showed strong associations with rocky habitats, their presence in other structured habitats suggest that their association with rocky habitats is likely due to their need to feed and graze on algae and invertebrates (in the case of *C. fasciatus)* from the surface of rocks and woody structures with their specialised sucking mouths (Skelton, 2001). Interestingly, the association of *P. acuticeps* with this mesohabitat disagrees with current literature that the species prefers vegetative river margins in slow-flowing sections (Skelton, 2001; Bruton *et al.*, 2018). This highlights the need for a greater assessment of species ecology in the region and indicates that *P. acuticeps* utilises a diverse range of habitats (Lamboj, 2004).

Numerous small-bodied fishes were associated with a specific mesohabitat types in the Kabompo River. Several species occurred in more than one habitat type but showed a stronger association with one or for some species two mesohabitat types. It is clear from the present study that, small-bodied fish in the Kabompo showed consistent associations with specific mesohabitat features. The results are consistent with findings from other large floodplain rivers in regions such as North America (Lapointe *et al.*, 2007) and South America (Arrington *et al.*, 2005; Schneider and Winemiller, 2008). This highlights the importance of preserving a diversity of freshwater habitats and maintaining habitat heterogeneity.

Indicators of change

Indicator species are a tool to monitor environmental change, provide warning signals for imminent ecological shifts and the effectiveness of management plans (Siddig *et al.*, 2016). The strong associations observed between species and mesohabitat types and environmental variables provide the opportunity to develop indicators of change within the catchment (Carignan and Villard, 2002). *Phragmites mauritianus* is an important species in reducing soil erosion during flooding and stabilising the riverbanks (van Ginkel and Cilliers, 2020). The annual flood cycle is an important driver of woody inputs in floodplain systems (Collins *et al.*, 2012). The excessive clearing of marginal vegetation and woodlands for agriculture, timber and charcoal production and the disruption of the intensity of the flood pulse will reduce available woody inputs and *Phragmites* (Timberlake, 2000). Although, eight species were associated with the woody habitat, three species *E. radiatus*, *E. unitaeniatus*, and *P. ngamensis* were almost exclusively associated with the wooded habitats and are potential indicator species. Similarly, three species (*E. kerstenii, E. lineomaculatus* and *S. depressirostris*) were almost exclusively associated with *P. mauritianus* and represent potential indicator species for this habitat. There are a large number of species share between these two mesohabitats, including the six potential indicator species mentioned above. Therefore, it may be more informative to monitor changes in assemblage structure between these two habitats in conjunction with species abundance. The wood and *P. mauritianus* mesohabitats contained different species assemblages despite some species occurring in both. Therefore, monitoring the simplification or convergences of these different assemblages provides a tool to assess environmental changes at a multispecies level (Pont *et al.*, 2006; Rashleigh *et al.*, 2009; Qadir and Malik, 2009). For example, the impacts of forest clearing have been associated with transitions in species assemblages from invertivores to algae/periphyton consumers and the simplification of food webs (da Costa *et al.*, 2020).

The rocky mesohabitat is susceptible to changes in flow and sediment loads, which can cause it to become smothered or restricting the available habitat area. This will result in species declines and may limit their presence to sections above the disturbance or to headwaters of the system. The significant association of nine species (*H. szaboi, P. longicapitis*, *L. cylindricus*, *O. zambezense*, *M. acutidens*, *A. uranoscopus, C. facsiatus, S. macrostoma* and *P. acuticeps*) with the rocky habitat, with some of these being stenotypic, provides potential indicators for monitoring the impacts of sedimentation and flow modification. However, of the nine species, only *H. szaboi*, *P. longicapitis L. cylindricus*, *A. uranoscopus*, and *C. fasciatus* likely represent good candidate species as indicators of change. These five species use rocky habitats almost exclusively during the low water periods for feeding and refuge and is an important spawning habitat for *A. uranoscopus* which attach or scatter their eggs among the substrate (Skelton, 2001; Marshall, 2011). *Petrocephalus longicapitis* is a common species in floodplains and shallow swamps, but rocky mesohabitats represent important habitats when the former is absent during the dry season (Kramer *et al.*, 2012). With regard to the other four species, two (*S.*

macrostoma and *P. acuticeps*) are generalist species while *O. zambezense* and *M. acutidens* are mid-water species not directly using the habitat (Skelton, 2001).

A number of species were recorded in water with strong current velocity. However, only *C. fasciatus* showed a statistically significant association with strong current velocity. This species and other *Chiloglanis* species have been proposed as indicators of changes in other southern African systems (Rashleigh *et al.*, 2009). Dams and other impoundments are considered a major threat to ecosystem health and biodiversity in aquatic environments (Watkins *et al.*, 2015), which negatively impact rheophilic species such as *Chiloglanis*. These impacts are emphasised in the disappearance of *Chiloglanis neumanni* that was once abundant in suitable habitats in the middle Zambezi River before the construction of Lake Kariba (Jackson, 1961c), but their failure to adapt to the lentic environment means the species is now absent from the lake (Bowmaker *et al.*, 1978). Similarly, although *O. zambezense* was not significantly associated with strong current velocities in the present study, their reliance on flowing environments is evident in their absence from Lake Kariba (Bowmaker *et al.*, 1978). These two species are therefore, potential indicator of reduced flow.

Our capacity to protect biodiversity is dependent on our ability to identify, predict and monitor the impacts of human activities on freshwater systems. To achieve this, we need to distinguish natural variation from human-induced changes. The middle Kabompo near Jivundu experiences low fishing pressure and small human population densities. This provides a unique opportunity to collect and develop baseline indices of fish species habitat use and assemblages in distinct low water mesohabitats. The presence of unique species assemblages and strong habitat association provides a valuable tool to conservationists and policymakers to implement science-based indicators of anthropogenic change. To confirm the effectiveness of these species as bio-indicators of anthropogenic impacts, it is recommended that replication of this dataset be done and further develop research on other species-environmental relationships. An initial step may be targeted assessment of species presence and abundance in selected areas of increasing anthropogenic stresses (e.g., water pollution, flow modification and habitat degradation) to develop a scoring system like the Zambian Invertebrate Scoring System (ZISS) (Dallas *et al.*, 2018). The potential use of fish indicators may yield more user-friendly results as local riverine communities generally have a greater knowledge of fish species than aquatic invertebrates. A step towards assisting Zambia and Africa in achieving sustainable development targets (e.g., Archi Biodiversity Targets and UN Sustainable Development Goals) and protecting an essential fisheries resource.

Chapter 4: General discussion

Discussion

The Kabompo River is the largest tributary of the Upper Zambezi in Zambia and provides essential services for communities, including capture fisheries, which are a major source of protein, micronutrients, and income. Few large Upper Zambezi River tributaries have received scientific attention in the past 60 years, with attention primarily focussed on economically important reaches (Barotse and Chobe floodplains) on the Upper Zambezi's mainstem. Consequently, relatively little is known about these large tributaries' fish faunal diversity, species distributions and ecology. The present study formed part of the first phase of a coordinated approach to fill the knowledge gap for these large tributaries starting with the Kabompo River. This study aimed to fill the current knowledge gaps on the diversity and habitat associations of fish communities in the Upper Zambezi, using the Kabompo River as a case study. This was achieved through two objectives i) provide an updated checklist of the Kabompo River fishes using a compilation of historical data and field surveys, and ii) assessing the habitat use of small-bodied fish communities during the low-flow period in 2019.

The Kabompo River hosts a rich diversity of freshwater fishes that are poorly documented scientifically. Sampling efforts have primarily focused in a small area in and around mining developments in the upper sections of the Mwafwe and middle Kabompo near the Ntambu Floodplain. Consequently, distribution records for species are incomplete and comprehensive sampling is required to understand species distributions better. Despite these short comings the synthesis of literature accompanied by museum collections and recent surveys detailed the occurrence and distribution of 83 fish species and 13 putative species within the Kabompo River. All these species have been recorded in the Upper Zambezi, with some of their ranges extending into the Middle (29 species) and Lower Zambezi (23 species) while other species (e.g., *'L'. hutereaui*) have more restricted distributions. The Cyprinidae and Cichlidae dominate diversity in the Kabompo, and several potentially undescribed species were collected, whose taxonomic distinctiveness need further investigation. Taxonomic conflicts are also highlighted for some of the taxa (*E. neefi, E. paludinosus, A. uranoscopus* and *C. neumanni*) that are considered to have broad geographic ranges or disjunct distributions. Consistent with findings from other studies within the region, the current taxonomy underestimates the diversity of fishes in the Kabompo River and Upper Zambezi (Tweddle *et al.*, 2004; Tweddle *et al.*, 2012). Despite the focus of literature and sampling in specific areas, the data collected to date provides valuable insight into species occurring in the Kabompo and re-emphasising the need for greater scientific focus in the region.

The general limited ecological knowledge for many fish species in the Kabompo River, is one of the major barriers to effective management and conservation in the system. Ecological data available has focused primarily on economically important species from fisheries regions or neighbouring systems. The assessment of mesohabitat use identified unique species assemblages within four of the five dominant mesohabitats i) *P. mauritianus*, ii) wood, iii) rock, and iv) *V. aethiopica*/ bare species assemblages related to the mesohabitats (Figure 24). Species diversity and abundance was greater in heterogeneous *P. mauritianus,* wooded, *Vallisneria* and rocky mesohabitats than homogenous bare substrate, congruent with current literature.

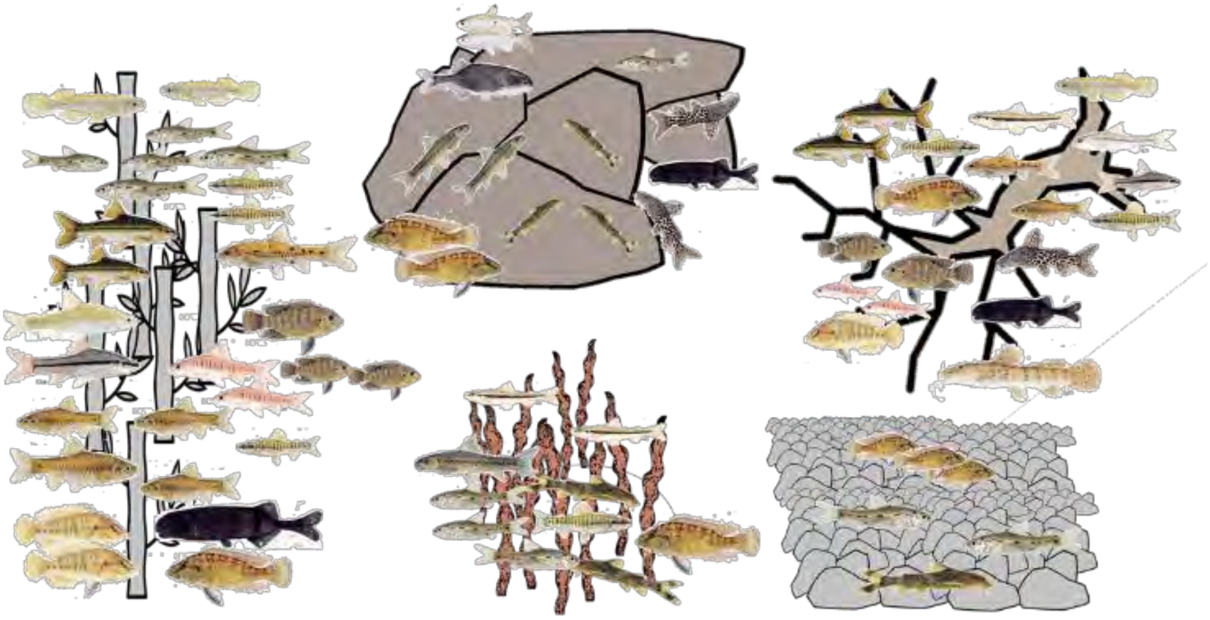

Figure 24: Stylistic diagram of species assemblages within the five mesohabitats. Species are represented by images from Skelton (2001).

Interestingly, 26 species showed significant associations with a specific mesohabitat type or environmental variable (current velocity or depth). Nine species were significantly associated with the rocky mesohabitat while three and four species were significantly associated with the wooded and *P. mauritianus* mesohabitats respectively. These mesohabitats are susceptible to anthropogenic change through disruptions in flow regimes, sediment load, and vegetation loss as a result of large-scale mining and power generation developments. The loss of which pose a considerable risk to the integrity of this system, which potentially threatens livelihoods and biodiversity and therefore, must be prioritised for protection. The strong associations indicate that this comprehensive baseline may be valuable indicators/ proxies for identifying anthropogenic induced change. Therefore, species like *H. szaboi*, *P. longicapitis* and *A. uranoscopus* are potential indicators for monitoring the integrity of rocky habitats under threat from sedimentation. Monitoring change in species assemblages of wooded and *P. mauritianus* habitats would be more informative than monitoring specific species. These data provide a basis to determine fish responses to regional environmental changes associated with human activities. While further analysis is required to determine the robustness or utility of these species as indicators, they provide evidence to aid managers and policymakers with implementing evidence-based decision making to protect biodiversity and livelihoods. Developing a fish-based indicator index may facilitate community involvement in environmental monitoring and use indigenous historical knowledge, as communities are often aware of changes in fish assemblages and presence before scientists. However, on a catchment scale, species-specific indicators may be unclear unless substantial degradation has taken place. Hocutt *et al*., (1994) proposed and developed a biomonitoring protocol for the Okavango River using 11 fish-based metrics. This protocol provides a large-scale assessment tool for the change in species assemblages at specific sentinel sites to monitor seasonal and long-term changes in species assemblages. The similarity in species between the Okavango and Upper Zambezi, including the Kabompo, means this biomonitoring protocol is likely transferable to the Upper Zambezi with few alterations.

Future research

The Kabompo River and greater Upper Zambezi River offer a unique opportunity to conduct novel research in fish taxonomy, biology, and ecology. Future biological and taxonomic work within the Kabompo River should focus on closing the sampling gaps in the Dongwe, Mwafwe, West Lunga and other west bank tributaries in the lower reaches. Greater geographical coverage will aid in understanding species distributions within the system, highlighting species with broad or restricted ranges. Comprehensive sampling in the section above Kabompo Gorge will assist in developing a better understanding of historical drainage connections between the Upper Zambezi and its neighbouring system.

Over the past 30 years several potentially undescribed species have been collected within the Kabompo. While this may pose a daunting task, effort should immediately focus on species groups with sufficient genetic material and museum specimens to facilitate a detailed preliminary analysis that enables the designation of molecular operational taxonomic units or formal species descriptions. The species groups highlighted within the families mentioned in Chapter 2 have sufficient genetic material and voucher specimens available at NRF-SAIAB to conduct these assessments. A greater knowledge of species diversity and relationships in the Kabompo and upper Zambezi is important in understanding species evolution within the system and its drivers. From a conservation perspective understanding species diversity and distribution within the Kabompo greatly assists management and conservation planning, by providing evidence of species with restricted distributions or species that are restricted to threatened habitats.

The development of robust indicators is a necessity for Kabompo and Upper Zambezi. Future studies should build on the findings of the present study to develop a comprehensive assessment tool to monitor the system's integrity. The development of this system should target sampling species through a degradation gradient allowing us to understand how changes in the system influence species. The establishment of mines in the catchment and sections along the river that are densely populated contrasted with vast sections of almost pristine riparian vegetation offer a unique opportunity to develop such indicators. These data can then be combined with current literature on histology, heavy metal contamination and other bioindicators to develop a comprehensive assessment tool (Chauke *et al.*, 2008; Marchand *et al.*, 2012; Dallas *et al.*, 2018).

The importance of fish to communities in the Upper Zambezi has prompted a lot of research into the biological and ecology of large commercially important species. However, this has left a gap in the biology of small-bodied fish species that are also used in the fishery. Fisheries catch assessments are underway in the Kabompo to quantify and estimate fish harvest in various sections of the Kabompo. The analysis of these data will highlight important species harvested by local communities which should be the focus for biological studies that assess one or more of the following aspects i) age and growth, ii) habitat use on a spatial-temporal scale, and iii) feeding/diet analyses. An understanding of these three key aspects will fill in gaps of basic species biology and ecology. This information is crucial to inform sustainable management of inland fisheries.

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Appendix 1

Table A1: The description, location and sampling methods use for biodiversity sampling within the Kabompo River and mesohabitat reaches in 2019.

Site no.	Site name	Date sampled	Coordinates	Method
CR19-A001	Dorians's camp	2019/09/07 and 2019/09/08	-12.510713, 24.881703	Electrofishing, rod and line
Site description. Variety of habitats including rocky substrate and marginal vegetation in a shallow section of the main channel				
CR19-A002	Large rocky rapids below Dorians's camp	2019/09/09	-12.514444, 24.864389	Electrofishing, rod and line
Site description. Rocky rapids with sand and cobble substrate				
CR19-A003	Nsengi River bridge	2019/09/09	-12.494036, 24.850937	Electrofishing, D-net
Site description. Small pools and stream with sand substrate, Lillie pads abundant and some woody substrate.				
CR19-A004	Kabompo River T5 road bridge.	2019/09/10	-11.888614, 25.250161	Electrofishing, angling
Site description. Shallow rocky run in the main channel. Bedrock and cobble are abundant with gravel.				
CR19-A005	Bought from local fisherman, near Dorians's camp.	2019/09/11	-12.521633, 24.876872	rod and line
Site description. Fishing off a rocky point in the main channel that drops into deep water.				
CR19-A006	Kabompo River floating floodplain vegetation	2019/09/13	-13.072947, 24.681142	Electrofishing
Site description. A small opening caused by feeding bushpigs in the floating vegetation. Dense vegetation.				
CR19-A007	West Lunga River. Rocks in the main channel	2019/09/14	-13.070311, 24.651931	Electrofishing
Site description. A large semi-submerged rocky island in the main channel that drops off into deep water.				
CR19-A008	West Lunga River. Island in the main channel with abundant phragmites	2019/09/14	-13.026625, 24.682192	Electrofishing
Site description. A large island in the main channel is surrounded predominantly by gravel.				

CR19-A009	Kabompo River, sandbank below Kabompo River lodge.	2019/09/15	-13.106319, 24.727203	Electrofishing, rod and line
Site description. Shallow gravel bar with cobble and submerged woody vegetation.				
Fishweir	West Lunga River, large fish weir upstream from Mwinilunga Town	2019/09/13	-11.661589, 24.466928	Electrofishing, D-net
Site description. Rocky rapids and cobble in a narrow main channel. There is a large fish weir across the whole channel.				
Watopa	Rapids upstream from Watopa pontoon	2019/09/02 and 2019/09/03	-14.025250, 23.695444	Electrofishing, rod and line
Site description. Rocky rapid comprising of bedrock and side channels containing cobble and sand. Abundant marginal vegetation and numerous small islands in the main channel.				
CRK001	Large rocky riffle 3.5 km upstream from Kabompo River lodge	2019/09/25 and 2019/11/03	-13.098758, 24.738103	Electrofishing
Site description. Approximately a 100m long rocky riffle section comprised of bedrock and cobble in the main channel. Substrates varied from sand to gravel. A few small logs were present.				
CRK002	Sandy beach near the bottom of the horseshoe bend at Jivundu	2019/09/29	-13.098300, 24.684628	Electrofishing
Site description. Small sandy beach with a small backwater channel that contained *Potamogeton crispus*. The main channel section was slow flowing with intermittent woody debris.				
CRK003	2nd large island downstream from Jivundu horseshoe bend	2019/09/30 and 2019/10/09	-13.100978, 24.679928	Electrofishing, rod and line
Site description. Island in the main channel with marginal phragmites and a shallow fast flowing section at the upstream most side containing patches of Vallisneria				
CRK004	Last island in the main channel before the West Lunga confluence (~1.5 km from the confluence)	2019/09/01	-13.114894, 24.658069	Electrofishing
Site description. Island largely covered in phragmites. Surrounding substrates was gravel covered with a thick mat of filamentous algae.				
CRK005	Croc island < 1 km upstream from Jivundu pontoon.	2019/09/02	13.108006, 24.700825	Electrofishing

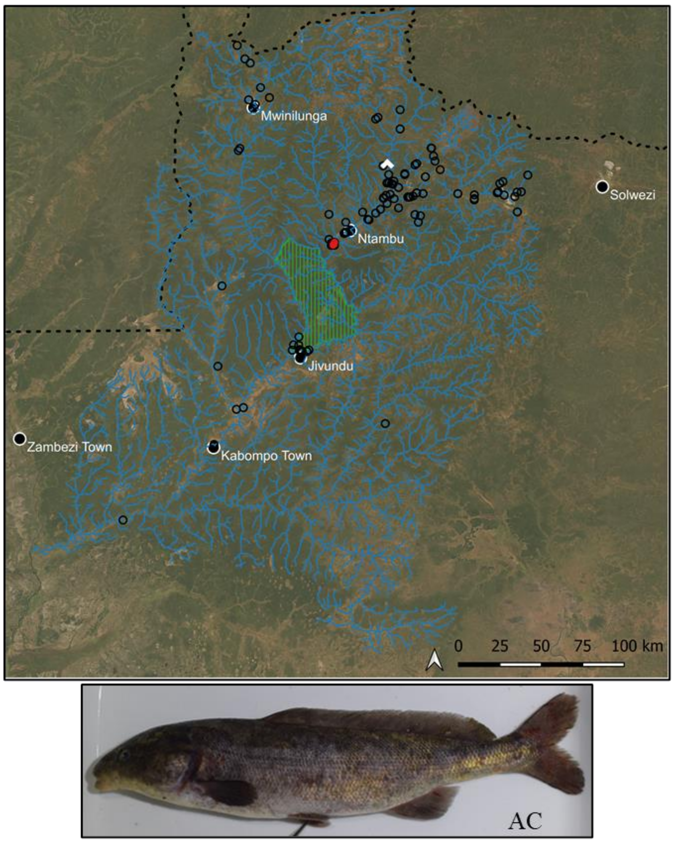
Site description. Upstream most section of the island is shallow and fast flowing with patches of *Vallisneria aethiopica* over sand. Medium sided backwater on the island was fringed with marginal vegetation dominated by phragmites, and the substrate was sand with leaf litter.				
CRK006	Left bank below Kabompo River lodge	2019/10/05	-13.115772, 24.738597	Electrofishing
Site description. Marginal vegetation was phragmites with sand and gravel substrate. Intermittent wood debris was also present in the form of stumps and branches.				
CRK007	Small island upstream from CRK002.	2019/10/04 and 2019/10/09	-13.095756, 24.681122	Electrofishing
Site description. Predominantly Vallisneria patches over sand and gravel. Small backwater was stagnant with woody structure and marginal phragmites.				
CRK008	Right bank below Kabompo River lodge	2019/10/06	-13.115350, 24.739350	Electrofishing
Site description. Section dominated by woody structures such as large logs and stumps with branches. The substrate was predominantly sand with leaf litter in the areas with little current.				
CRK009	Small sand beach used by local fishers	2019/10/07	-13.108611, 24.671983	Electrofishing
Site description. Small sandy beach with cobble and logs. Used as a landing site but local fisherman to park their makoros.				
CRK010	Two small islands just below the rock section downstream from Jivundu.	2019/10/07 and 2019/10/30	-13.100975, 24.683750	Electrofishing, rod and line
Site description. Islands in the main channel. *Vallisneria* patches in moderate current fringe the left of the island. The right island is largely fringed by cobble and bedrock with a strong current and a deep drop off. The backwater behind the two islands contains cobble and bedrock with little current.				
CRK011	Large island above the rocky riffles of CRK001.	2019/10/08	-13.098292, 24.733689	Electrofishing
Site description. Largely marginal *Phragmites* producing small overhangs over sandy bottoms with intermittent gravel. Current moderate velocity				
CRK012	Rocky shelf below new river lodge development.	2019/10/10	-13.123622, 24.719347	Electrofishing
Site description. Large logs in the main channel over a bedrock shelf. The area is used for fishing by construction workers.				

<table>
<tr><td>CRK013</td><td>Bend below Jivundu village washing area just above the rocky riffle.</td><td>2019/10/30</td><td>-13.101936, 24.686953</td><td>Electrofishing</td></tr>
<tr><td colspan="5">Site description. A shallow section of cobble and gravel with intermittent leaf litter. Very little marginal vegetation. Low current velocity.</td></tr>
<tr><td>CRK014</td><td>Jivundu pontoon</td><td>2019/11/04</td><td>-13.101289, 24.693711</td><td>Electrofishing</td></tr>
<tr><td colspan="5">Site description. Cobble and boulders at the Jivundu pontoon slipway. Moderate current velocity.</td></tr>
</table>

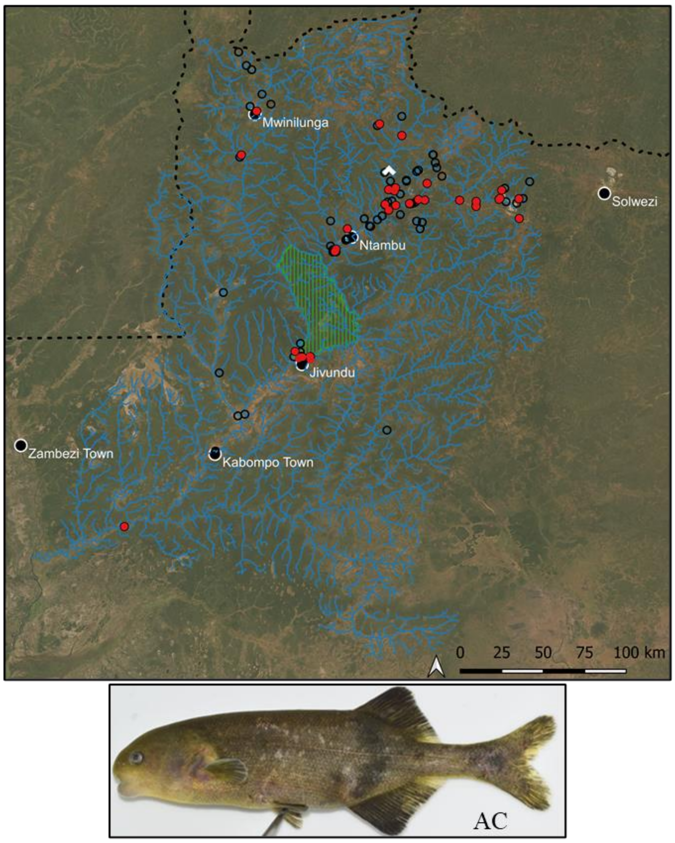
Appendix 2

Plate 1-23: Distribution range of fishes of the Kabompo River based on surveys conducted from 1983 to 2019 with live colour photographs where available. Open black circles: sample localities, red circle: indicate species resent

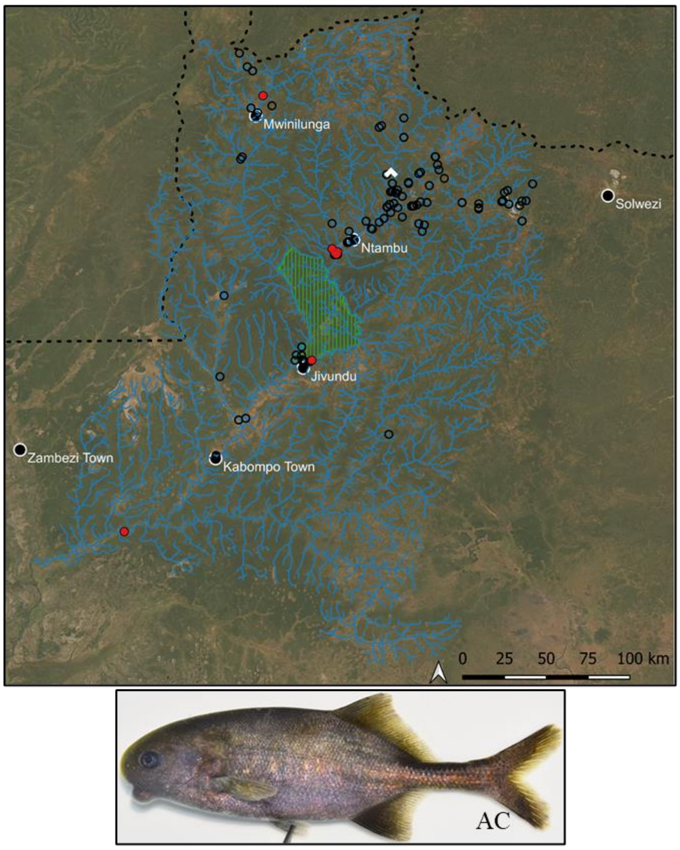
Plate1



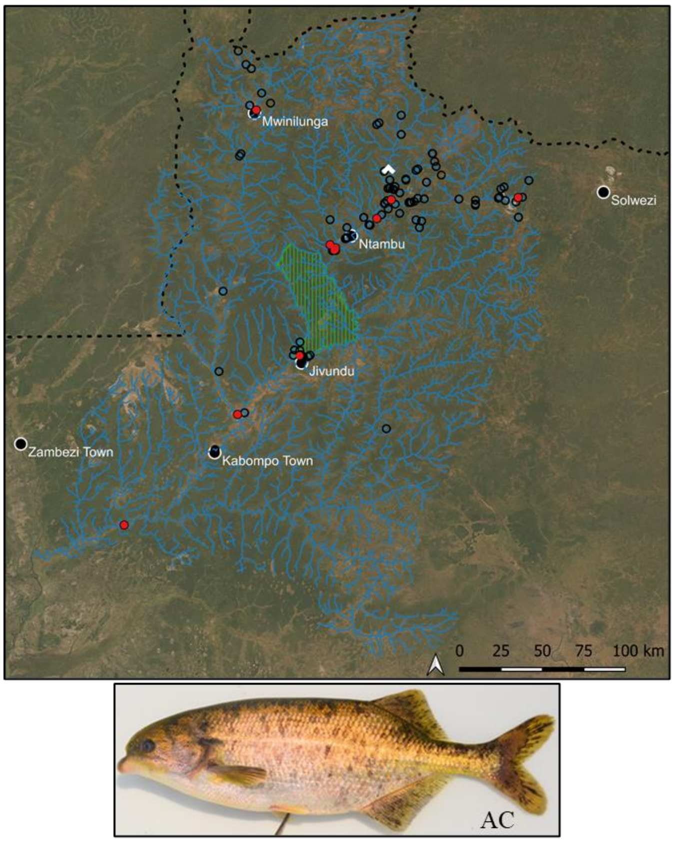
Mormyrus lacerda



Hippopotamyrus szaboi



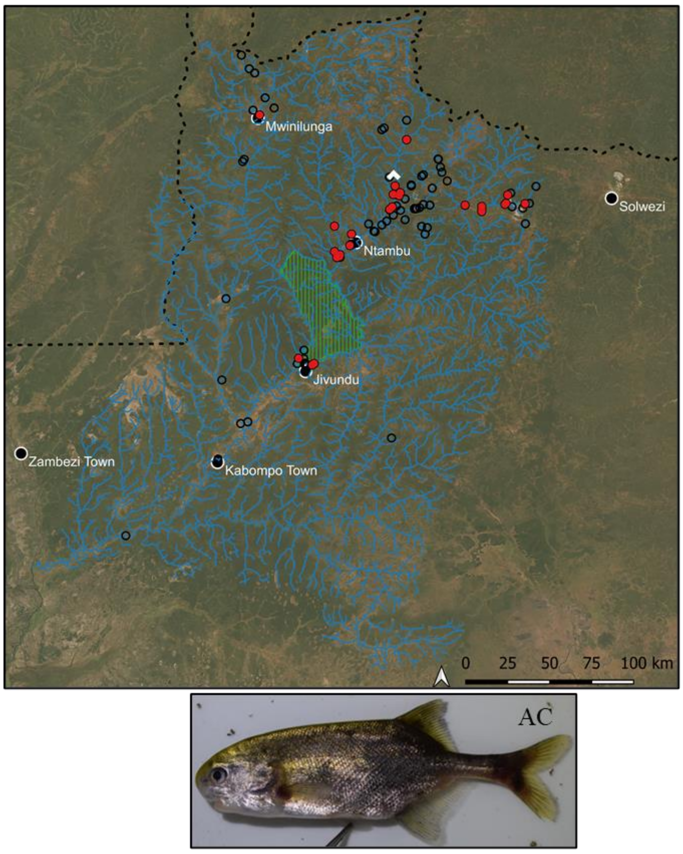
Cyphomyrus cubangoensis



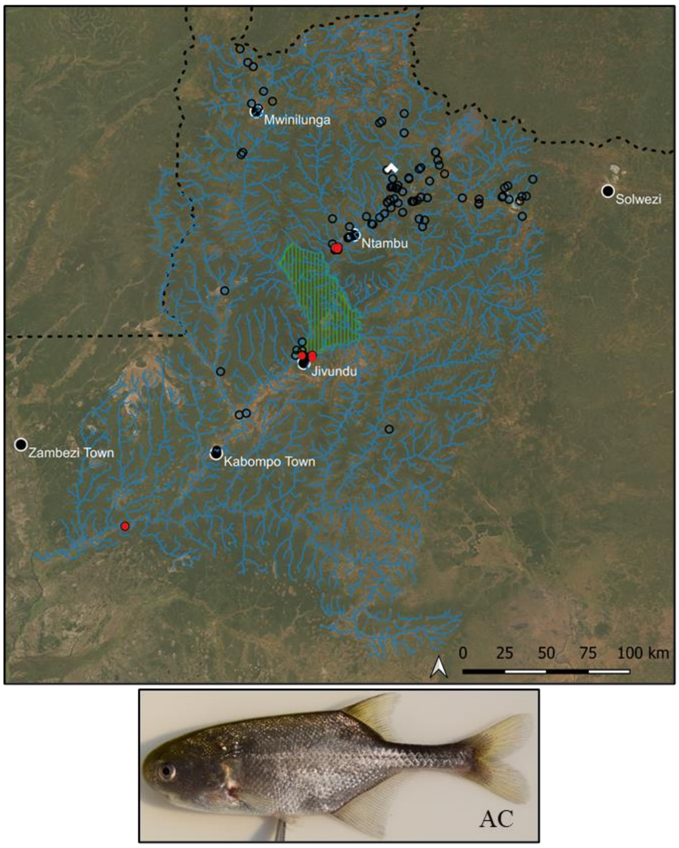
Marcusenius altisambesi

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

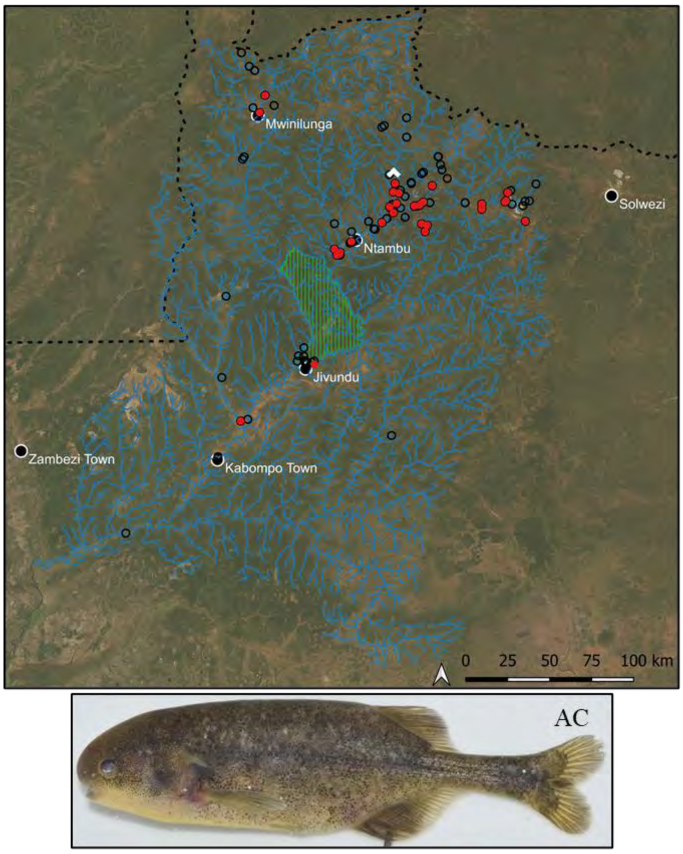
Plate 2



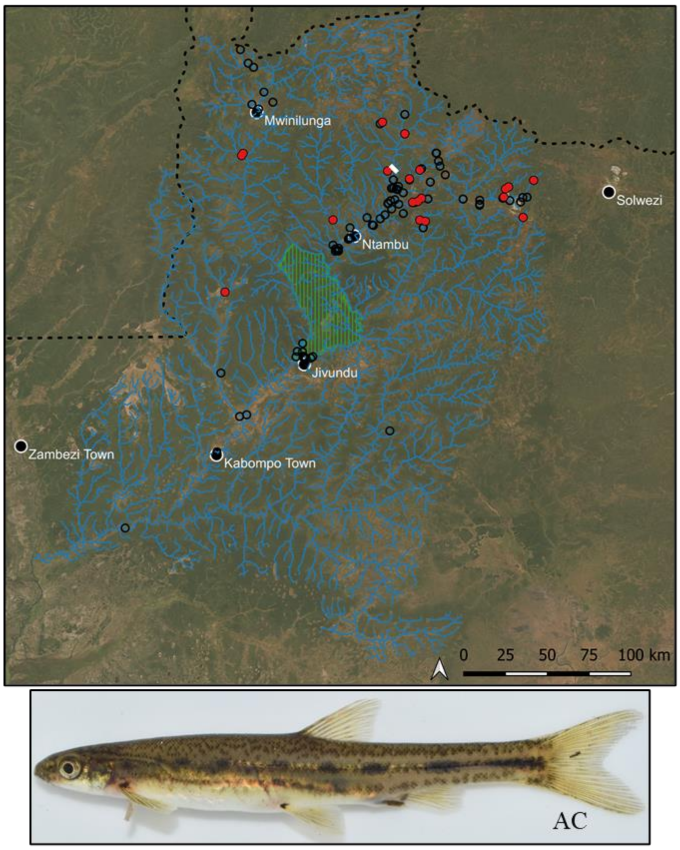
Petrocephalus longicapitis



Petrocephalus okavangoensis



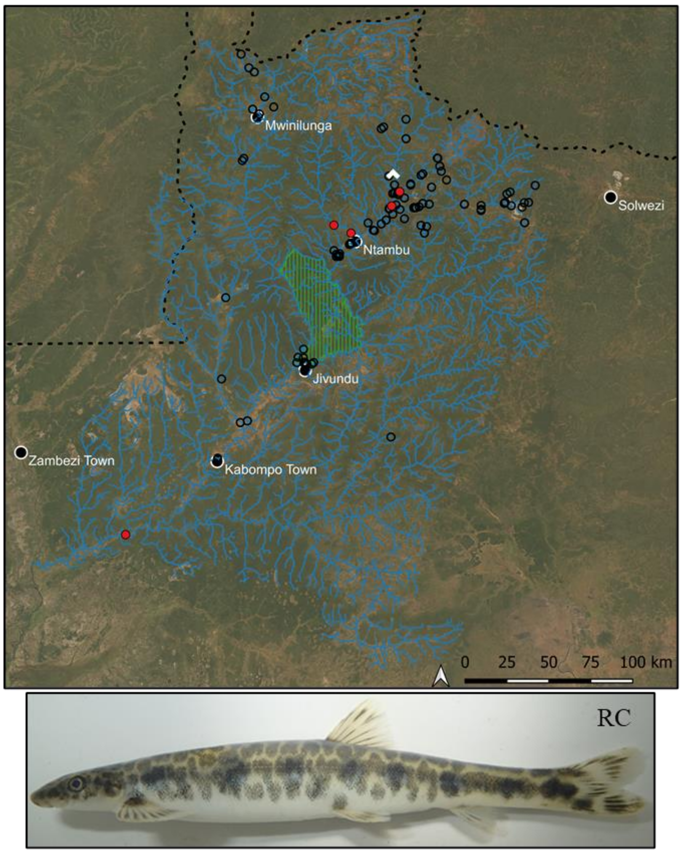
Pollimyrus marianne



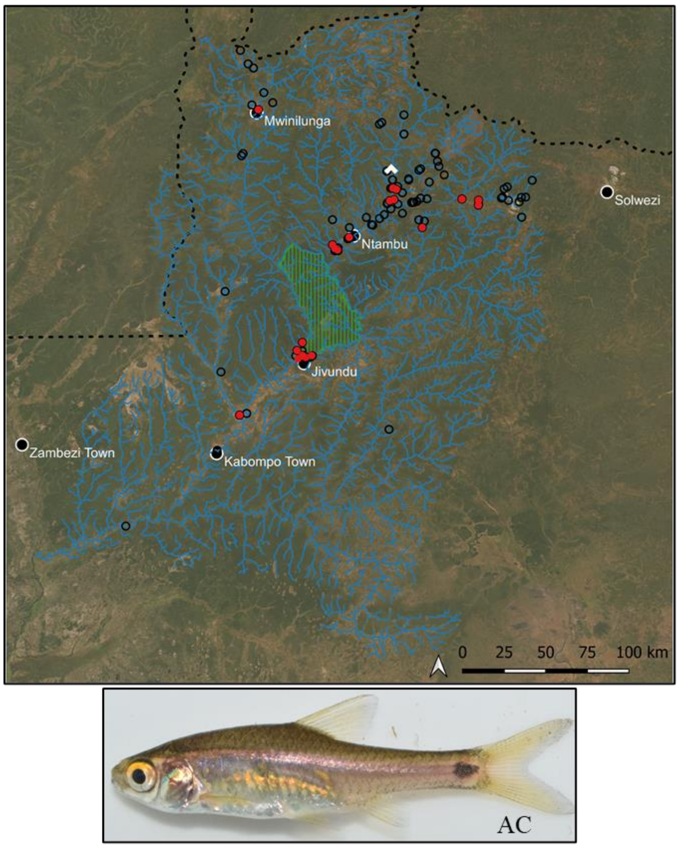
Kneria polli

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

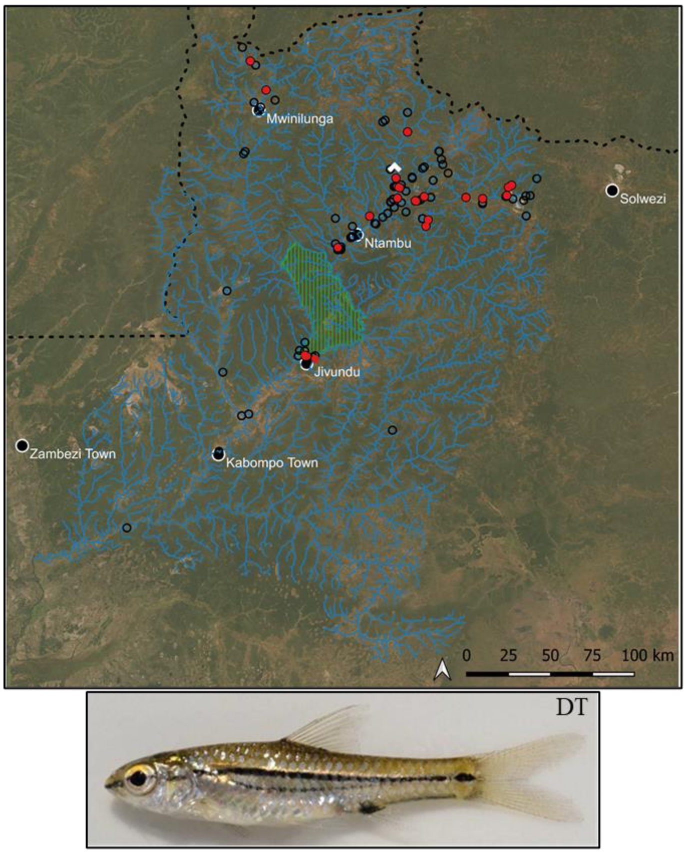
Plate 3



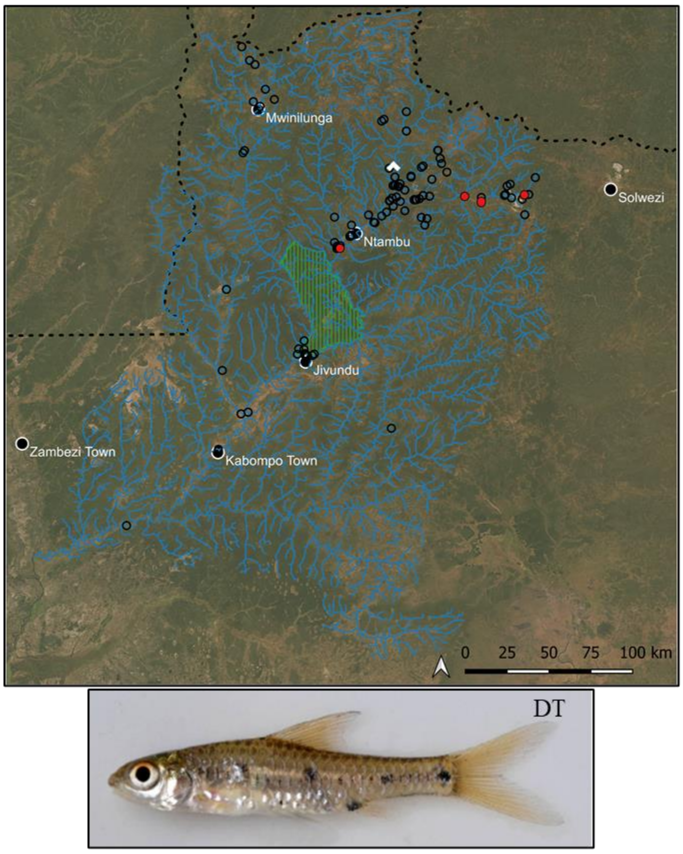
Parakneria fortuita



Enteromius afrovernayi



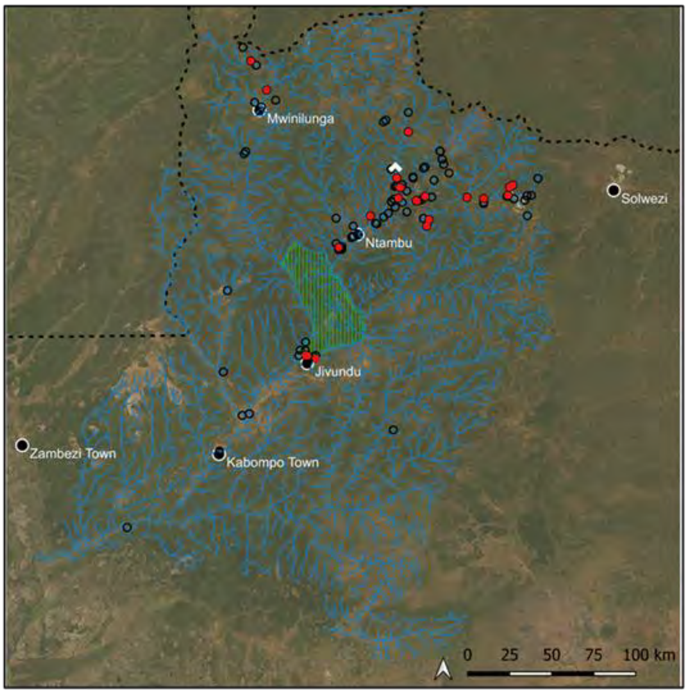
Enteromius barnardi



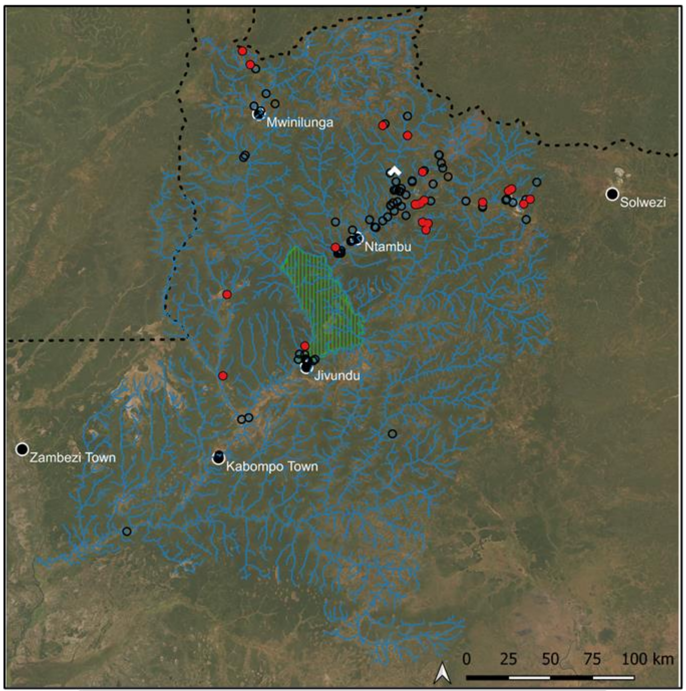
Enteromius barotseensis

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

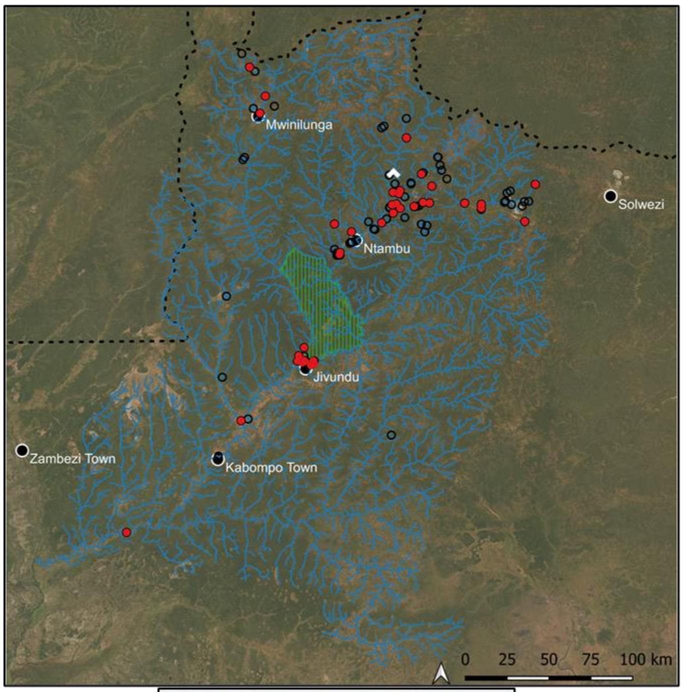
Plate 4



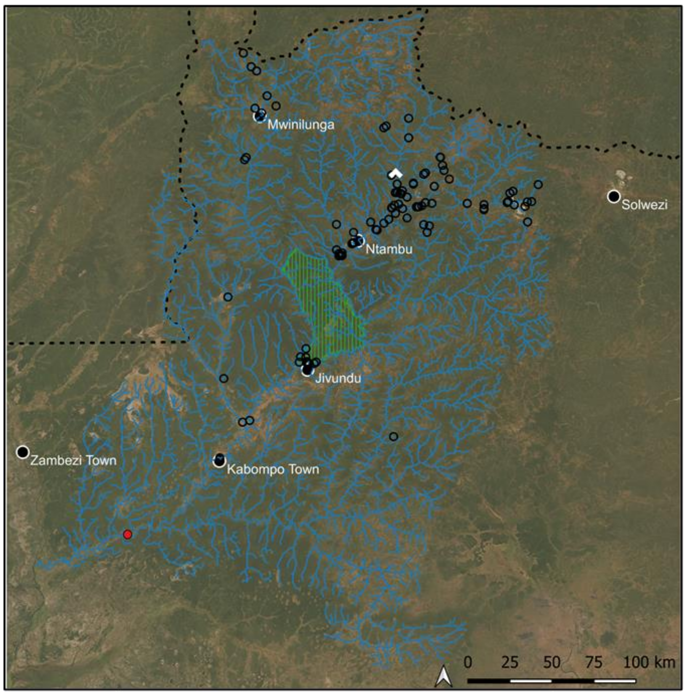
Enteromius bifrenatus



Enteromius brevidorsalis



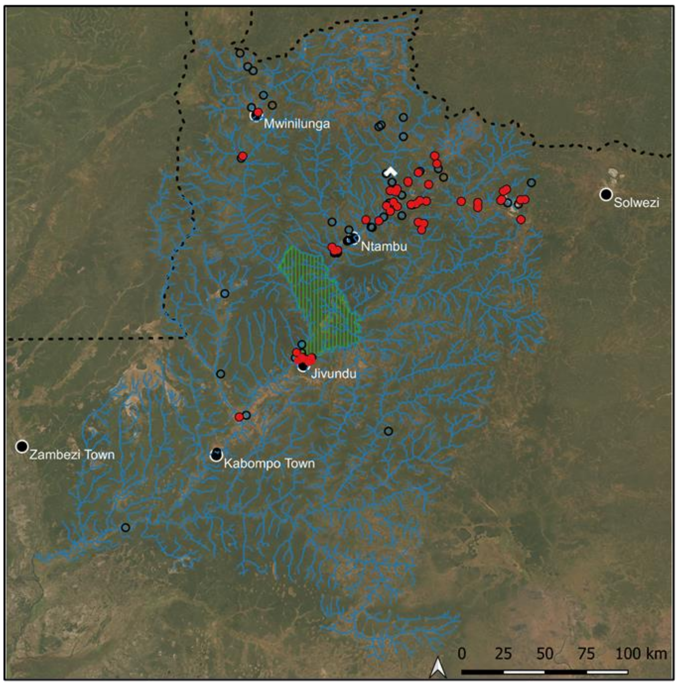
Enteromius eutaenia



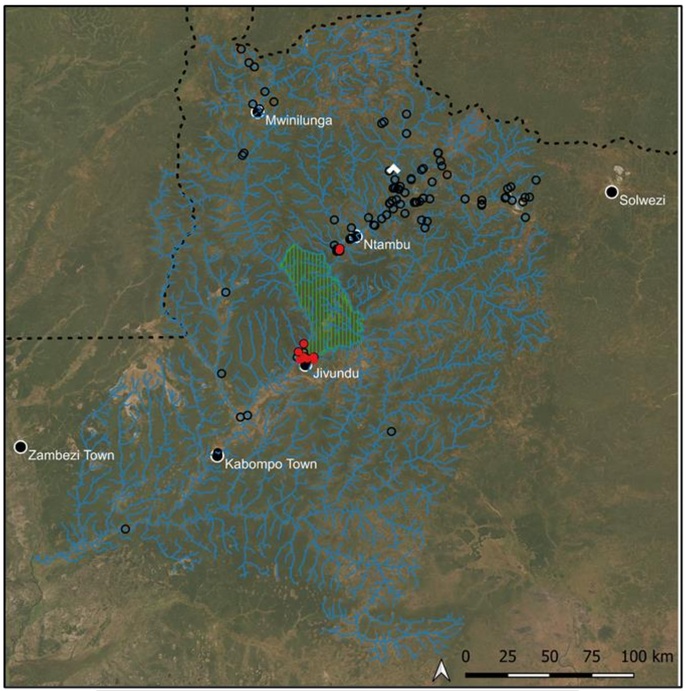
Enteromius eutaenia ‘red-eye’

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

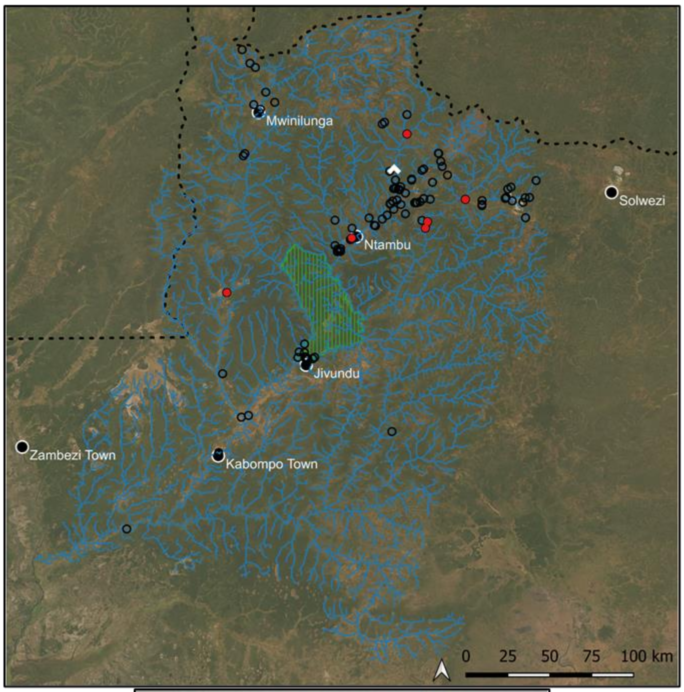
Plate 5



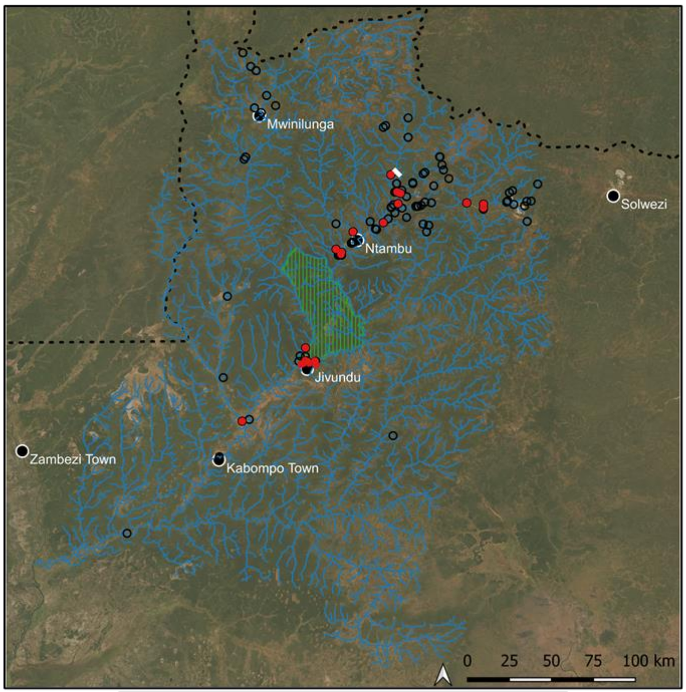
Enteromius fasciolatus



Enteromius greenwoodi



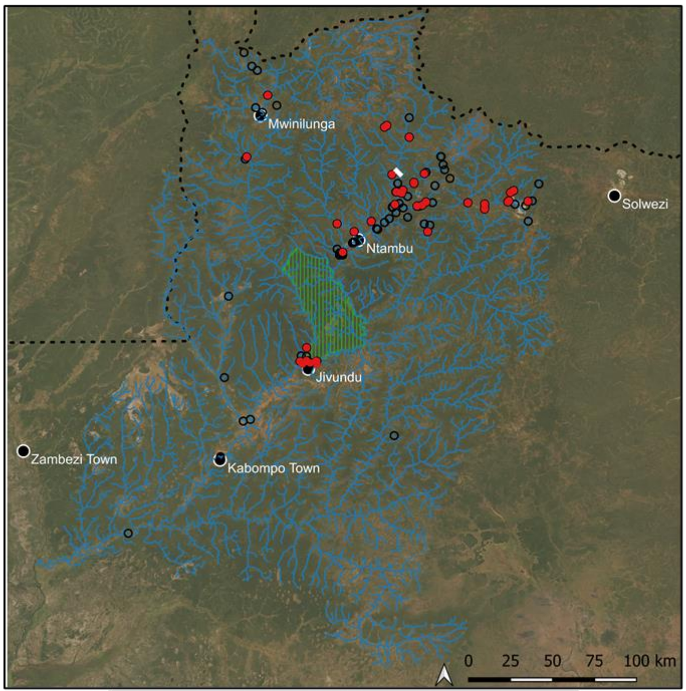
Enteromius haasianus



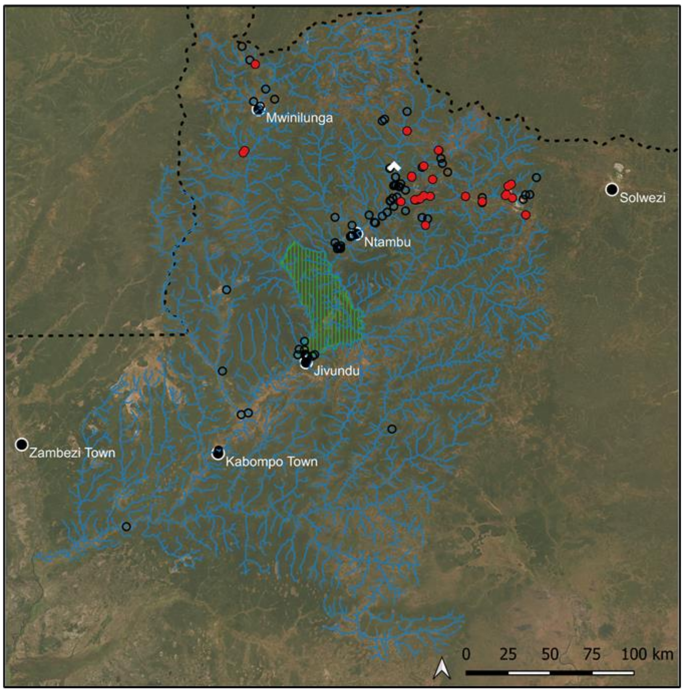
Enteromius kerstenii

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

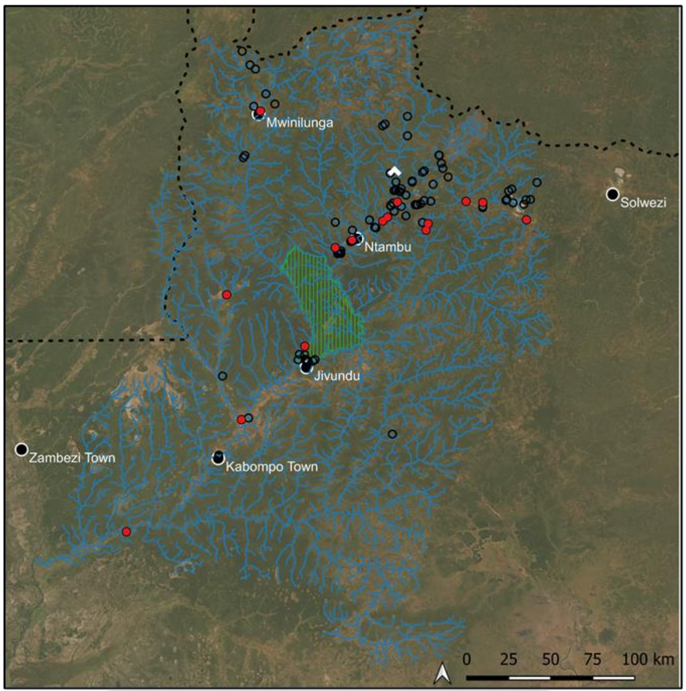
Plate 6



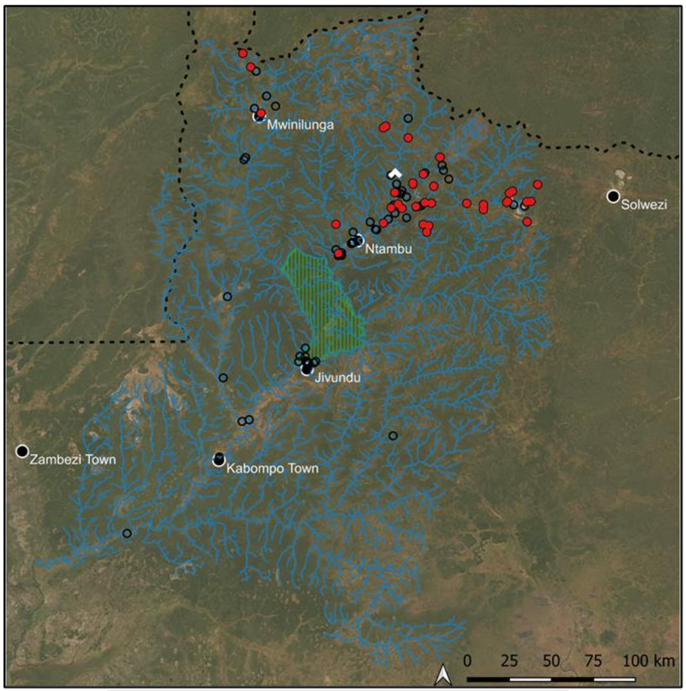
Enteromius lineomaculatus



Enteromius miolepis



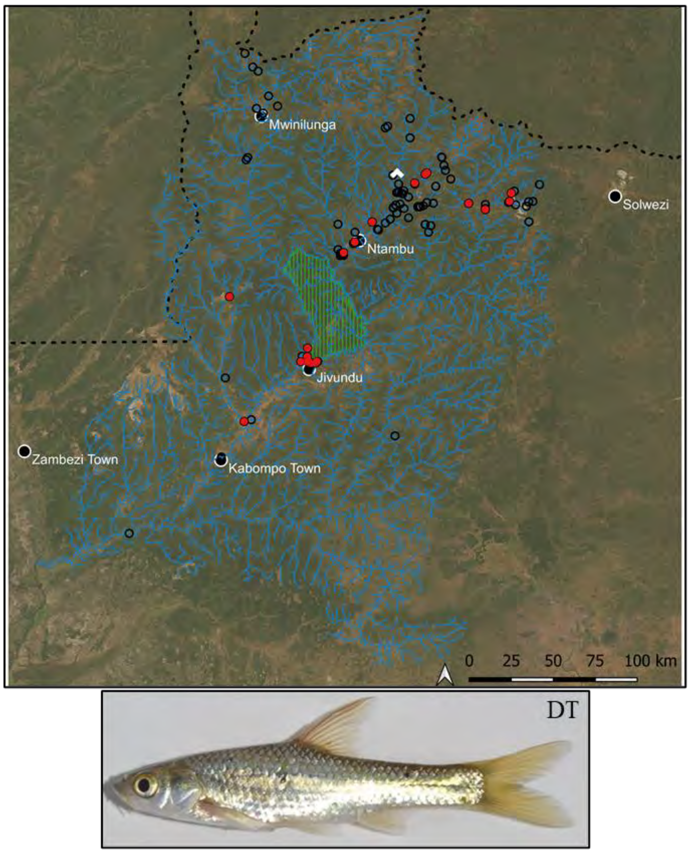
Enteromius multilineatus



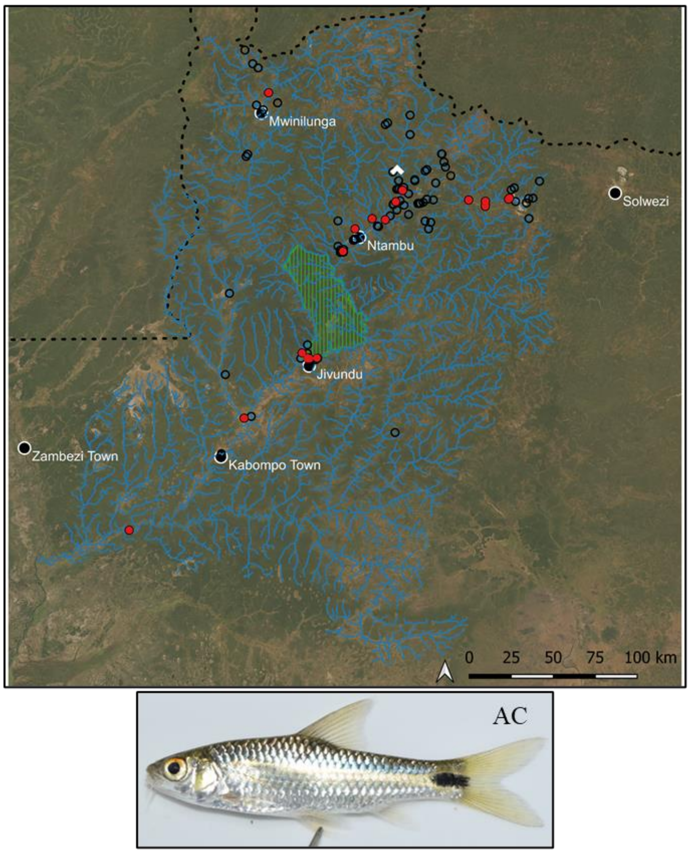
Enteromius neefi

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

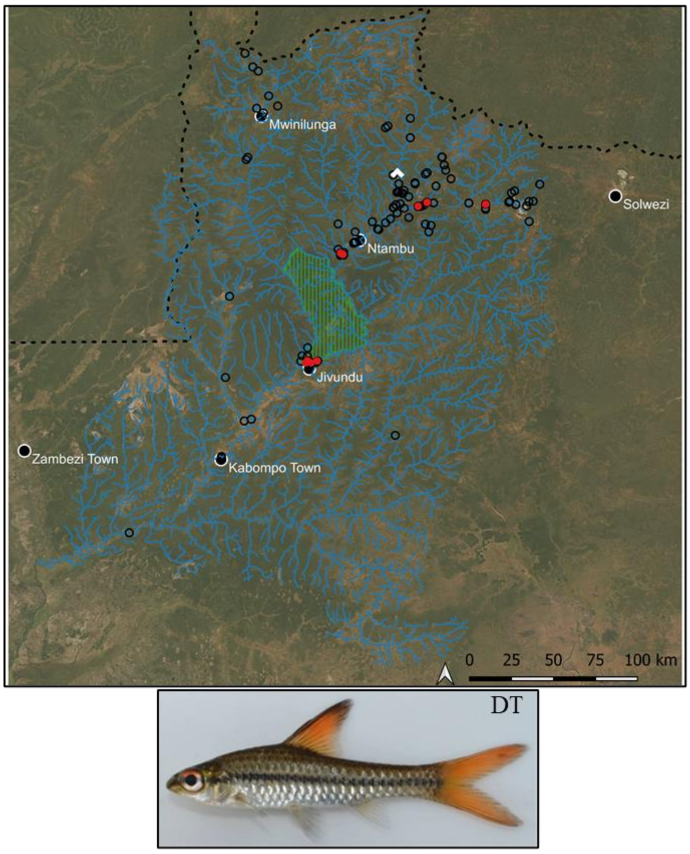
Plate 7



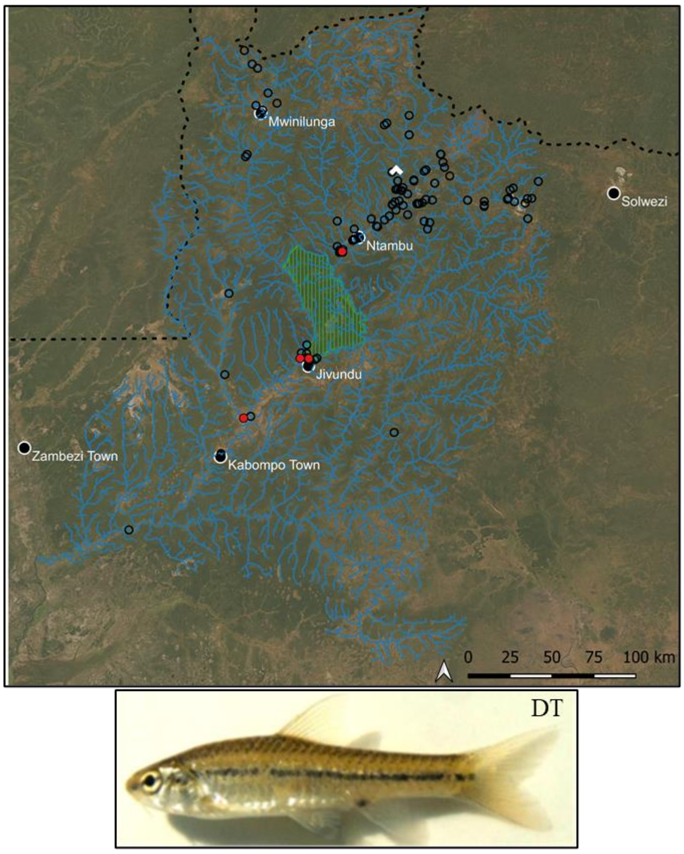
Enteromius paludinosus



Enteromius poechii



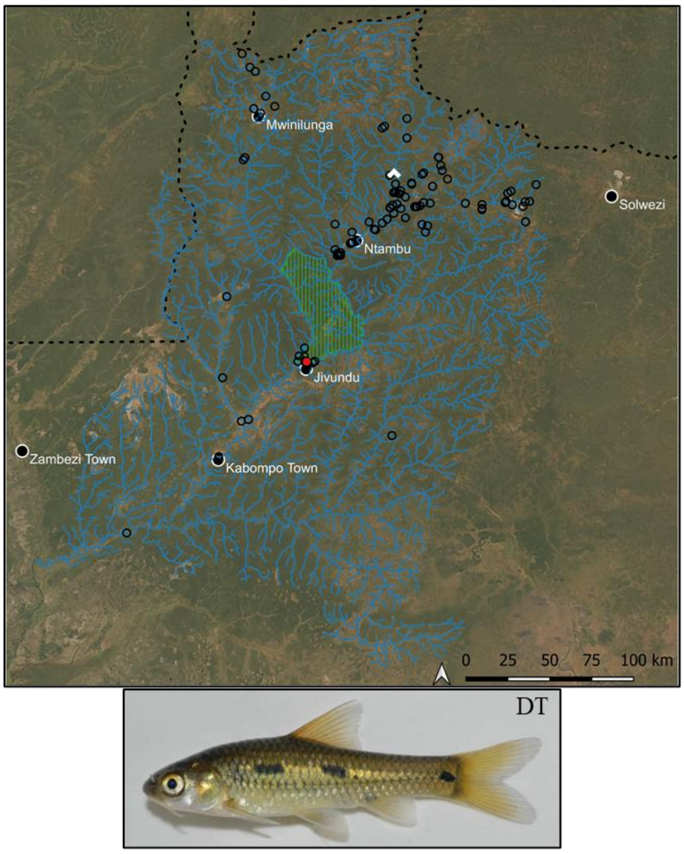
Enteromius radiatus



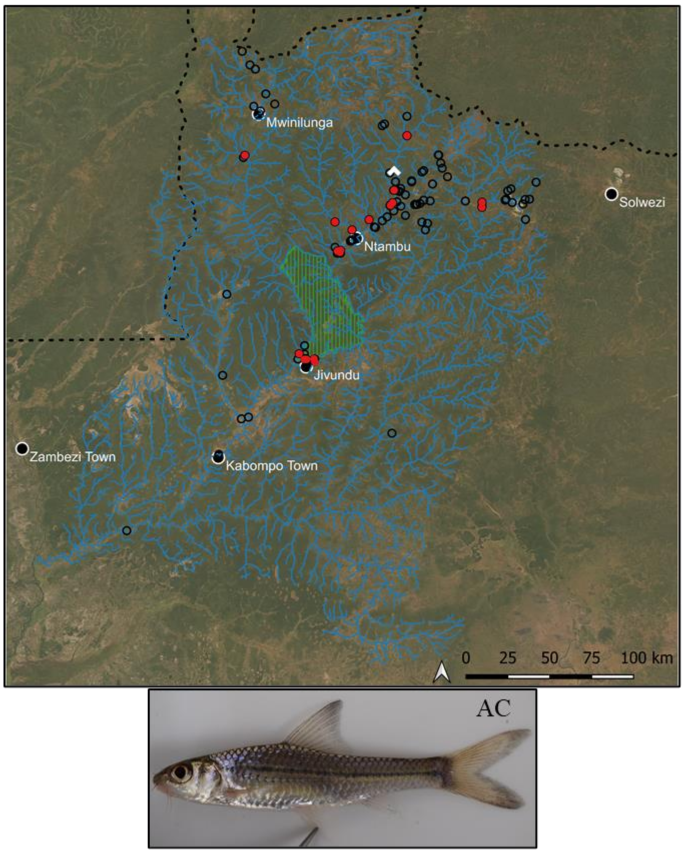
Enteromius thamalakanensis

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

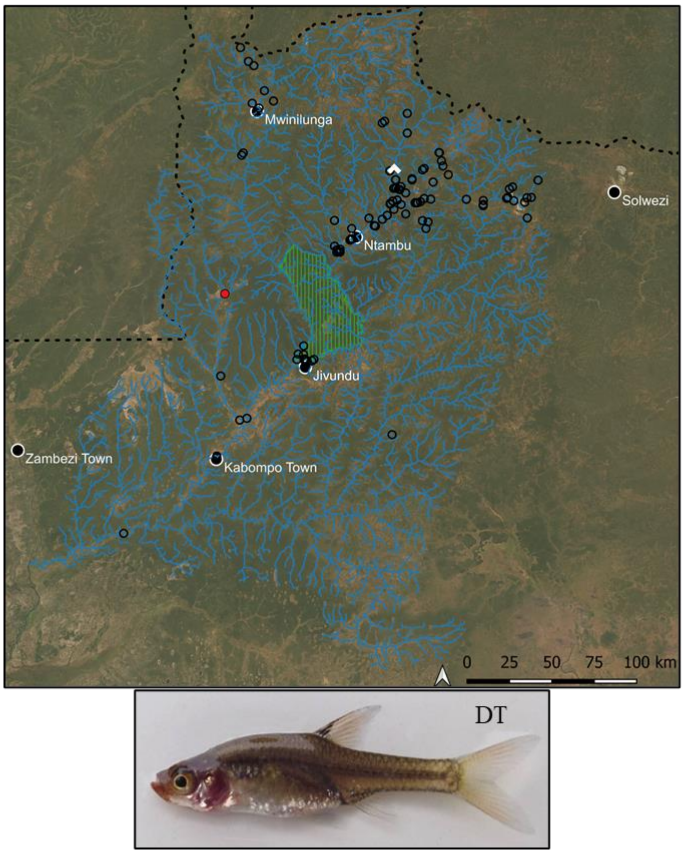
Plate 8



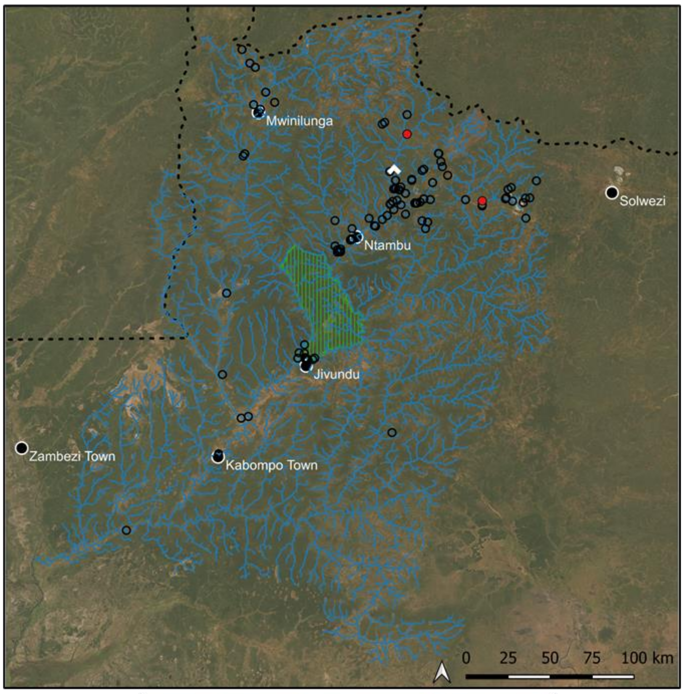
Enteromius trimaculatus



Enteromius unitaeniatus



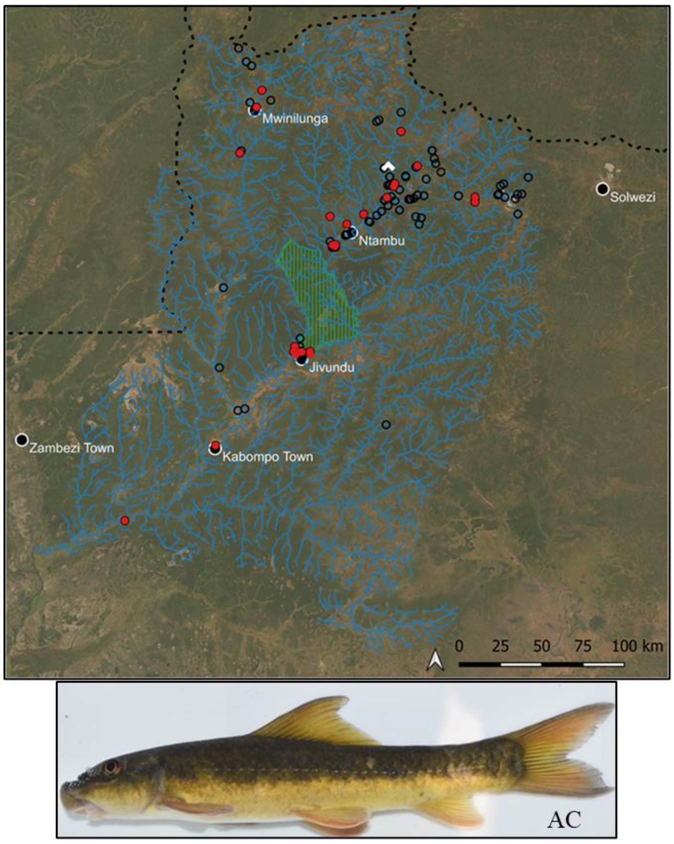
Coptostomabarbus wittei



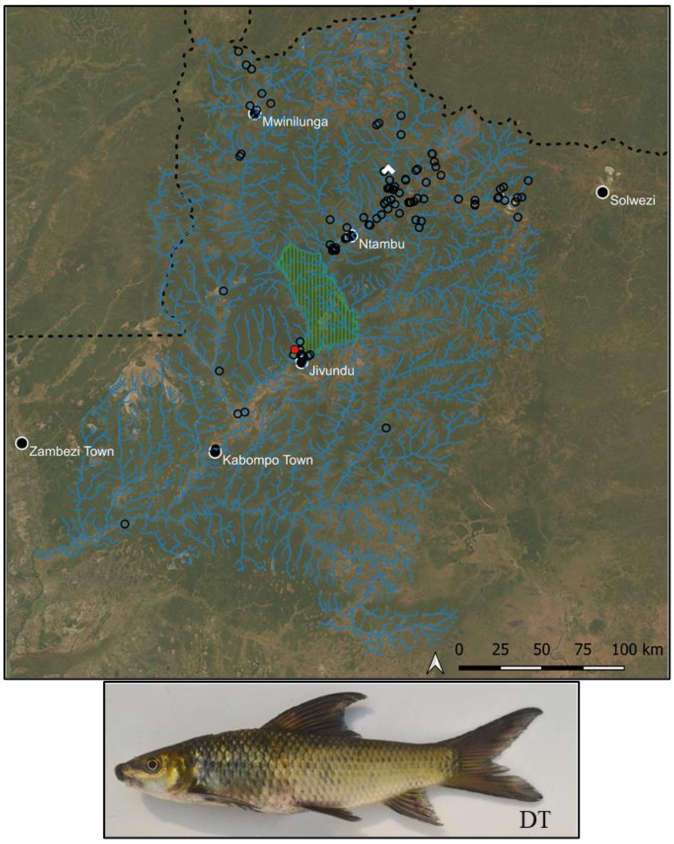
Clypeobarbus bellcrossi

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

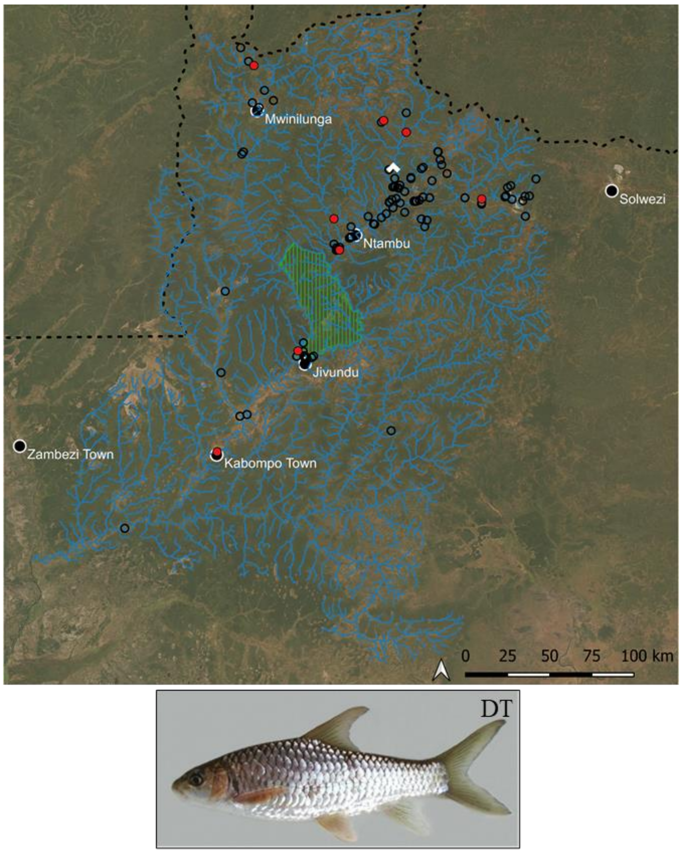
Plate 9



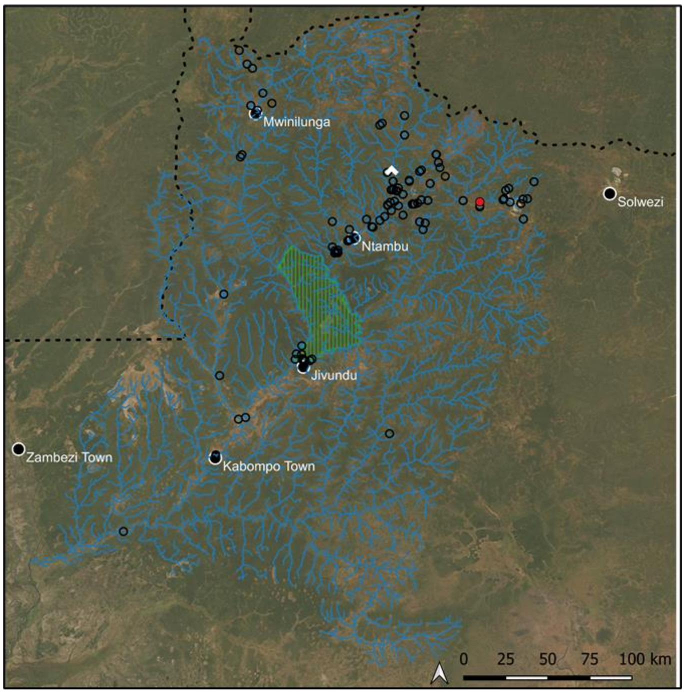
Labeo cylindricus



Labeo lunatus



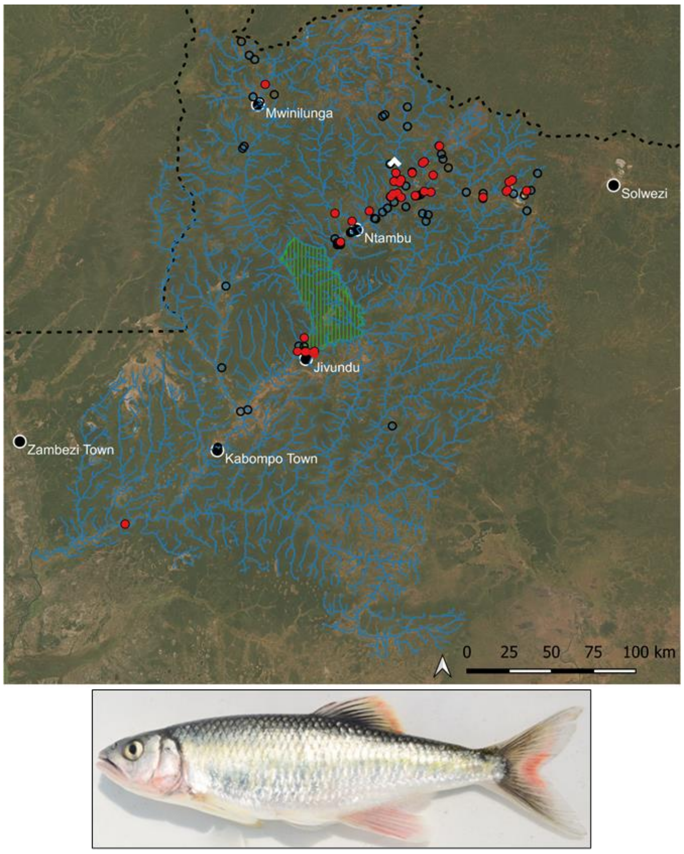
Labeobarbus codringtonii



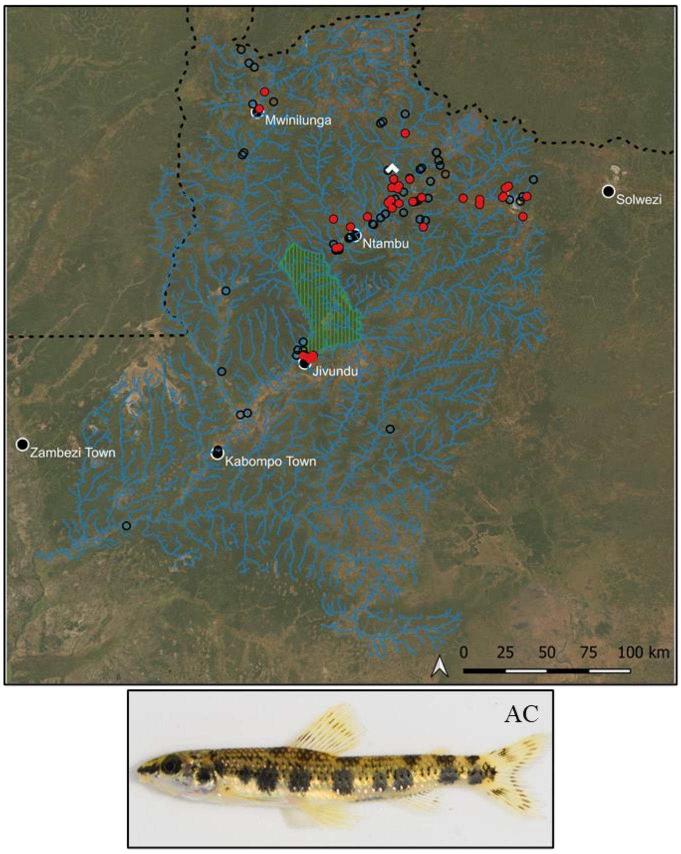
Engraulicypris brevianalis

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

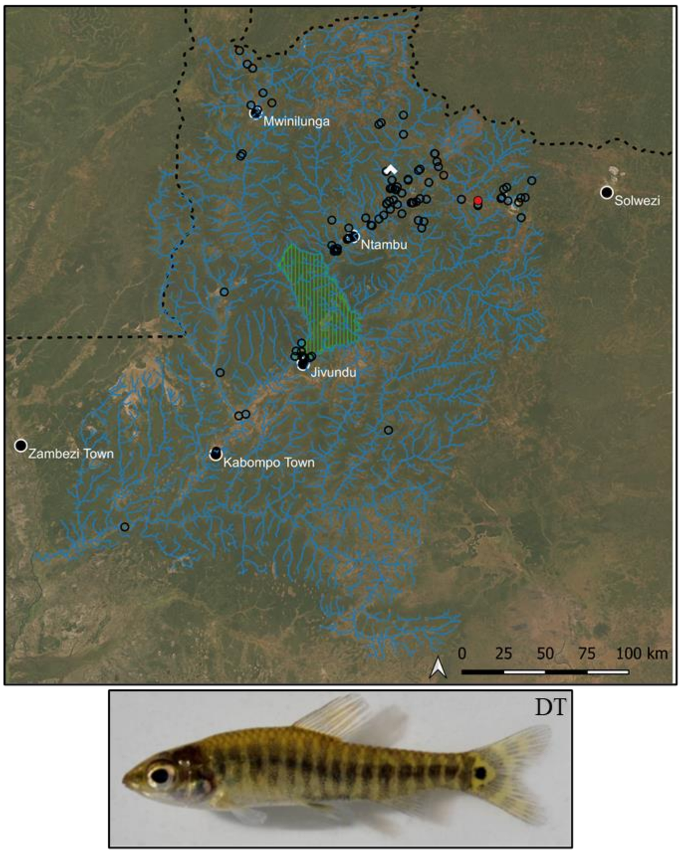
Plate 10



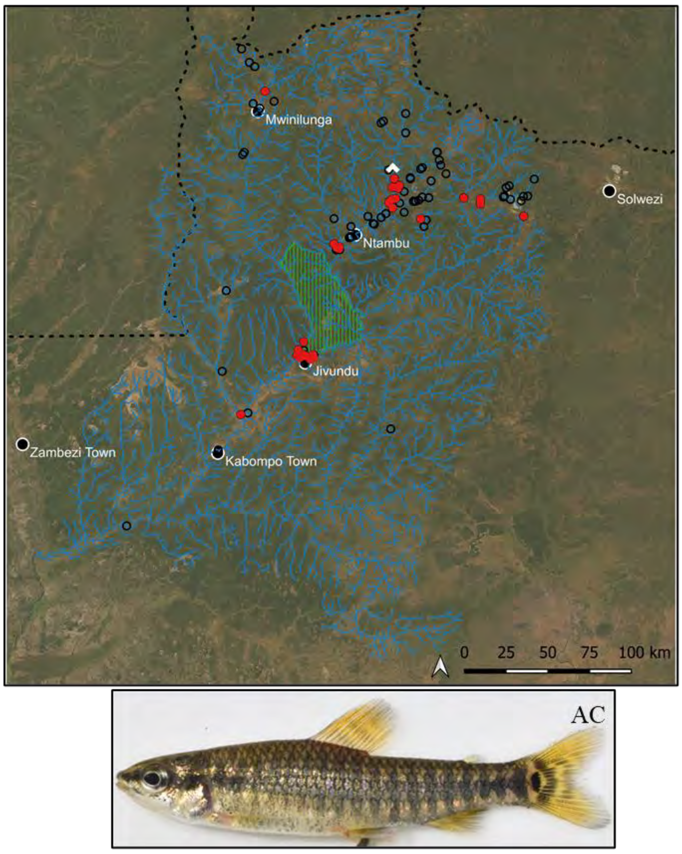
Opsaridium zambezense



Nannocharax dageti



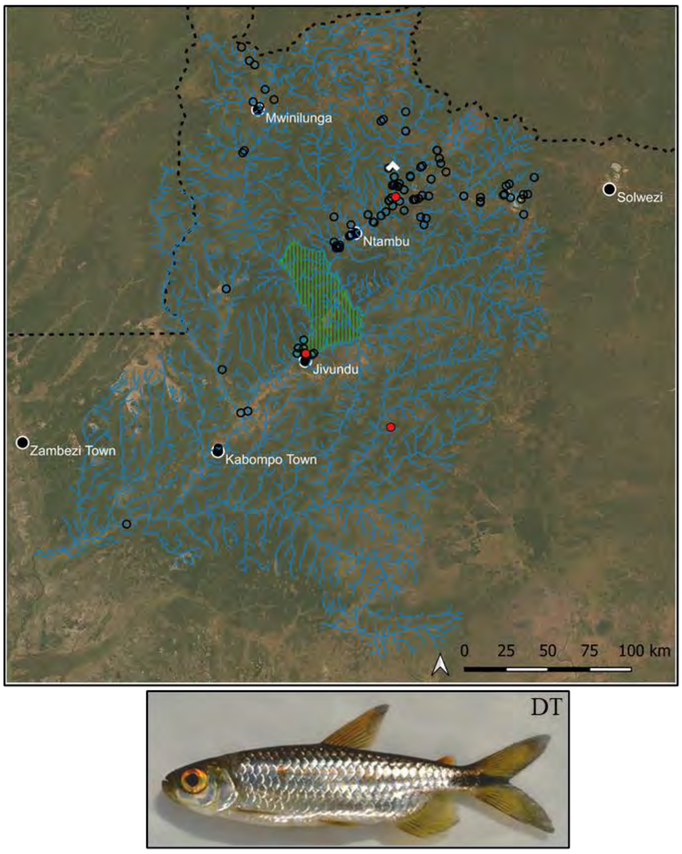
Nannocharax machadoi



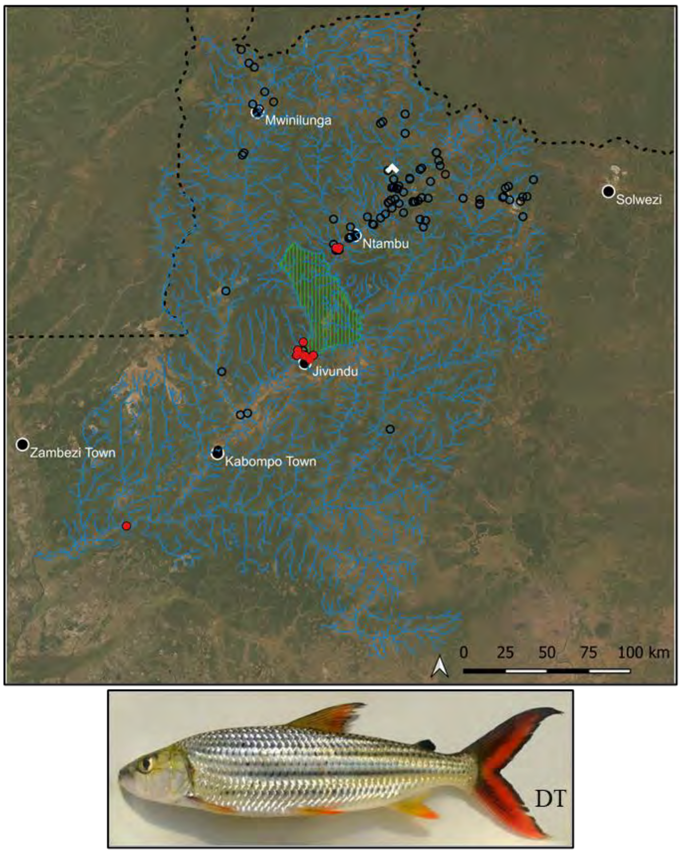
Nannocharax multifasciatus

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

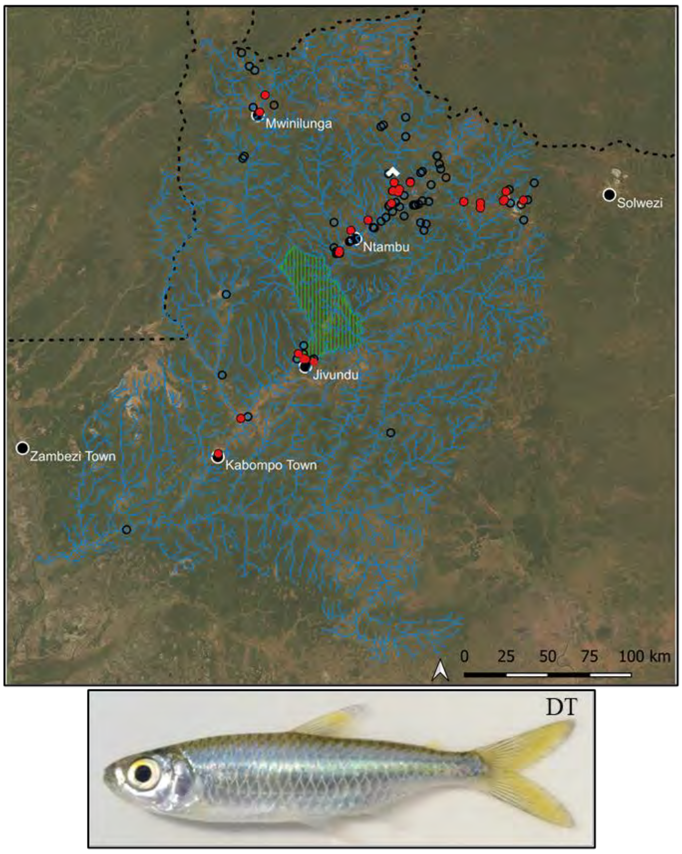
Plate 11



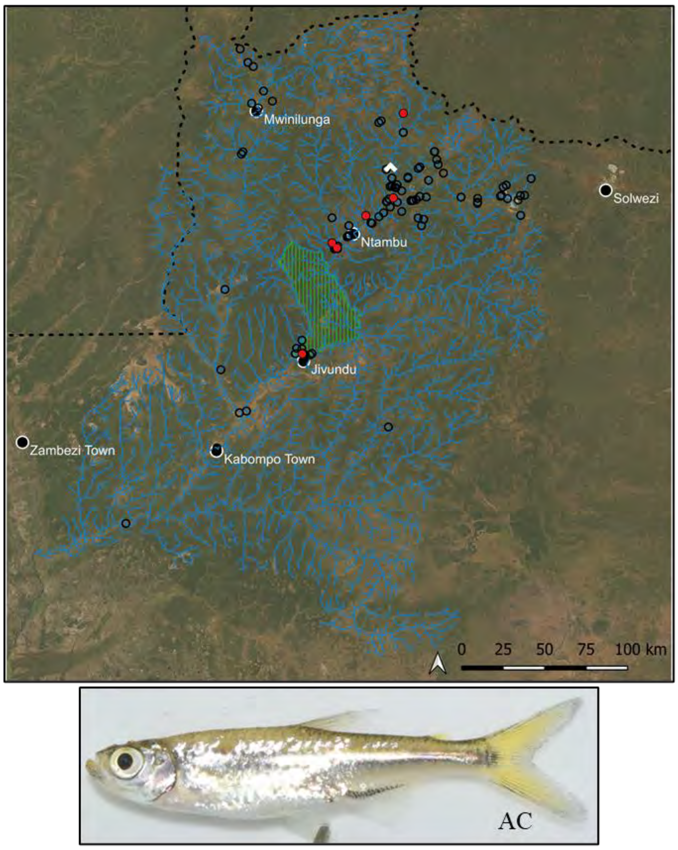
Brycinus lateralis



Hydrocynus vittatus



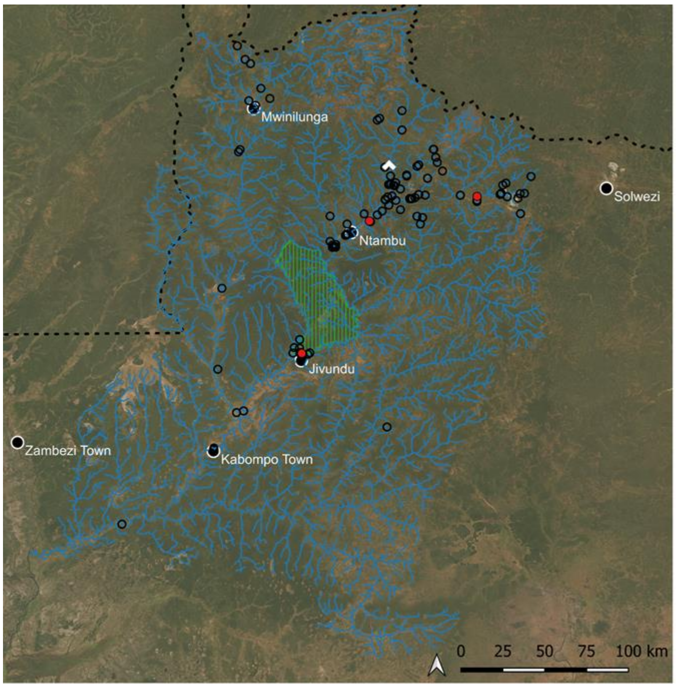
Micralestes acutidens



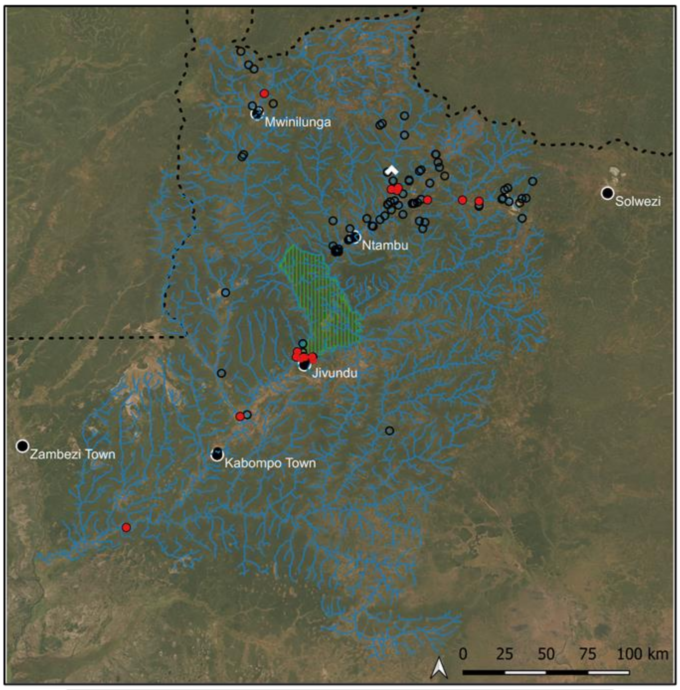
Rhabdalestes maunensis

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

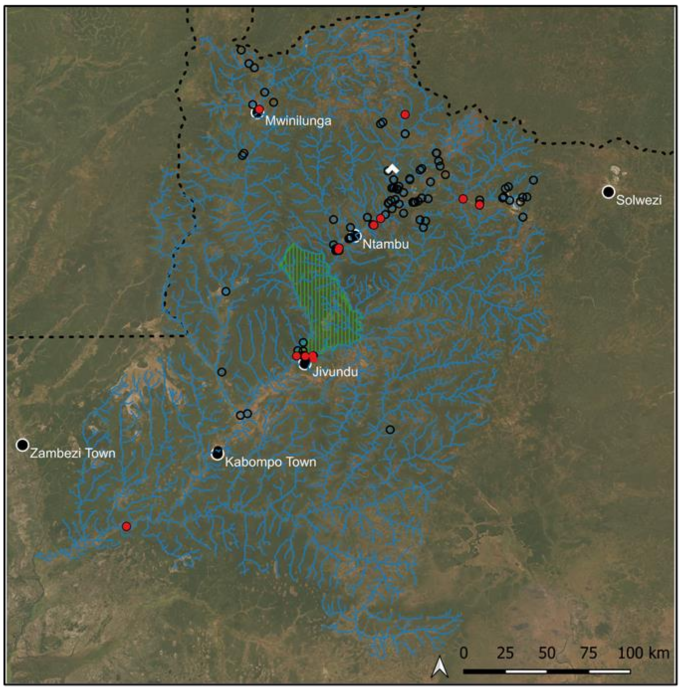
Plate 12



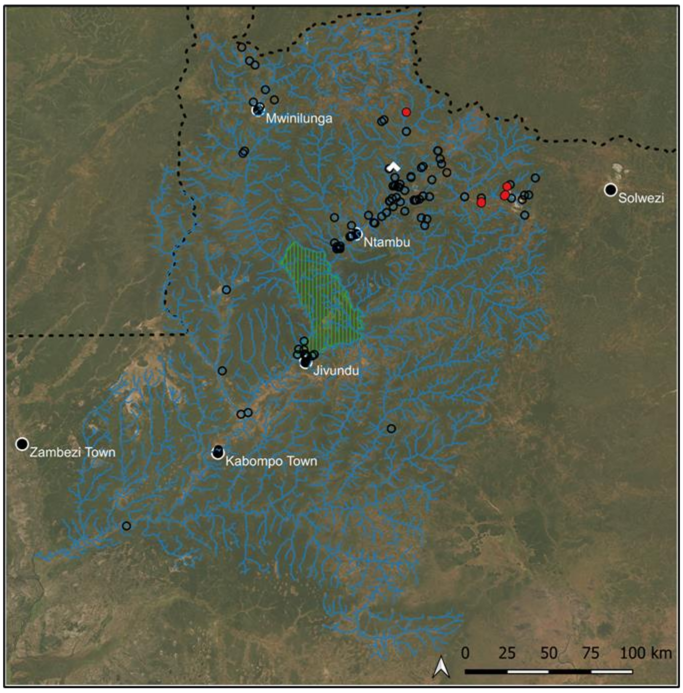
Hepsetus cuvieri



Parauchenoglanis ngamensis



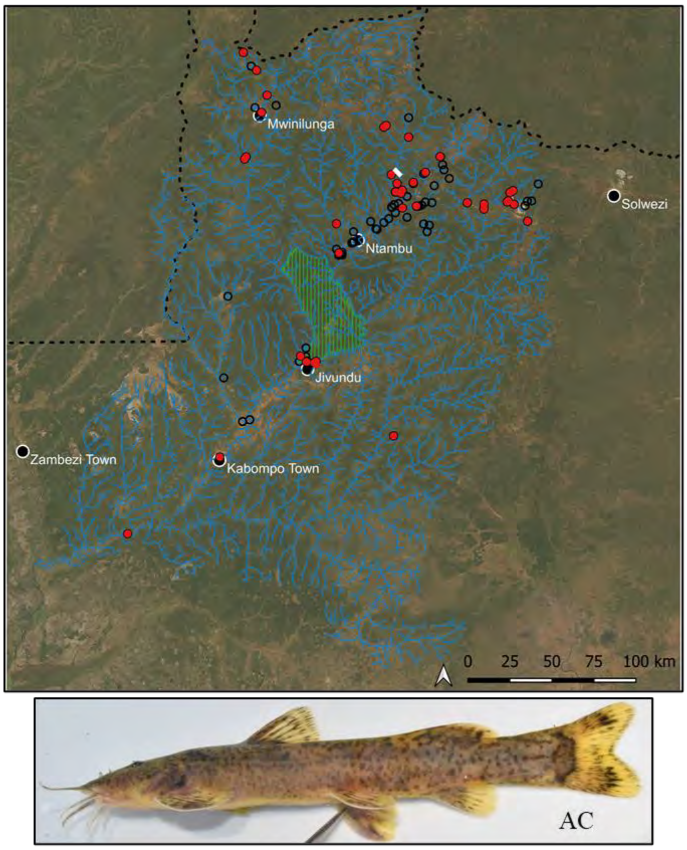
Schilbe depressirostris



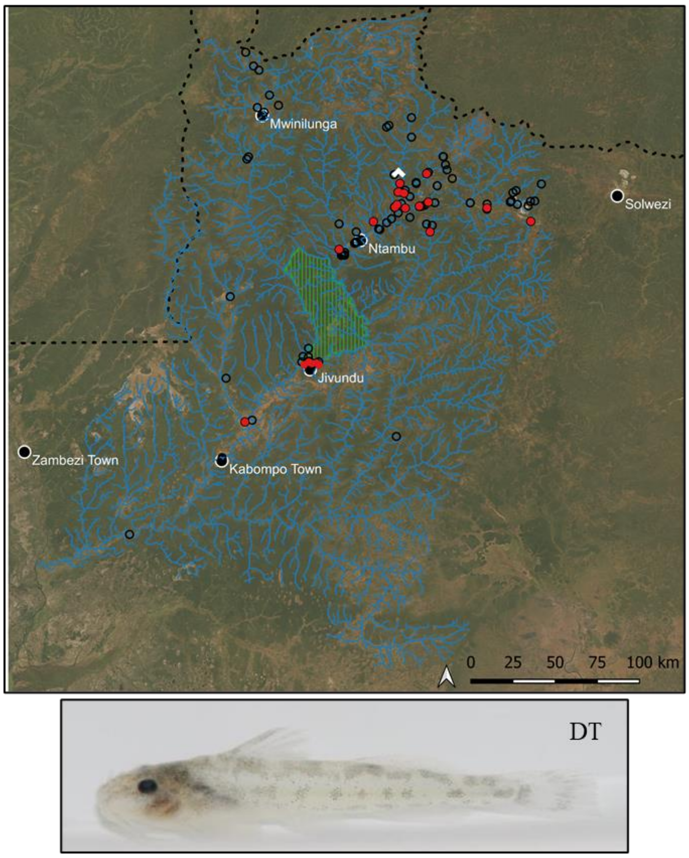
Schilbe yangambianus

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

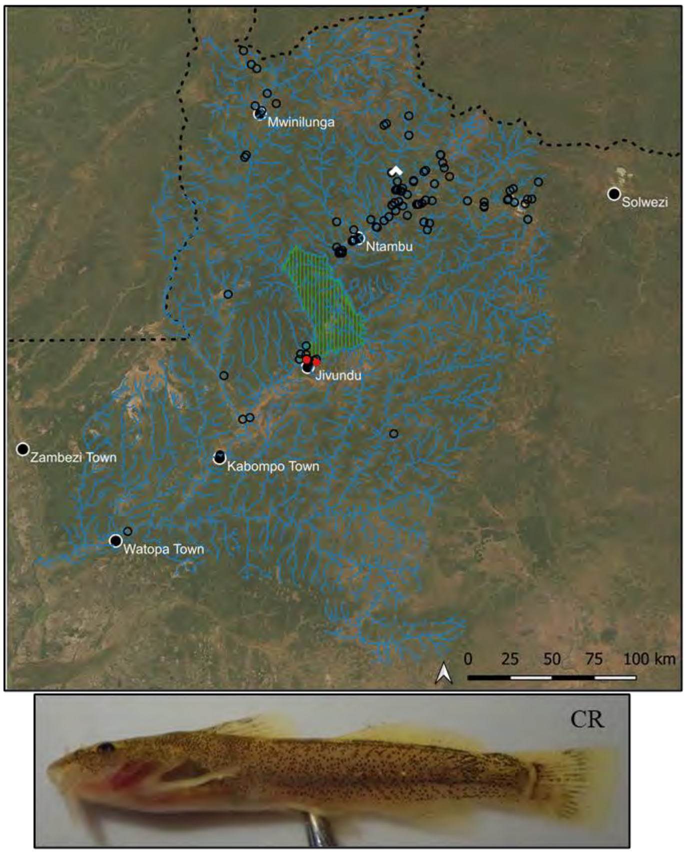
Plate 13



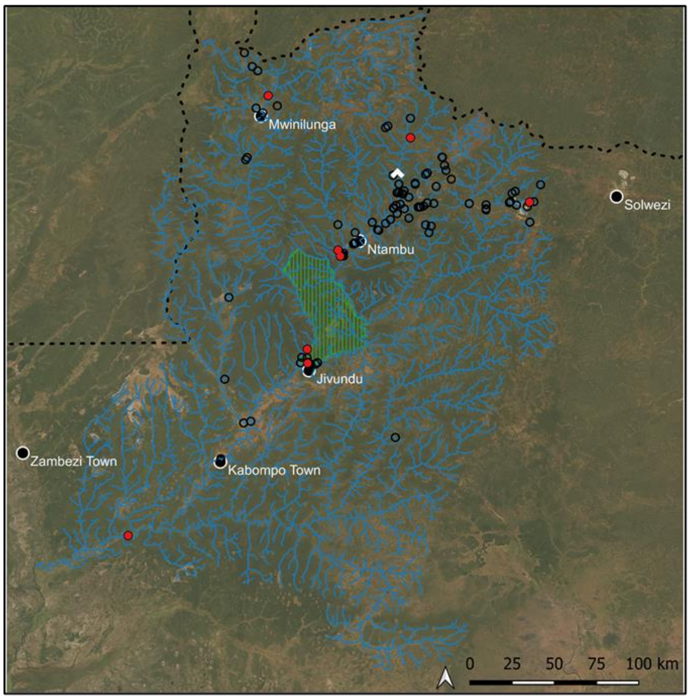
Amphilius uranoscopus



Zaireichthys pallidus



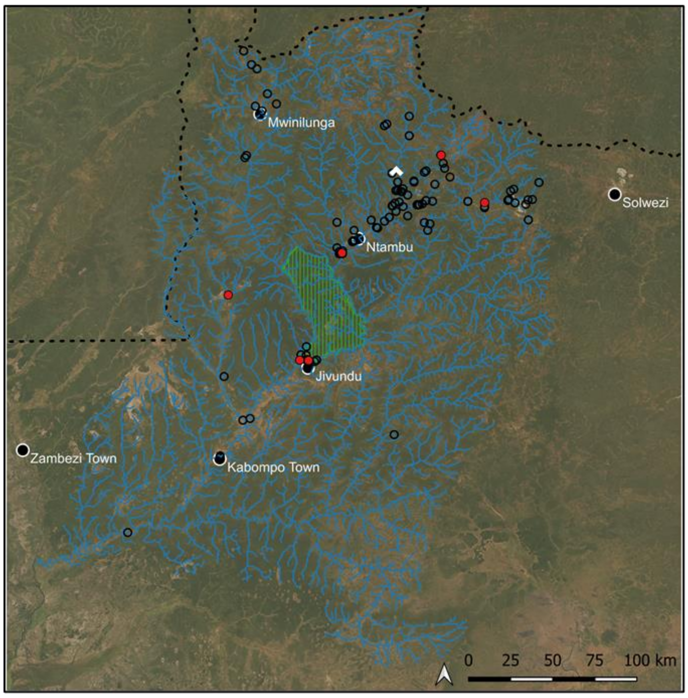
Zaireichthys sp. 'brown north'



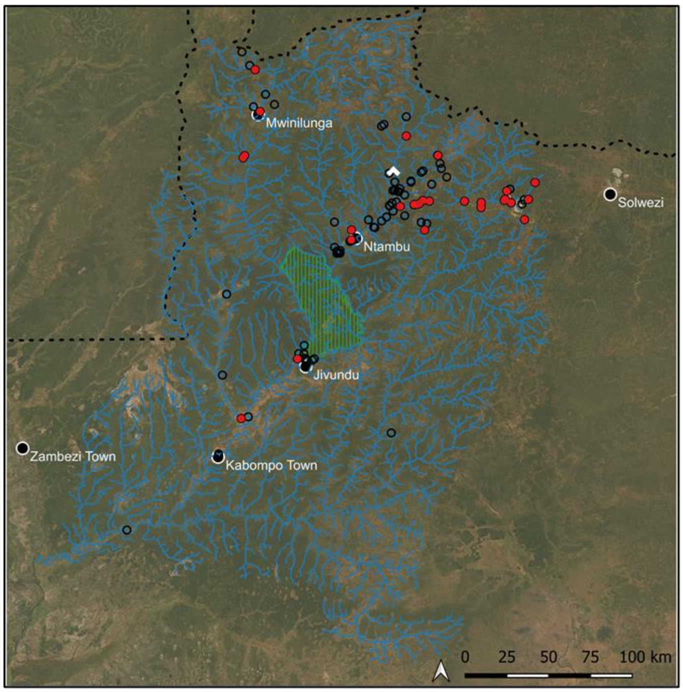
Clariallabes platyprosopos

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

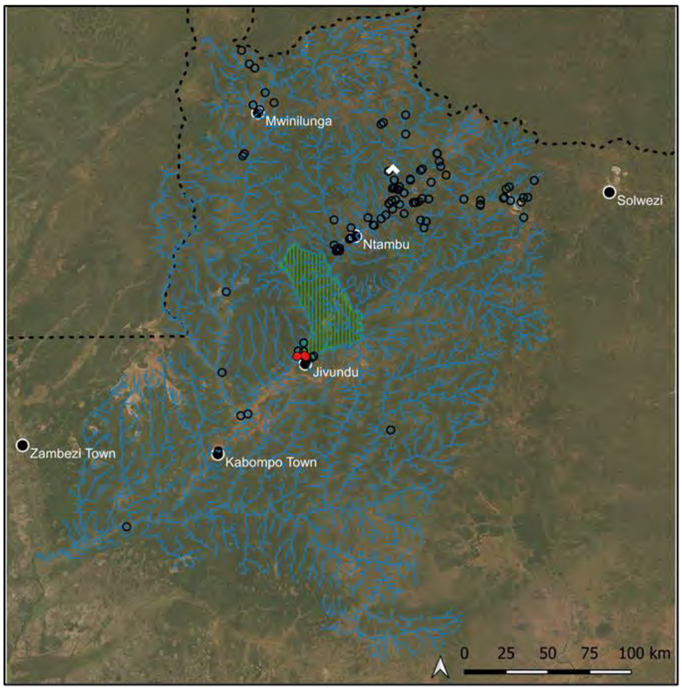
Plate 14



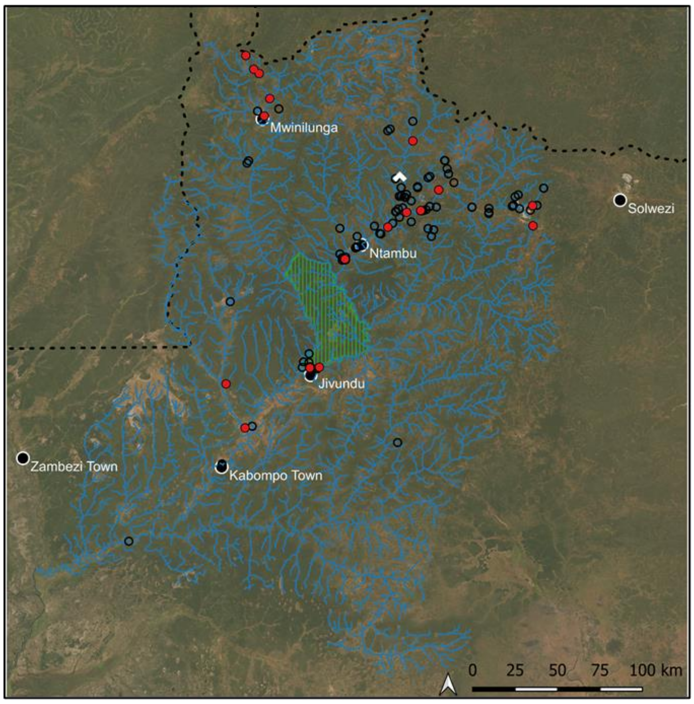
Clarias gariepinus



Clarias liocephalus



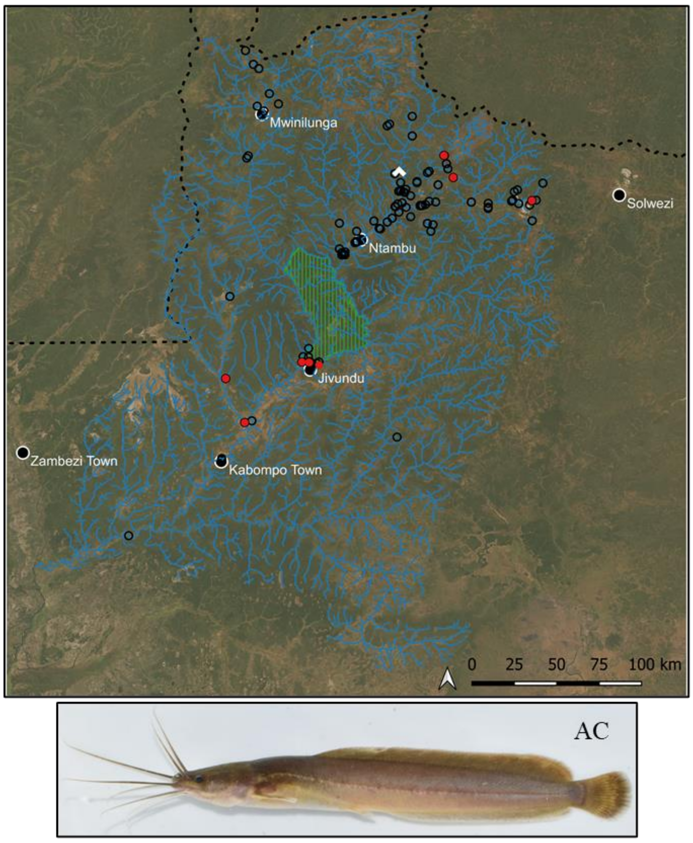
Clarias ngamensis



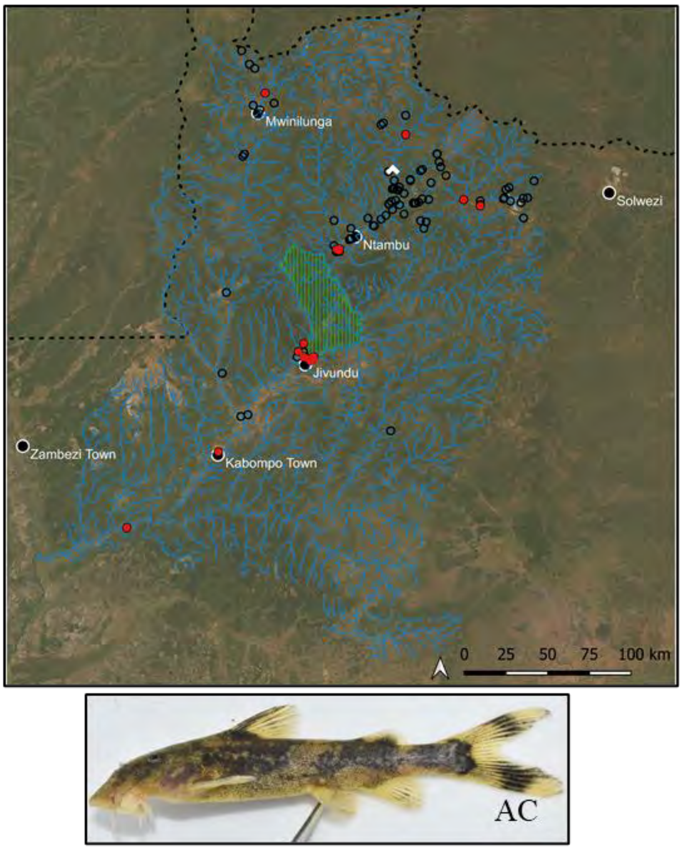
Clarias stappersii

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

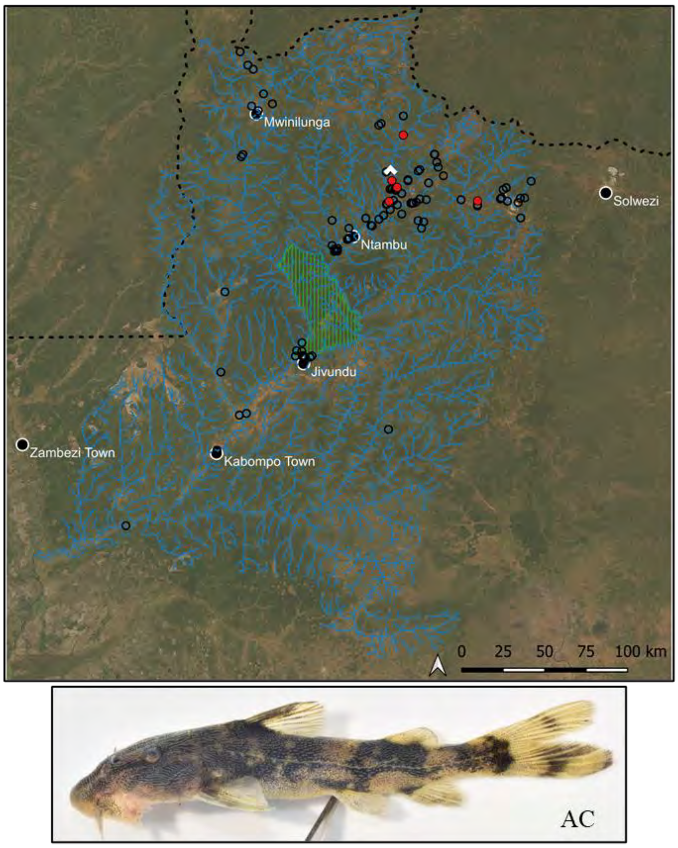
Plate 15



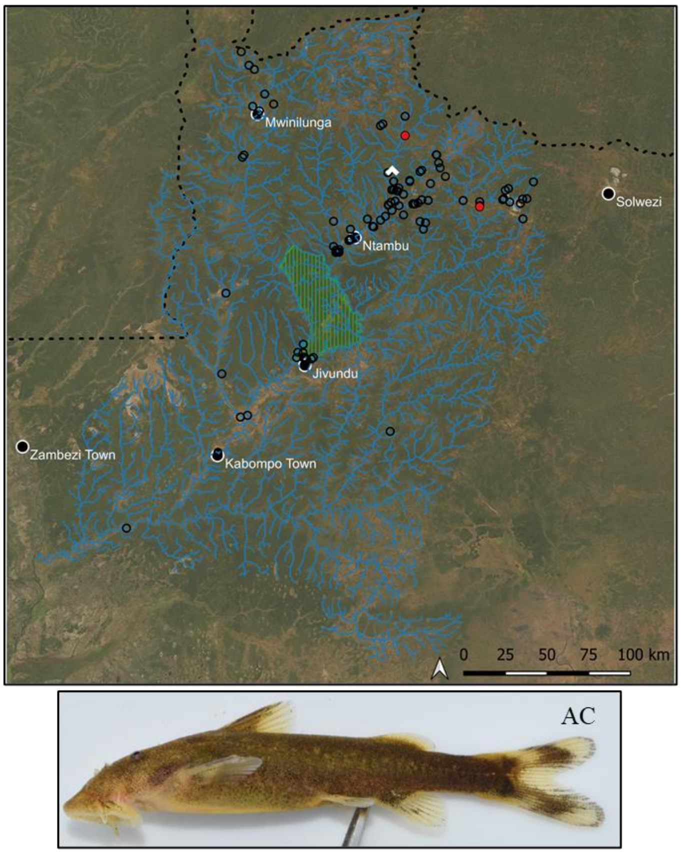
Clarias theodorae



Chiloglanis fasciatus



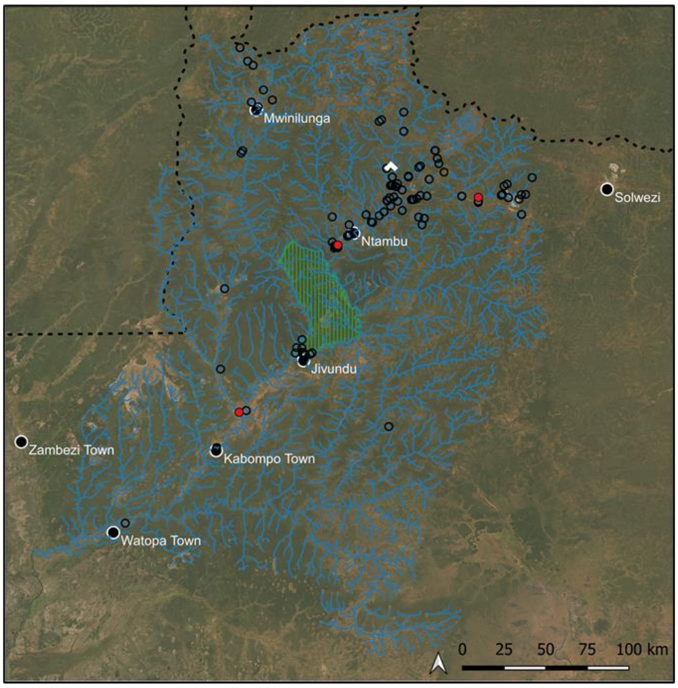
Chiloglanis neumanni



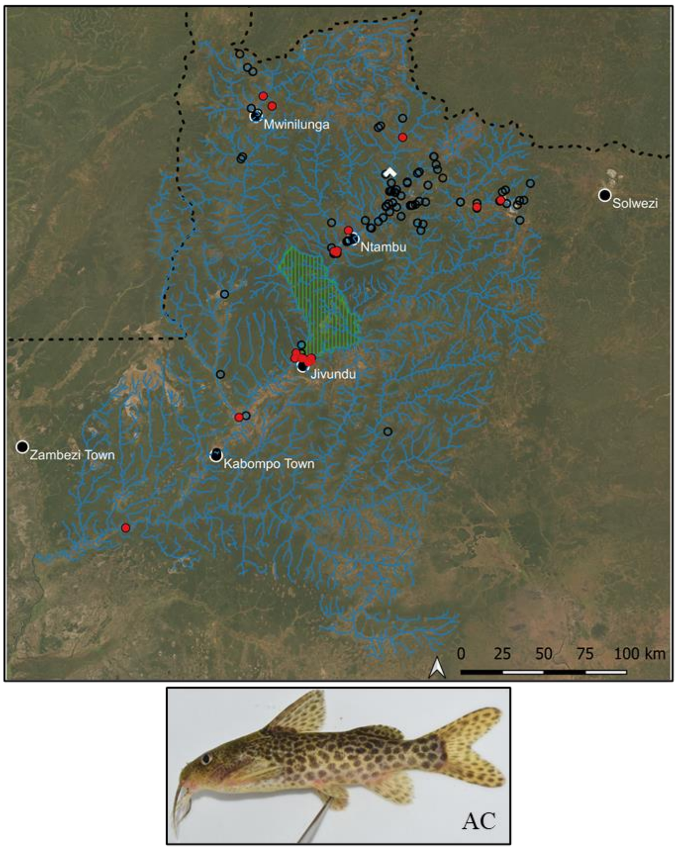
Chiloglanis sp. 'plain, small eye'

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

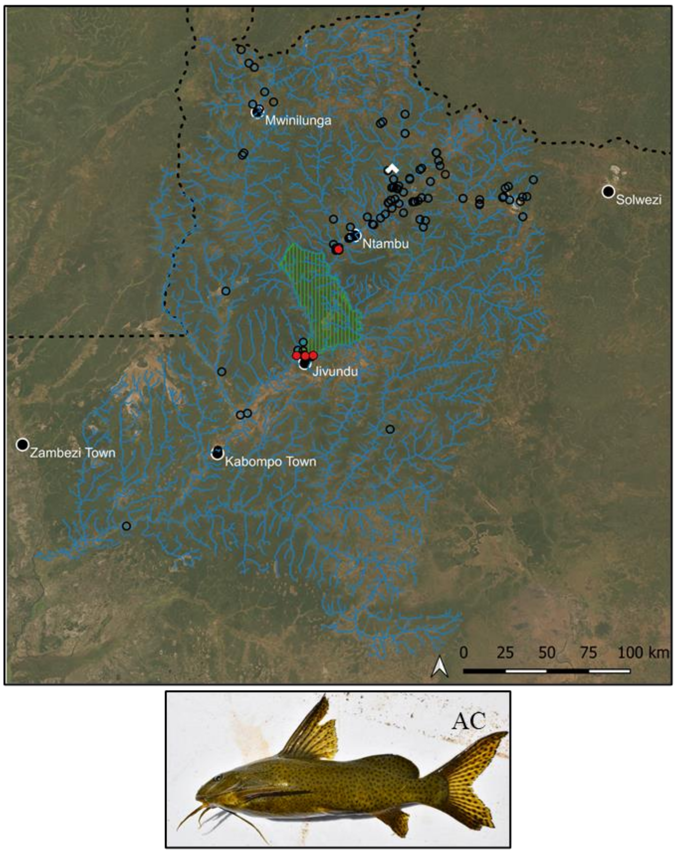
Plate 16



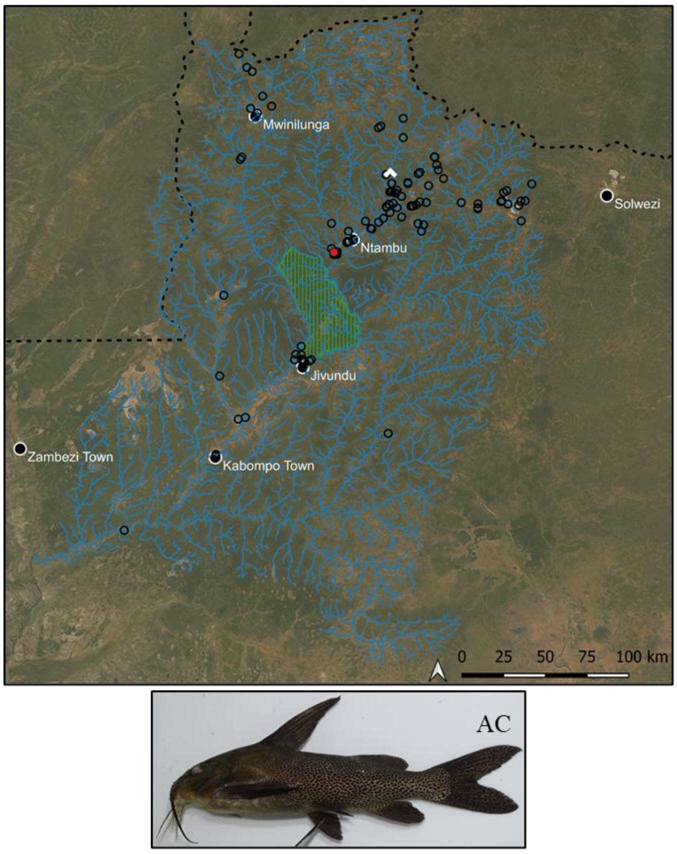
Synodontis macrostigma



Synodontis macrostoma



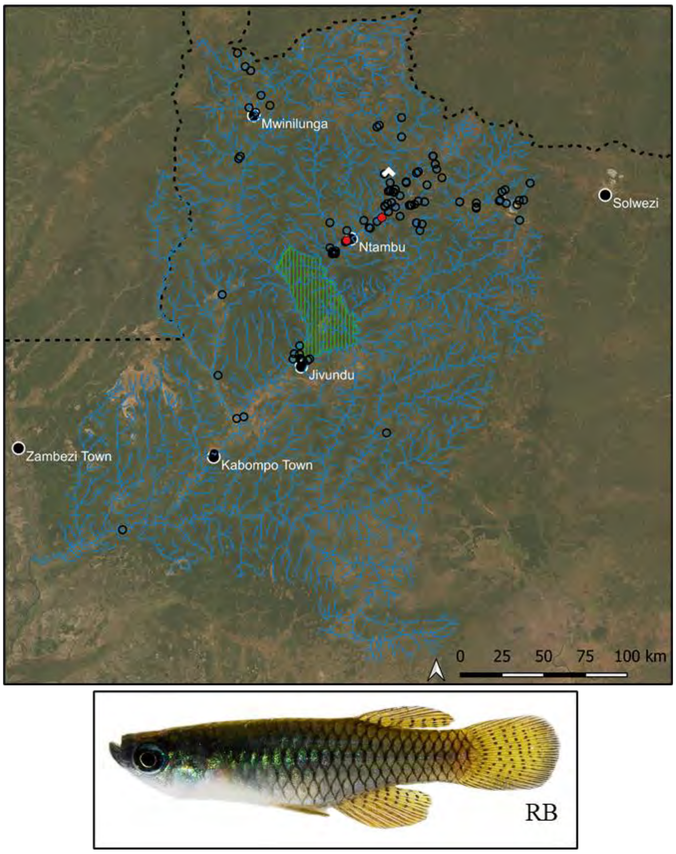
Synodontis nigromaculatus



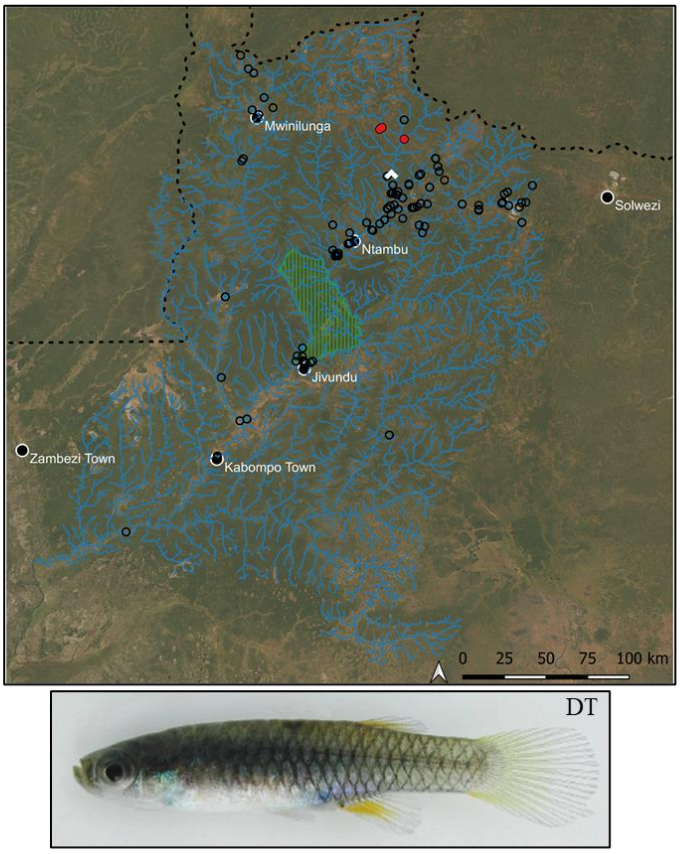
Synodontis woosnami

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

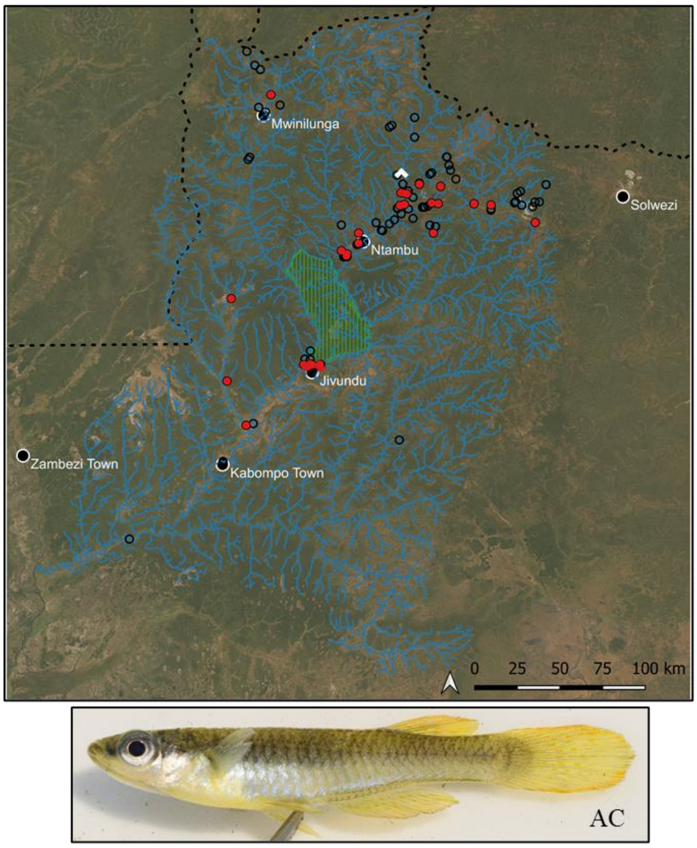
Plate 17



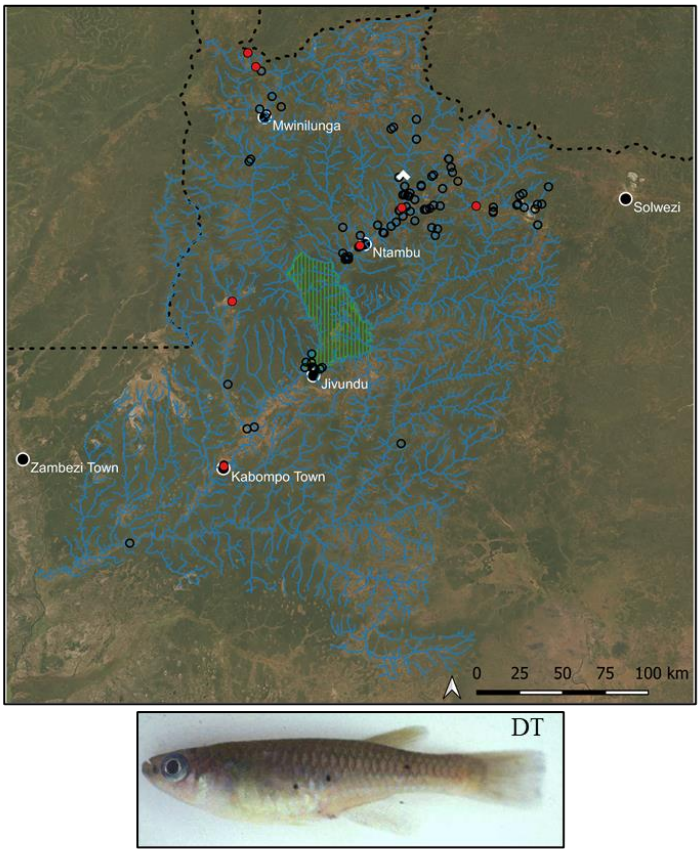
Lacustricola’ chobensis



‘Lacustricola’ hutereaui



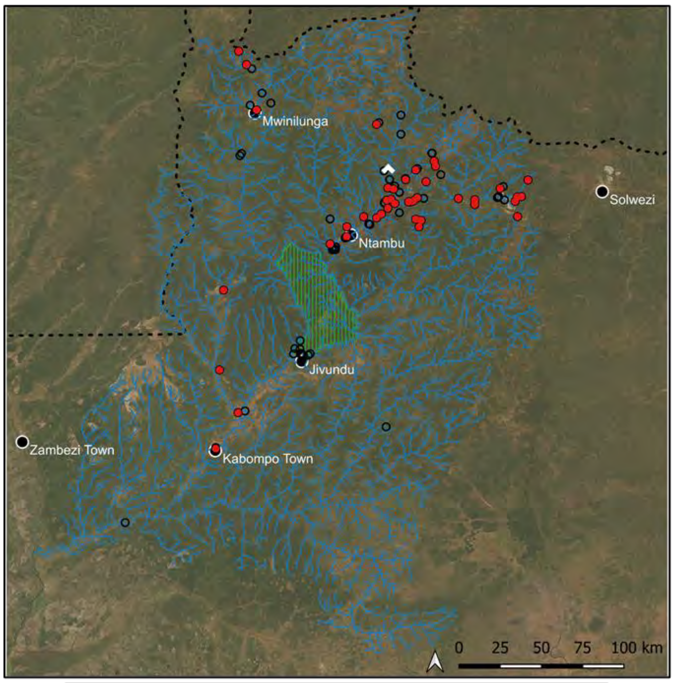
‘Lacustricola’ johnstoni



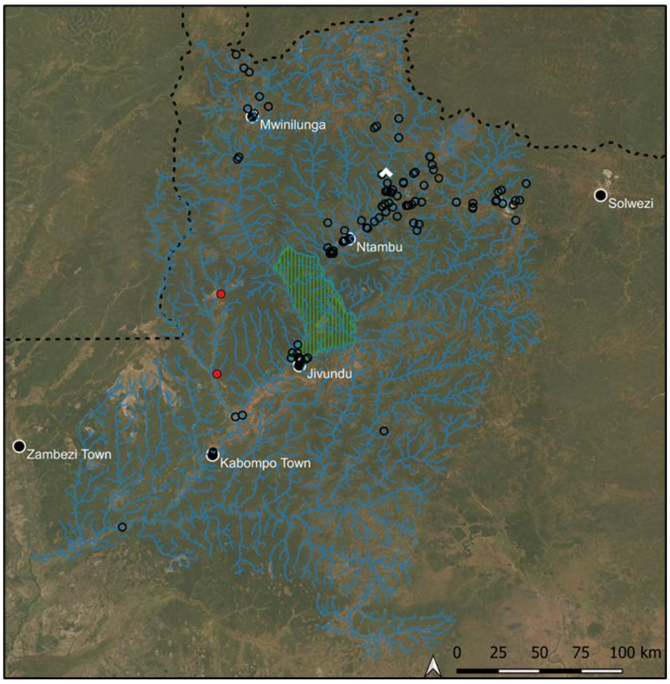
‘Lacustricola’ jubbi

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

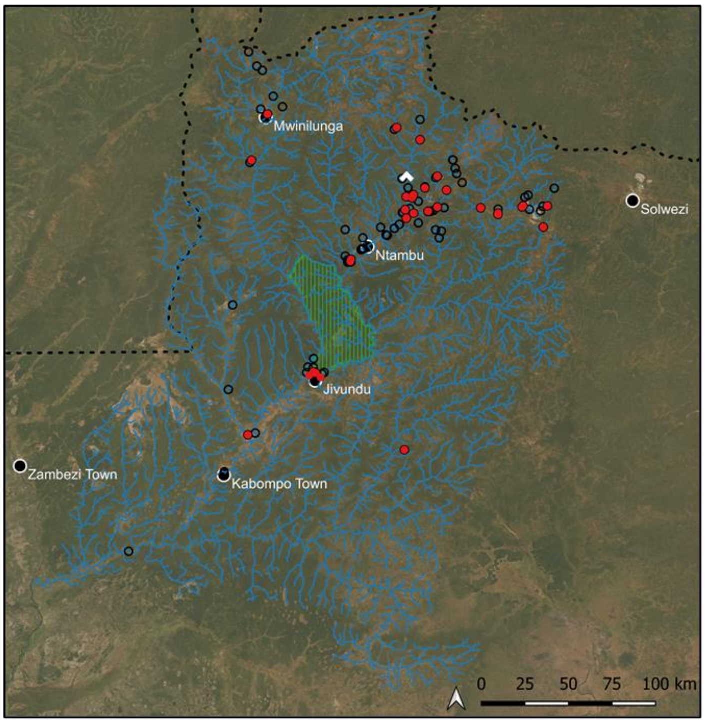
Plate 18



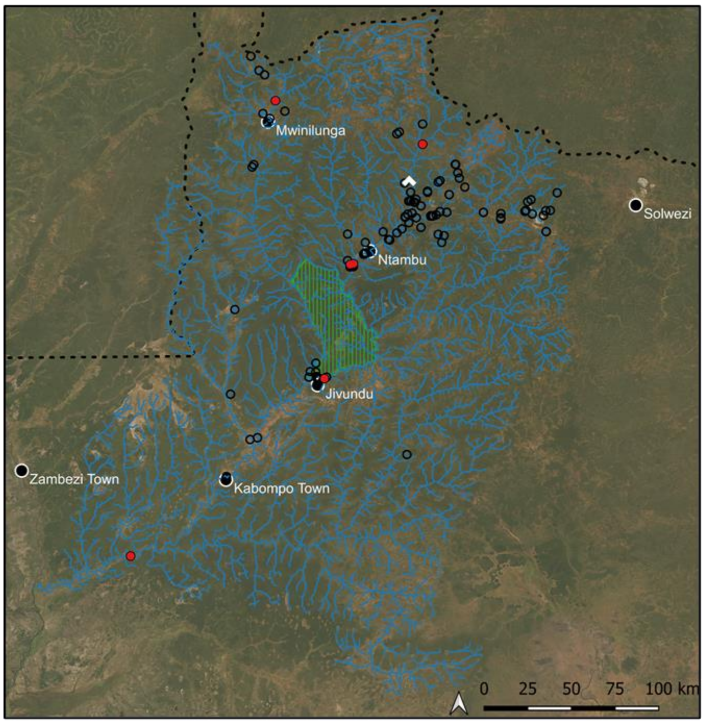
'Lacustricola' katangae



'Lacustricola' pygmaeus



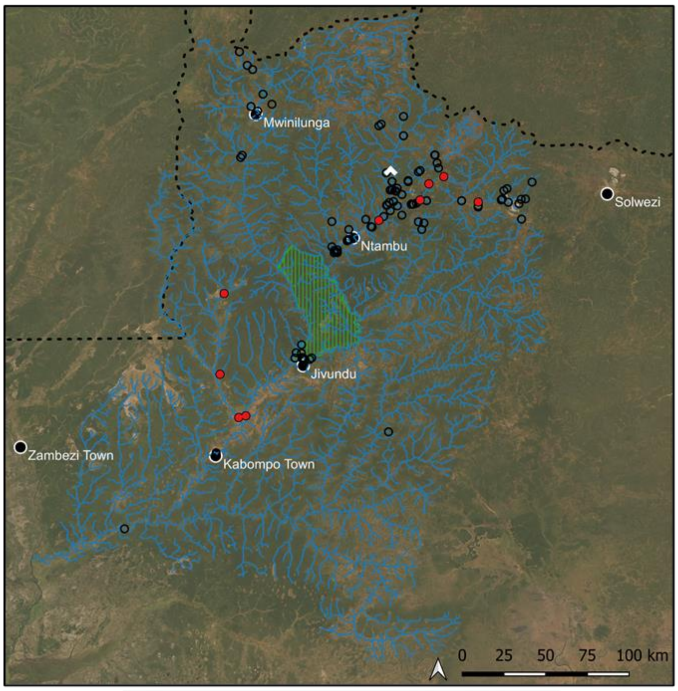
Mastacembelus frenatus



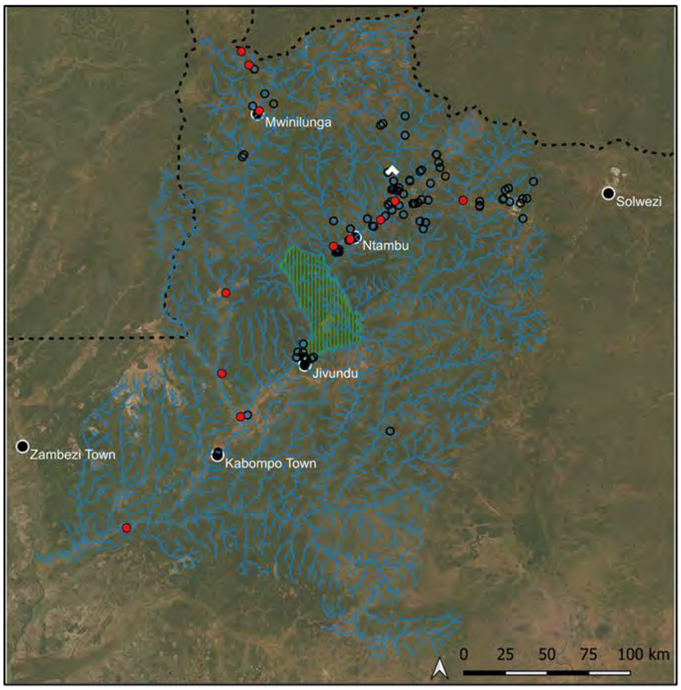
Mastacembelus vanderwaali

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

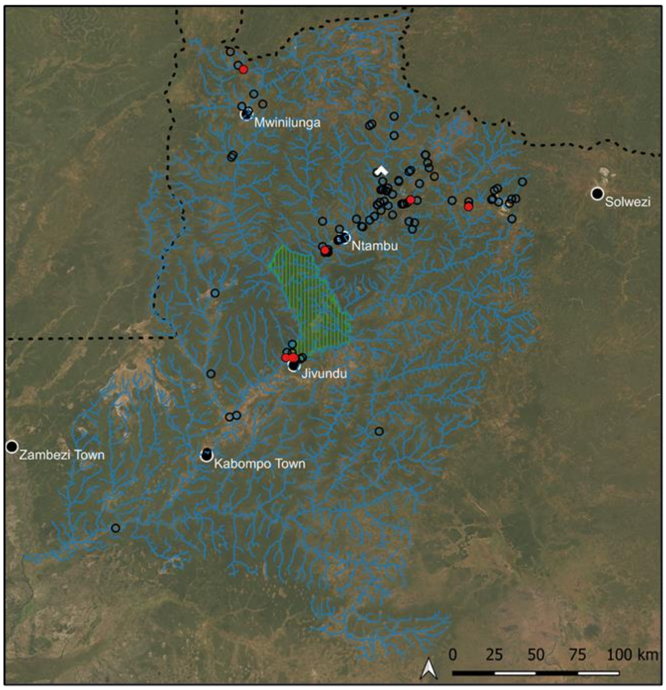
Plate 19



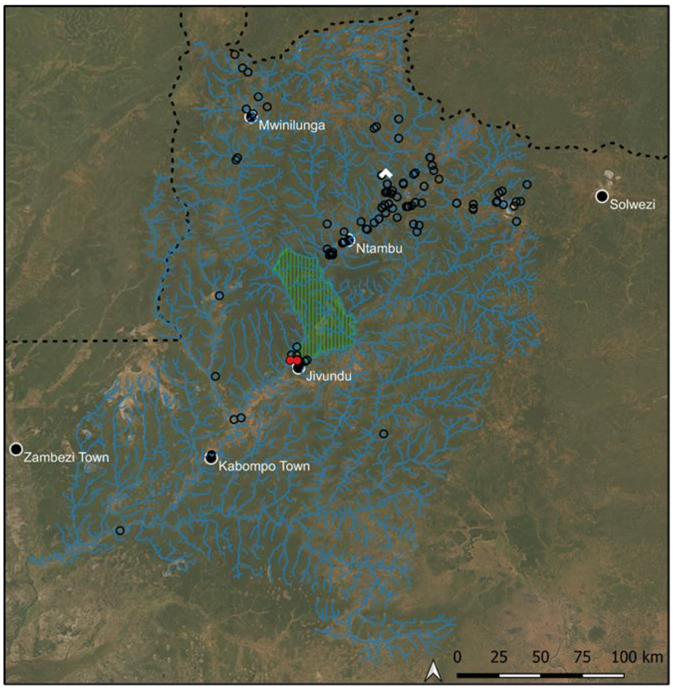
Ctenopoma multispine



Microctenopoma intermedium



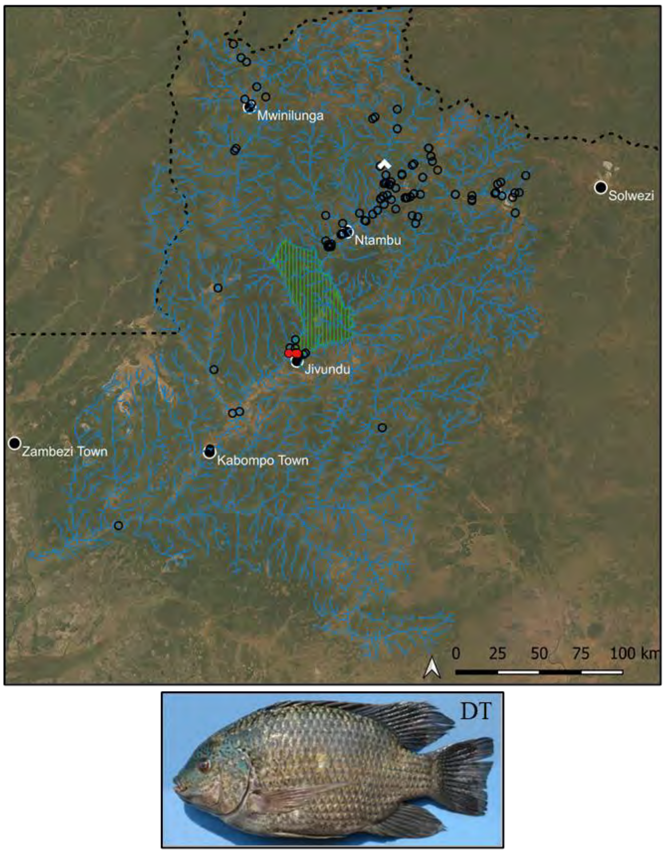
Coptodon rendalli



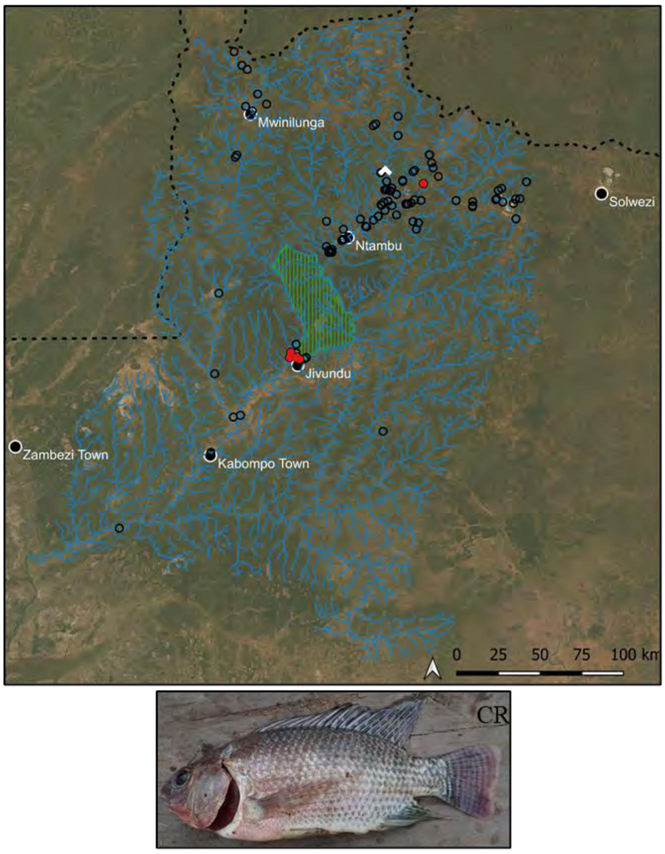
Oreochromis andersonii

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

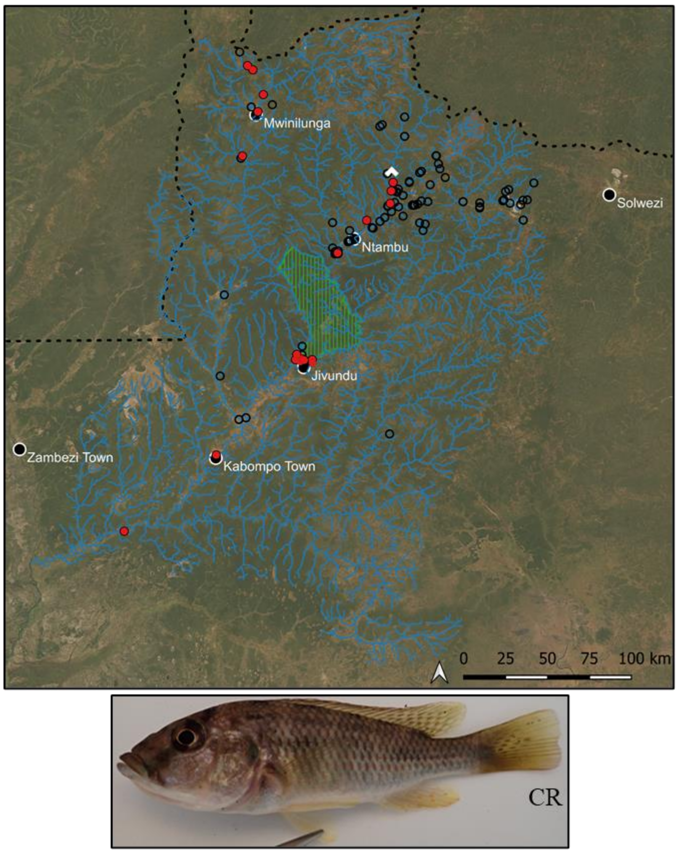
Plate 20



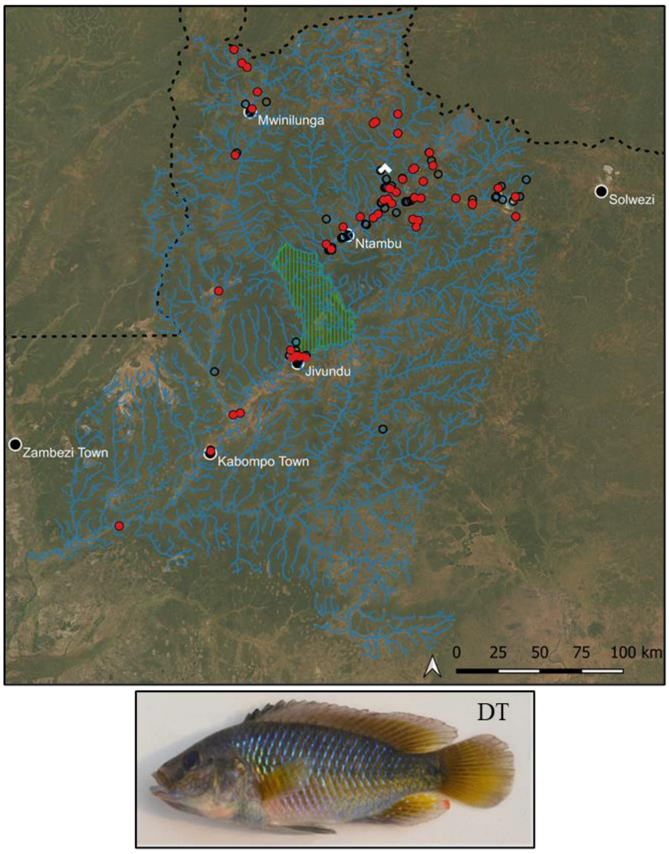
Oreochromis macrochir



Oreochromis niloticus



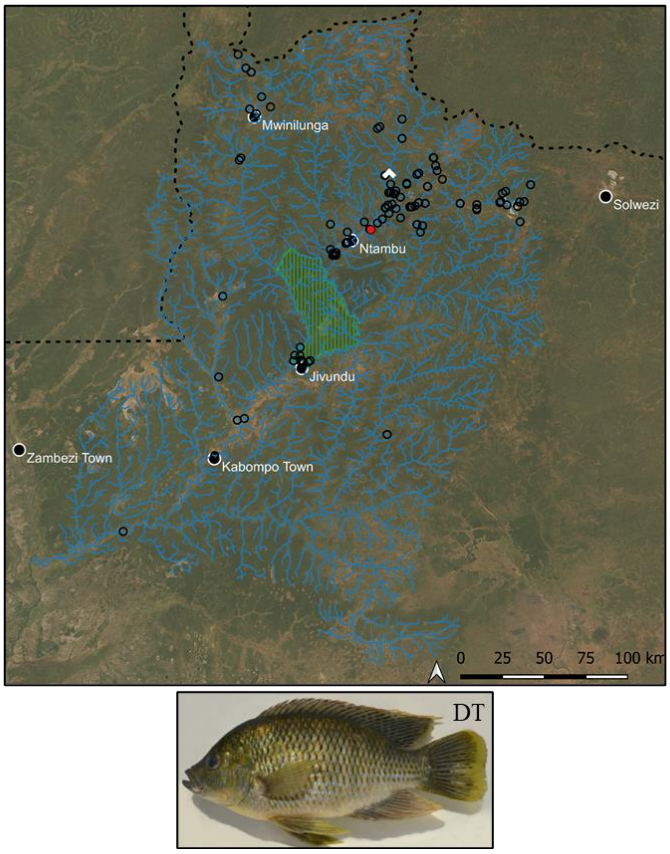
Pharyngochromis acuticeps



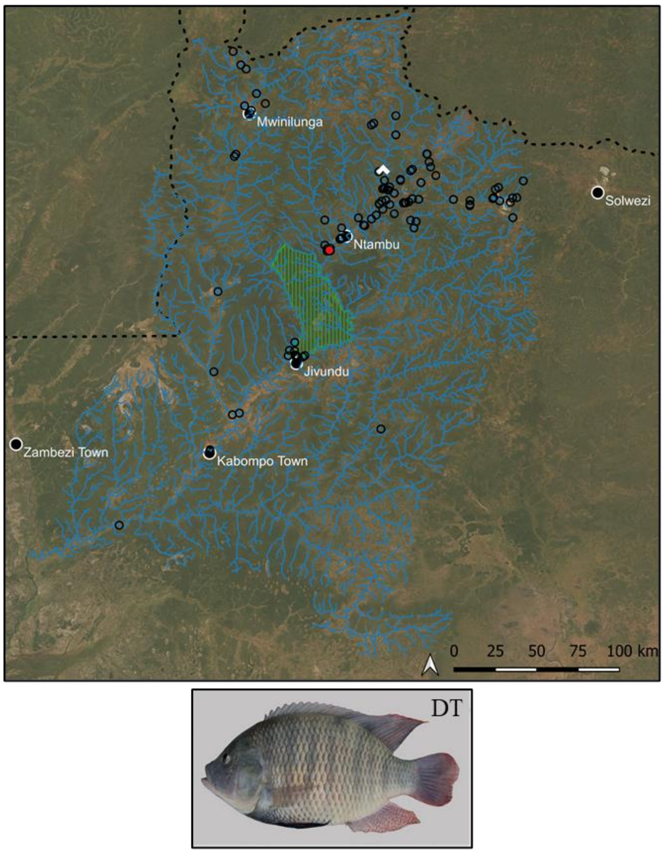
Pseudocrenilabrus philander

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

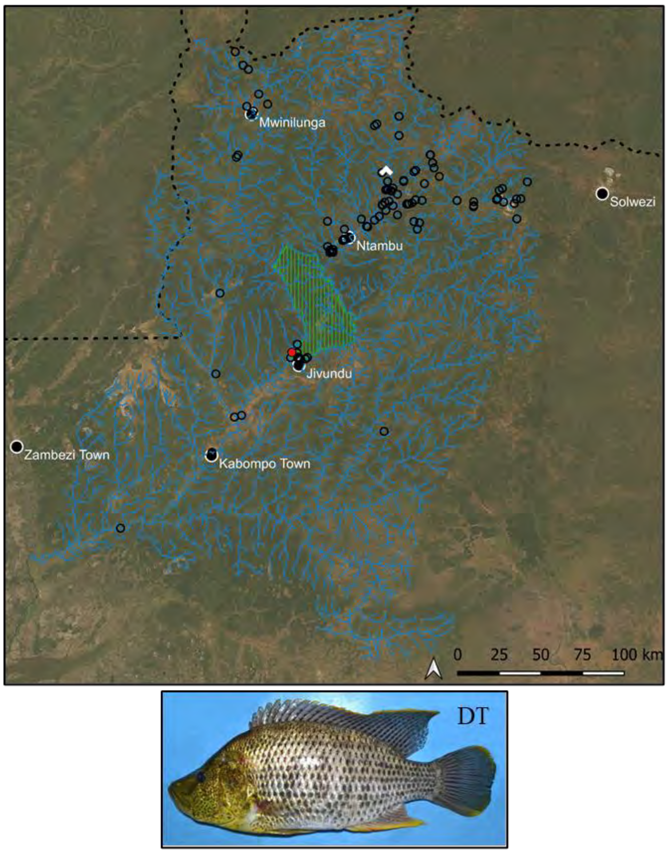
Plate 21



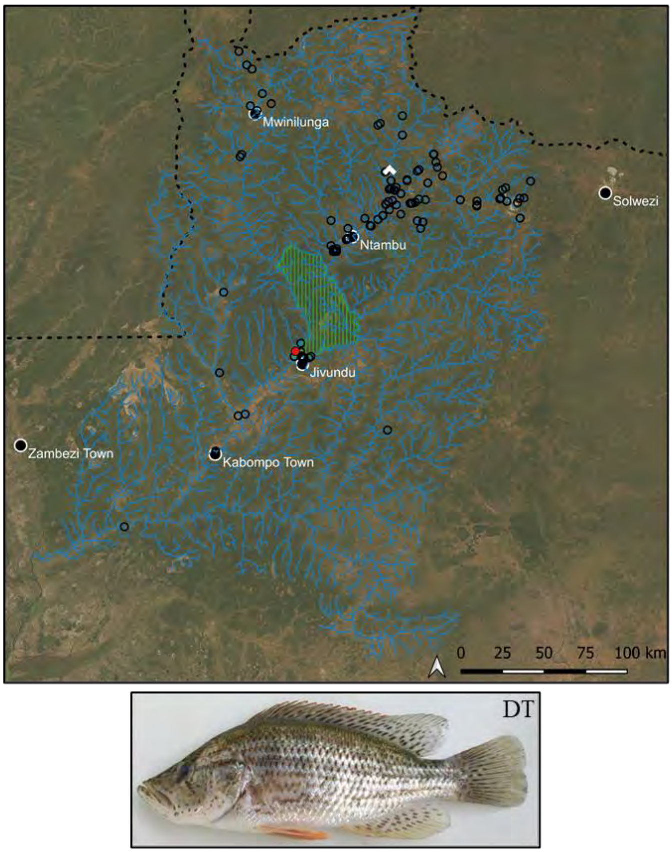
Sargochromis carlottae



Sargochromis giardi



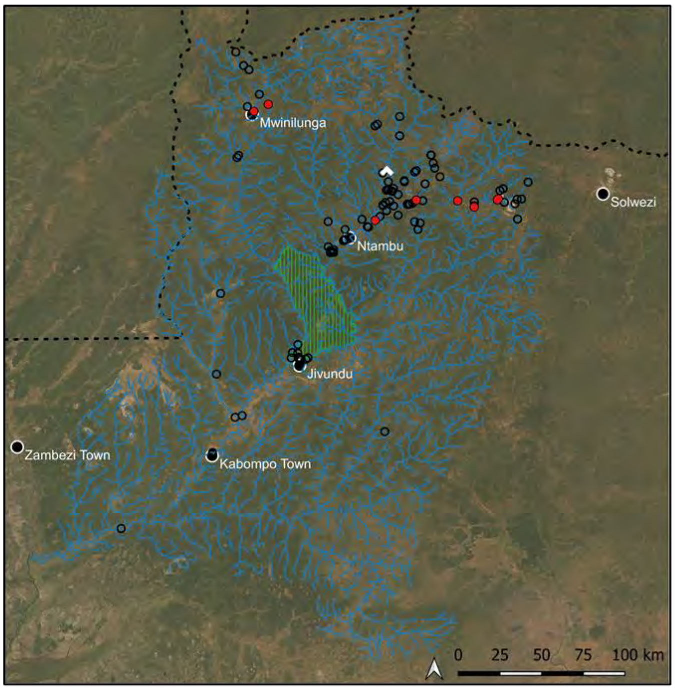
Serranochromis altus



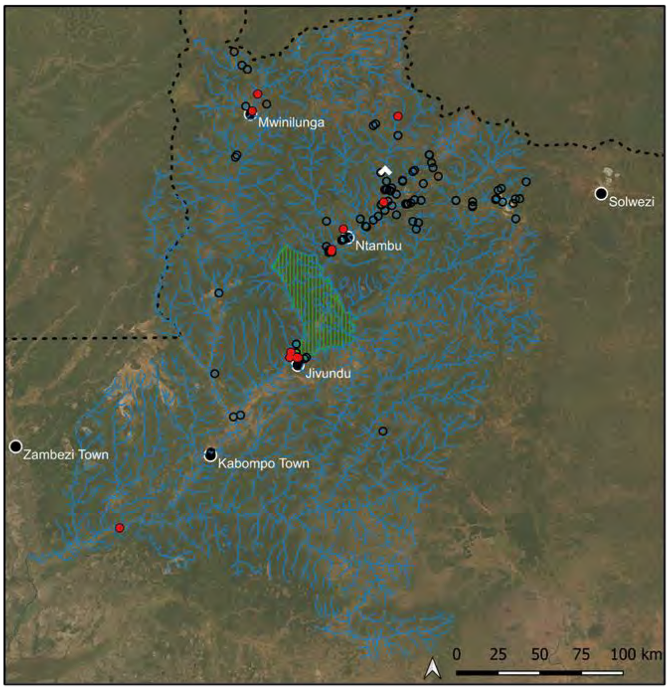
Serranochromis angusticeps

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

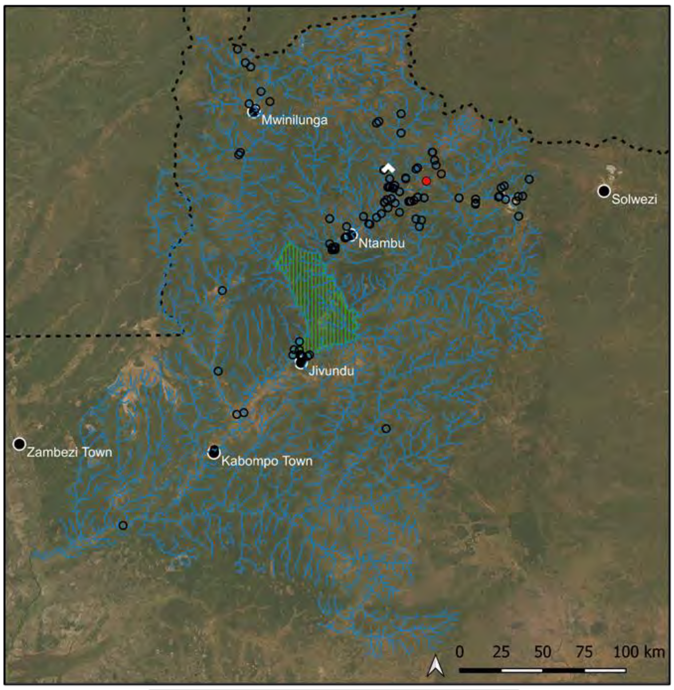
Plate 22

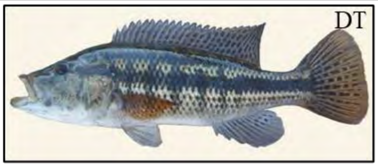


Serranochromis jallae

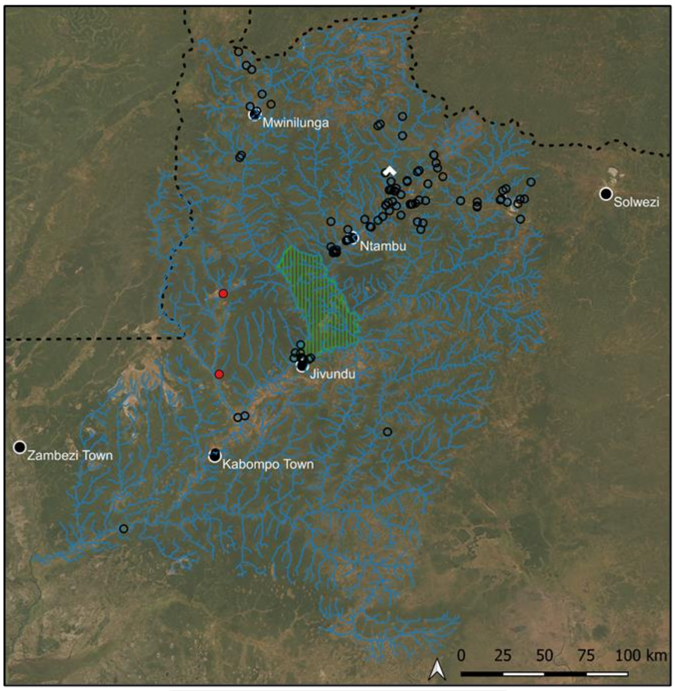


Serranochromis macrocephalus



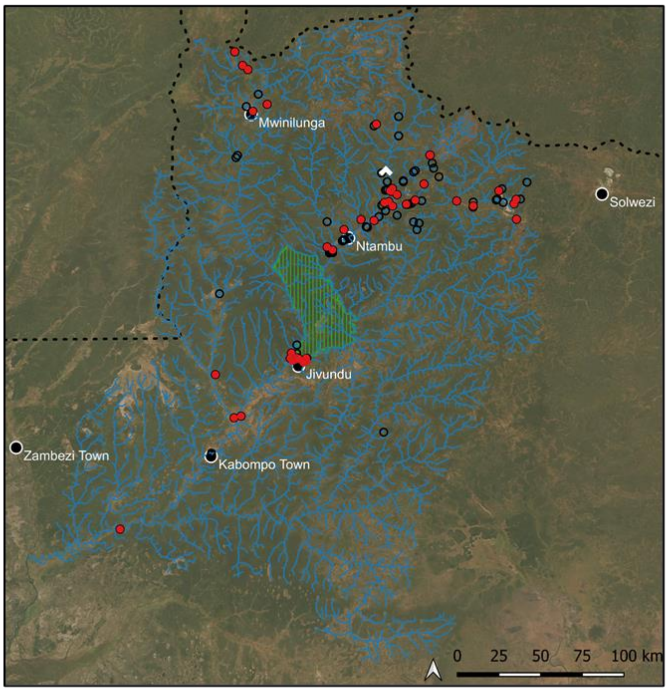


Serranochromis thumbergi



Tilapia ruweti

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie



Tilapia sparrmanii

Photograph credits: AC: Dr Albert Chakona; DT: Denis Tweddle; RC: Dr Russell Chalmers; CR: Craig Rennie

Supplementary 1

Table S1: Pairwise Wilcox test for catch per unit effort from five main low water Kabompo River habitats.

Habitat	Bare	Phrag	Rock	Vall
Phrag	0.003			
Rock	0.004	0.378		
Vall	0.001	0.197	0.019	
Wood	0.019	0.190	0.377	0.001

Table S2: Pairwise Wilcox test for Sample species richness from five main low water Kabompo River habitats.

Habitat	Bare	Phrag	Rock	Vall
Phrag	<0.001			
Rock	0.001	0.006		
Vall	0.009	<0.001	<0.004	
Wood	<0.001	0.798	0.0131	<0.001

Table S3: Pairwise Wilcox test for Shannon diversity index from five main low water Kabompo River habitats.

Habitat	Bare	Phrag	Rock	Vall
Phrag	<0.001			
Rock	0.001	0.006		
Vall	0.009	<0.001	<0.004	
Wood	<0.001	0.798	0.0131	<0.001

Table S4: Pairwise Wilcox test for Pielou’s evenness from five main low water Kabompo River habitats.

Habitats	Bare	Phrag	Rock	Vall
Phrag	<0.001			
Rock	<0.001	0.221		
Vall	0.003	<0.001	<0.001	
Wood	<0.001	0.777	0.565	<0.001

Table S5: Summary of the Pairwise Adonis tables performed on the five main habitats sampled for the nMDS.

A) Bare-Phrag

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	2.18	2.18	7.32	0.16	**0.001**
Residuals	38	11.34	0.30		0.84	
Total	39	13.53			1	

B) Bare-Rock

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	2.29	2.29	7.27	0.15	**0.001**
Residuals	42	13.23	0.32		0.85	
Total	43	15.52			1	

C) Bare- *V. aethiopica*

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	0.39	0.39	1.66	0.04	0.128
Residuals	40	9.48	0.24		0.96	
Total	41	9.87			1	

D) Bare-Wood

F) Phrag-*V. aethiopica*

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	4.13	4.13	16.62	0.23	**0.001**
Residuals	56	13.92	0.25		0.77	
Total	57	18.05			1	

G) Phrag-Wood

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	0.66	0.66	2.06	0.04	**0.013**
Residuals	55	17.68	0.32		0.96	
Total	56	18.35			1	

H) Rock-*V. aethiopica*

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	3.79	3.79	14.38	0.19	**0.001**
Residuals	60	15.81	0.26		0.81	
Total	61	19.59			1	

I) Rock-Wood

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	2.04	2.04	6.02	0.13	**0.001**
Residuals	39	13.24	0.34		0.87	
Total	40	15.29			1	

E) Phrag-Rock

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	3.90	3.90	12.81	0.18	**0.001**
Residuals	58	17.67	0.30		0.82	
Total	59	21.57			1	

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	2.54	2.54	7.64	0.11	**0.001**
Residuals	59	19.57	0.33		0.89	
Total	60	22.11			1	

J) *V. aethiopica* -Wood

	Df	SS	MeanSqs	F. Model	R2	Pr(>F)
Habitat	1	3.93	3.93	14.15	0.20	**0.001**
Residuals	57	15.82	0.28		0.80	
Total	58	19.74			1	

Table S6: SIMPER analysis for the comparison in species composition in Bare and phragmites mesohabitats based on Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.190	0.167	1.138	0.423	0.106	0.210	0.002
CJUV	0.105	0.138	0.760	0.205	0.022	0.326	0.001
CFAS	0.102	0.184	0.554	0.199	0.009	0.439	0.321
ELIN	0.057	0.090	0.635	0.000	0.115	0.502	0.068
EKER	0.053	0.050	1.066	0.000	0.106	0.561	0.004
PACU	0.045	0.136	0.333	0.083	0.009	0.611	0.653
NMUL	0.044	0.045	0.973	0.000	0.088	0.660	0.299
EEUT	0.042	0.071	0.592	0.000	0.084	0.706	0.268
TSPA	0.032	0.036	0.883	0.012	0.060	0.741	0.637
SDEP	0.029	0.065	0.448	0.000	0.058	0.773	0.244
PPHI	0.028	0.055	0.506	0.022	0.039	0.804	0.124
EFAS	0.021	0.028	0.730	0.000	0.041	0.827	0.175
EUNI	0.020	0.069	0.293	0.000	0.040	0.849	0.494
MFRE	0.019	0.063	0.301	0.038	0.000	0.870	0.530
LJOH	0.018	0.029	0.613	0.018	0.022	0.890	0.180
EPAL	0.016	0.044	0.368	0.000	0.033	0.907	0.185
HSZA	0.016	0.047	0.340	0.000	0.032	0.925	0.879
EAFR	0.014	0.031	0.459	0.000	0.029	0.941	0.139
ERAD	0.011	0.027	0.407	0.000	0.022	0.953	0.600
NDAG	0.010	0.037	0.274	0.000	0.020	0.964	0.965
PNGA	0.010	0.036	0.276	0.000	0.020	0.975	0.893
EPOE	0.010	0.029	0.340	0.000	0.020	0.986	0.382
MACU	0.004	0.022	0.192	0.000	0.008	0.991	0.816
SYOMA	0.004	0.014	0.276	0.000	0.008	0.995	1.000
OZAM	0.003	0.016	0.192	0.000	0.006	0.999	0.758
LCYL	0.001	0.007	0.192	0.000	0.003	1.000	1.000
AURA	0.000	0.000	NaN	0.000	0.000	1.000	1.000
PLON	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S7: SIMPER analysis for the comparison in species composition in bare and rock mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.203	0.183	1.110	0.423	0.041	0.222	0.001
CFAS	0.145	0.161	0.899	0.199	0.170	0.381	0.022
CJUV	0.103	0.142	0.725	0.205	0.004	0.493	0.001
PACU	0.095	0.152	0.622	0.083	0.127	0.597	0.053
LCYL	0.093	0.121	0.768	0.000	0.186	0.699	0.018
SYOMA	0.036	0.044	0.815	0.000	0.072	0.738	0.097
MFRE	0.029	0.068	0.423	0.038	0.024	0.769	0.221
PLON	0.028	0.052	0.529	0.000	0.055	0.800	0.038
HSZA	0.026	0.046	0.567	0.000	0.052	0.828	0.488
TSPA	0.023	0.057	0.400	0.012	0.037	0.853	0.916
AURA	0.018	0.050	0.365	0.000	0.037	0.873	0.144
PPHI	0.016	0.042	0.389	0.022	0.013	0.891	0.500
EEUT	0.013	0.053	0.249	0.000	0.026	0.906	0.983
MACU	0.013	0.037	0.345	0.000	0.026	0.920	0.292
LJOH	0.012	0.030	0.411	0.018	0.008	0.933	0.555
PNGA	0.011	0.037	0.312	0.000	0.023	0.946	0.884
OZAM	0.011	0.028	0.394	0.000	0.022	0.958	0.166
NMUL	0.010	0.034	0.280	0.000	0.019	0.968	1.000
EKER	0.008	0.031	0.259	0.000	0.016	0.977	1.000
EPOE	0.006	0.031	0.179	0.000	0.011	0.983	0.689
ELIN	0.005	0.024	0.218	0.000	0.010	0.989	1.000
ERAD	0.002	0.010	0.245	0.000	0.005	0.991	0.986
NDAG	0.002	0.013	0.179	0.000	0.005	0.994	0.999
EAFR	0.002	0.012	0.179	0.000	0.004	0.997	0.933
EFAS	0.002	0.006	0.258	0.000	0.003	0.998	1.000
EPAL	0.002	0.009	0.179	0.000	0.003	1.000	0.940
EUNI	0.000	0.000	NaN	0.000	0.000	1.000	1.000
SDEP	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S8: SIMPER analysis for the comparison in species composition in bare and Vallisneria mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.184	0.130	1.417	0.423	0.422	0.267	0.004
CFAS	0.153	0.158	0.963	0.199	0.199	0.489	0.010
CJUV	0.112	0.141	0.791	0.205	0.052	0.651	0.001
PACU	0.074	0.145	0.513	0.083	0.078	0.759	0.192
NDAG	0.049	0.119	0.410	0.000	0.097	0.830	0.312
MFRE	0.029	0.073	0.399	0.038	0.025	0.872	0.227
LCYL	0.019	0.059	0.327	0.000	0.039	0.900	0.964
NMUL	0.019	0.062	0.309	0.000	0.038	0.928	0.986
LJOH	0.012	0.030	0.384	0.018	0.007	0.945	0.626
ELIN	0.011	0.047	0.245	0.000	0.023	0.961	0.981
PPHI	0.011	0.036	0.301	0.022	0.000	0.977	0.761
TSPA	0.010	0.031	0.335	0.012	0.010	0.993	0.998
MACU	0.004	0.017	0.247	0.000	0.008	0.999	0.765
SYOMA	0.001	0.006	0.185	0.000	0.002	1.000	1.000
AURA	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EAFR	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EEUT	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EFAS	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EKER	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EPAL	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EPOE	0.000	0.000	NaN	0.000	0.000	1.000	1.000
ERAD	0.000	0.000	NaN	0.000	0.000	1.000	1.000
EUNI	0.000	0.000	NaN	0.000	0.000	1.000	1.000
HSZA	0.000	0.000	NaN	0.000	0.000	1.000	1.000
OZAM	0.000	0.000	NaN	0.000	0.000	1.000	1.000
PNGA	0.000	0.000	NaN	0.000	0.000	1.000	1.000
PLON	0.000	0.000	NaN	0.000	0.000	1.000	1.000
SDEP	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S9: SIMPER analysis for the comparison in species composition in bare and wood mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.202	0.180	1.126	0.423	0.094	0.220	0.001
CFAS	0.111	0.181	0.611	0.199	0.041	0.340	0.224
CJUV	0.103	0.140	0.735	0.205	0.008	0.453	0.001
PACU	0.048	0.136	0.354	0.083	0.015	0.505	0.587
TSPA	0.044	0.066	0.673	0.012	0.086	0.553	0.263
PNGA	0.040	0.085	0.469	0.000	0.080	0.596	0.141
NMUL	0.037	0.043	0.850	0.000	0.073	0.636	0.583
EEUT	0.035	0.053	0.651	0.000	0.070	0.674	0.503
NDAG	0.034	0.071	0.485	0.000	0.069	0.711	0.583
EUNI	0.034	0.081	0.415	0.000	0.068	0.748	0.186
MFRE	0.030	0.076	0.396	0.038	0.026	0.781	0.212
EKER	0.025	0.043	0.594	0.000	0.051	0.808	0.775
SYOMA	0.023	0.044	0.520	0.000	0.046	0.833	0.602
HSZA	0.023	0.036	0.635	0.000	0.046	0.858	0.626
PPHI	0.020	0.042	0.484	0.022	0.022	0.880	0.366
SDEP	0.019	0.077	0.249	0.000	0.038	0.901	0.456
LJOH	0.019	0.032	0.575	0.018	0.023	0.921	0.133
ERAD	0.018	0.033	0.549	0.000	0.036	0.940	0.178
EFAS	0.017	0.037	0.463	0.000	0.034	0.959	0.330
ELIN	0.014	0.028	0.506	0.000	0.028	0.974	0.956
EPOE	0.006	0.018	0.331	0.000	0.012	0.981	0.651
EPAL	0.006	0.021	0.272	0.000	0.012	0.987	0.701
EAFR	0.004	0.013	0.332	0.000	0.009	0.992	0.822
LCYL	0.004	0.017	0.263	0.000	0.009	0.997	0.999
AURA	0.003	0.017	0.189	0.000	0.006	1.000	0.865
MACU	0.000	0.000	NaN	0.000	0.000	1.000	1.000
OZAM	0.000	0.000	NaN	0.000	0.000	1.000	1.000
PLON	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S10: SIMPER analysis for the comparison in species composition in phragmites and rock mesohabitats based on Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
LCYL	0.093	0.120	0.773	0.003	0.186	0.102	0.001
CFAS	0.084	0.107	0.790	0.009	0.170	0.194	0.704
PACU	0.063	0.110	0.570	0.009	0.127	0.263	0.273
ELIN	0.059	0.089	0.663	0.115	0.010	0.327	0.001
EKER	0.054	0.050	1.094	0.106	0.016	0.387	0.001
EGRE	0.050	0.042	1.203	0.106	0.041	0.441	1.000
EEUT	0.050	0.078	0.638	0.084	0.026	0.496	0.028
NMUL	0.047	0.047	0.996	0.088	0.019	0.547	0.125
TSPA	0.041	0.055	0.750	0.060	0.037	0.592	0.322
SYOMA	0.036	0.043	0.850	0.008	0.072	0.632	0.018
HSZA	0.036	0.056	0.650	0.032	0.052	0.672	0.033
SDEP	0.029	0.065	0.448	0.058	0.000	0.703	0.178
PLON	0.028	0.052	0.529	0.000	0.055	0.733	0.001
PPHI	0.024	0.052	0.472	0.039	0.013	0.760	0.081
EFAS	0.021	0.028	0.752	0.041	0.003	0.783	0.081
EUNI	0.020	0.069	0.294	0.040	0.000	0.805	0.603
PNGA	0.020	0.048	0.418	0.020	0.023	0.827	0.757
AURA	0.018	0.050	0.365	0.000	0.037	0.847	0.051
EPAL	0.017	0.044	0.395	0.033	0.003	0.866	0.039
MACU	0.016	0.041	0.397	0.008	0.026	0.884	0.065
EAFR	0.016	0.032	0.493	0.029	0.004	0.901	0.009
EPOE	0.015	0.040	0.370	0.020	0.011	0.917	0.090
OZAM	0.013	0.031	0.442	0.006	0.022	0.932	0.013
LJOH	0.013	0.019	0.698	0.022	0.008	0.946	0.489
ERAD	0.013	0.027	0.465	0.022	0.005	0.960	0.520
CJUV	0.012	0.039	0.319	0.022	0.004	0.974	0.979
NDAG	0.012	0.038	0.320	0.020	0.005	0.987	0.994
MFRE	0.012	0.038	0.310	0.000	0.024	1.000	0.842

Table S11: SIMPER analysis for the comparison in species composition in phragmites and Vallisneria mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.164	0.118	1.391	0.106	0.422	0.189	0.004
CFAS	0.100	0.113	0.882	0.009	0.199	0.303	0.317
ELIN	0.063	0.092	0.684	0.115	0.023	0.376	0.001
NDAG	0.055	0.118	0.471	0.020	0.097	0.439	0.112
NMUL	0.054	0.060	0.914	0.088	0.038	0.502	0.005
EKER	0.053	0.050	1.067	0.106	0.000	0.563	0.001
EEUT	0.042	0.071	0.593	0.084	0.000	0.611	0.206
PACU	0.042	0.083	0.503	0.009	0.078	0.659	0.803
CJUV	0.035	0.082	0.428	0.022	0.052	0.700	0.520
TSPA	0.033	0.039	0.836	0.060	0.010	0.737	0.673
SDEP	0.029	0.065	0.448	0.058	0.000	0.771	0.184
EFAS	0.021	0.028	0.731	0.041	0.000	0.794	0.102
LCYL	0.020	0.059	0.347	0.003	0.039	0.818	0.995
EUNI	0.020	0.069	0.294	0.040	0.000	0.841	0.620
PPHI	0.020	0.049	0.402	0.039	0.000	0.864	0.353
EPAL	0.016	0.044	0.369	0.033	0.000	0.883	0.074
HSZA	0.016	0.047	0.340	0.032	0.000	0.901	0.941
EAFR	0.014	0.031	0.460	0.029	0.000	0.918	0.042
LJOH	0.013	0.019	0.675	0.022	0.007	0.932	0.533
MFRE	0.012	0.047	0.262	0.000	0.025	0.946	0.841
ERAD	0.011	0.027	0.407	0.022	0.000	0.959	0.694
PNGA	0.010	0.036	0.276	0.020	0.000	0.971	0.971
EPOE	0.010	0.029	0.341	0.020	0.000	0.982	0.449
MACU	0.008	0.026	0.306	0.008	0.008	0.991	0.640
SYOMA	0.005	0.014	0.327	0.008	0.002	0.997	1.000
OZAM	0.003	0.016	0.192	0.006	0.000	1.000	0.877
AURA	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S12: SIMPER analysis for the comparison in species composition in phragmites and wood mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.065	0.085	0.765	0.106	0.094	0.081	1.000
ELIN	0.060	0.085	0.704	0.115	0.028	0.156	0.003
EEUT	0.058	0.068	0.854	0.084	0.070	0.228	0.002
EKER	0.054	0.046	1.168	0.106	0.051	0.295	0.001
TSPA	0.050	0.060	0.835	0.060	0.086	0.358	0.053
EUNI	0.049	0.096	0.512	0.040	0.068	0.419	0.001
NMUL	0.048	0.041	1.172	0.088	0.073	0.479	0.094
PNGA	0.046	0.085	0.537	0.020	0.080	0.536	0.011
SDEP	0.044	0.091	0.489	0.058	0.038	0.592	0.002
NDAG	0.041	0.073	0.557	0.020	0.069	0.643	0.462
HSZA	0.033	0.050	0.665	0.032	0.046	0.684	0.113
EFAS	0.029	0.037	0.791	0.041	0.034	0.720	0.001
PPHI	0.027	0.050	0.545	0.039	0.022	0.755	0.043
SYOMA	0.025	0.043	0.567	0.008	0.046	0.785	0.576
ERAD	0.024	0.035	0.692	0.022	0.036	0.816	0.001
CFAS	0.023	0.061	0.384	0.009	0.041	0.845	1.000
EPAL	0.021	0.046	0.449	0.033	0.012	0.871	0.005
LJOH	0.018	0.023	0.762	0.022	0.023	0.893	0.075
EAFR	0.017	0.031	0.557	0.029	0.009	0.914	0.004
EPOE	0.014	0.031	0.468	0.020	0.012	0.933	0.119
CJUV	0.014	0.040	0.359	0.022	0.008	0.950	0.970
MFRE	0.013	0.051	0.253	0.000	0.026	0.967	0.779
PACU	0.011	0.020	0.545	0.009	0.015	0.980	1.000
LCYL	0.006	0.018	0.317	0.003	0.009	0.987	1.000
MACU	0.004	0.022	0.192	0.008	0.000	0.992	0.890
AURA	0.003	0.017	0.189	0.000	0.006	0.996	0.945
OZAM	0.003	0.016	0.192	0.006	0.000	1.000	0.862
PLON	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S13: SIMPER analysis for the comparison in species composition in rock and Vallisneria mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.193	0.119	1.612	0.041	0.422	0.226	0.001
CFAS	0.118	0.107	1.103	0.170	0.199	0.364	0.025
LCYL	0.098	0.118	0.831	0.186	0.039	0.479	0.001
PACU	0.084	0.115	0.731	0.127	0.078	0.578	0.012
NDAG	0.050	0.118	0.427	0.005	0.097	0.637	0.202
SYOMA	0.036	0.043	0.827	0.072	0.002	0.679	0.020
CJUV	0.028	0.078	0.352	0.004	0.052	0.711	0.766
PLON	0.028	0.052	0.529	0.055	0.000	0.743	0.001
NMUL	0.027	0.066	0.408	0.019	0.038	0.775	0.978
HSZA	0.026	0.046	0.568	0.052	0.000	0.806	0.515
MFRE	0.023	0.056	0.402	0.024	0.025	0.832	0.361
TSPA	0.022	0.060	0.371	0.037	0.010	0.858	0.979
AURA	0.018	0.050	0.365	0.037	0.000	0.880	0.025
MACU	0.016	0.039	0.416	0.026	0.008	0.899	0.054
ELIN	0.016	0.050	0.319	0.010	0.023	0.917	0.984
EEUT	0.013	0.052	0.250	0.026	0.000	0.933	0.997
PNGA	0.011	0.037	0.312	0.023	0.000	0.946	0.971
OZAM	0.011	0.028	0.394	0.022	0.000	0.959	0.064
EKER	0.008	0.031	0.259	0.016	0.000	0.968	1.000
LJOH	0.007	0.017	0.415	0.008	0.007	0.977	0.983
PPHI	0.007	0.027	0.245	0.013	0.000	0.984	0.983
EPOE	0.006	0.031	0.180	0.011	0.000	0.991	0.830
ERAD	0.002	0.010	0.245	0.005	0.000	0.994	1.000
EAFR	0.002	0.012	0.180	0.004	0.000	0.996	0.986
EFAS	0.002	0.006	0.258	0.003	0.000	0.998	1.000
EPAL	0.002	0.009	0.180	0.003	0.000	1.000	0.988
EUNI	0.000	0.000	NaN	0.000	0.000	1.000	1.000
SDEP	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S14: SIMPER analysis for the comparison in species composition in rock and wood mesohabitats based on Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
LCYL	0.093	0.119	0.780	0.186	0.009	0.104	0.001
CFAS	0.089	0.108	0.818	0.170	0.041	0.204	0.600
PACU	0.063	0.109	0.579	0.127	0.015	0.275	0.248
TSPA	0.053	0.075	0.704	0.037	0.086	0.334	0.024
EGRE	0.053	0.092	0.572	0.041	0.094	0.393	1.000
PNGA	0.047	0.085	0.551	0.023	0.080	0.445	0.003
SYOMA	0.044	0.046	0.941	0.072	0.046	0.494	0.001
EEUT	0.043	0.065	0.661	0.026	0.070	0.542	0.182
NMUL	0.040	0.046	0.875	0.019	0.073	0.588	0.470
HSZA	0.038	0.045	0.839	0.052	0.046	0.630	0.022
NDAG	0.036	0.070	0.509	0.005	0.069	0.670	0.625
EUNI	0.034	0.081	0.415	0.000	0.068	0.708	0.103
EKER	0.030	0.046	0.650	0.016	0.051	0.742	0.623
PLON	0.028	0.052	0.529	0.055	0.000	0.773	0.001
MFRE	0.023	0.060	0.392	0.024	0.026	0.799	0.283
AURA	0.021	0.051	0.407	0.037	0.006	0.822	0.012
ERAD	0.019	0.032	0.597	0.005	0.036	0.844	0.035
SDEP	0.019	0.077	0.249	0.000	0.038	0.865	0.510
EFAS	0.018	0.037	0.490	0.003	0.034	0.885	0.273
ELIN	0.018	0.033	0.542	0.010	0.028	0.905	0.970
PPHI	0.016	0.036	0.456	0.013	0.022	0.923	0.587
LJOH	0.014	0.024	0.601	0.008	0.023	0.939	0.359
MACU	0.013	0.037	0.345	0.026	0.000	0.954	0.228
OZAM	0.011	0.028	0.394	0.022	0.000	0.966	0.054
EPOE	0.011	0.034	0.326	0.011	0.012	0.979	0.311
EPAL	0.007	0.022	0.320	0.003	0.012	0.987	0.720
EAFR	0.006	0.017	0.372	0.004	0.009	0.994	0.768
CJUV	0.005	0.017	0.321	0.004	0.008	1.000	0.998

Table S15: SIMPER analysis for the comparison in species composition in Vallisneria and wood mesohabitats based on the Bray-Curtis dissimilarity index.

Species code	average	sd	ratio	ava	avb	cumsum	p
EGRE	0.188	0.121	1.564	0.422	0.094	0.213	0.001
CFAS	0.104	0.112	0.932	0.199	0.041	0.331	0.195
NDAG	0.072	0.119	0.606	0.097	0.069	0.413	0.002
NMUL	0.049	0.060	0.805	0.038	0.073	0.468	0.068
TSPA	0.045	0.068	0.668	0.010	0.086	0.519	0.146
PACU	0.044	0.082	0.530	0.078	0.015	0.568	0.779
PNGA	0.040	0.085	0.470	0.000	0.080	0.613	0.051
EEUT	0.035	0.053	0.652	0.000	0.070	0.652	0.529
EUNI	0.034	0.081	0.415	0.000	0.068	0.691	0.136
CJUV	0.029	0.078	0.377	0.052	0.008	0.724	0.714
EKER	0.025	0.043	0.594	0.000	0.051	0.752	0.883
MFRE	0.024	0.065	0.366	0.025	0.026	0.779	0.291
ELIN	0.024	0.049	0.482	0.023	0.028	0.806	0.861
SYOMA	0.023	0.044	0.535	0.002	0.046	0.832	0.640
LCYL	0.023	0.059	0.388	0.039	0.009	0.858	0.993
HSZA	0.023	0.036	0.635	0.000	0.046	0.884	0.708
SDEP	0.019	0.077	0.249	0.000	0.038	0.906	0.499
ERAD	0.018	0.033	0.549	0.000	0.036	0.926	0.072
EFAS	0.017	0.037	0.463	0.000	0.034	0.946	0.329
LJOH	0.014	0.024	0.580	0.007	0.023	0.961	0.447
PPHI	0.011	0.028	0.386	0.000	0.022	0.973	0.879
EPOE	0.006	0.018	0.332	0.000	0.012	0.980	0.777
EPAL	0.006	0.021	0.272	0.000	0.012	0.987	0.788
EAFR	0.004	0.013	0.333	0.000	0.009	0.992	0.916
MACU	0.004	0.017	0.247	0.008	0.000	0.996	0.880
AURA	0.003	0.017	0.189	0.000	0.006	1.000	0.923
OZAM	0.000	0.000	NaN	0.000	0.000	1.000	1.000
PLON	0.000	0.000	NaN	0.000	0.000	1.000	1.000

Table S16: Pearson correlation coefficient results for the 14 habitat variables recorded at the microhabitat site. Values in bold are greater than the 0.7 cut-off assigned.

	Bare	Phragmites	Rock	Vallisneria	Wood	Site Area	Current velocity	Depth	Sub_ sand	Sub_ rock	Sub_leaf litter	Sub_gravel	Sub_ wood	Algae density
Bare	1.00	-0.16	-0.17	-0.17	-0.16	0.13	0.01	0.21	-0.35	-0.19	-0.15	**0.72**	-0.14	0.40
Phragmites	-0.16	1.00	-0.30	-0.29	-0.28	-0.17	-0.36	-0.17	0.18	-0.25	0.33	-0.04	-0.14	-0.05
Rock	-0.17	-0.30	1.00	-0.31	-0.31	0.34	0.05	0.07	-0.48	**0.79**	-0.07	-0.03	-0.26	-0.42
Vallisneria	-0.17	-0.29	-0.31	1.00	-0.29	-0.06	0.56	-0.27	0.62	-0.34	-0.28	-0.14	-0.26	-0.04
Wood	-0.16	-0.28	-0.31	-0.29	1.00	-0.21	-0.27	0.24	-0.07	-0.10	0.13	-0.27	**0.76**	0.27
Site Area	0.13	-0.17	0.34	-0.06	-0.21	1.00	0.09	0.14	-0.17	0.23	-0.11	0.07	-0.08	-0.21
Current velocity	0.01	-0.36	0.05	0.56	-0.27	0.09	1.00	-0.07	0.27	-0.10	-0.42	0.08	-0.21	0.06
Depth	0.21	-0.17	0.07	-0.27	0.24	0.14	-0.07	1.00	-0.18	0.10	-0.08	0.07	0.15	0.52
Sub_ sand	-0.35	0.18	-0.48	0.62	-0.07	-0.17	0.27	-0.18	1.00	-0.55	-0.13	-0.53	-0.08	0.03
Sub_ rock	-0.19	-0.25	**0.79**	-0.34	-0.10	0.23	-0.10	0.10	-0.55	1.00	-0.09	-0.17	-0.18	-0.33
Sub_leaf litter	-0.15	0.33	-0.07	-0.28	0.13	-0.11	-0.42	-0.08	-0.13	-0.09	1.00	-0.23	0.04	-0.09
Sub_gravel	**0.72**	-0.04	-0.03	-0.14	-0.27	0.07	0.08	0.07	-0.53	-0.17	-0.23	1.00	-0.26	0.18
Sub_ wood	-0.14	-0.14	-0.26	-0.26	**0.76**	-0.08	-0.21	0.15	-0.08	-0.18	0.04	-0.26	1.00	0.26
Algae density	0.40	-0.05	-0.42	-0.04	0.27	-0.21	0.06	0.52	0.03	-0.33	-0.09	0.18	0.26	1.00

Table S17: Forward selection stepwise model of environmental variable for the CCA performed on log-transformed abundance data 28 fish species using 999 permutations.

Start: LgAbn10 ~ 1

	Df	AIC	F	Pr(>F)
+Habitat_	4	301.20	5.9482	**0.005**
+Current	1	304.58	13.7645	**0.005**
+ Sub_Leaf litter	1	312.97	4.9007	**0.005**
+Depth	1	314.15	3.7035	**0.005**
+ Sub_Sand	1	314.98	2.8616	**0.005**
+Algae	1	315.47	2.3737	**0.005**

Step: LgAbn10 ~ Habitat

	Df	AIC	F	Pr(>F)
+Current	1	292.73	10.4010	**0.005**
+Depth	1	299.75	3.3311	**0.005**
+Sub_Leaf litter	1	300.05	3.0436	**0.005**
+Algae	1	300.94	2.1780	**0.005**
+Sub_Sand	1	301.74	1.4011	0.115

Step: LgAbn10 ~ Habitat + Current

	Df	AIC	F	Pr(>F)
+Depth	1	290.95	3.6300	**0.005**
+Algae	1	292.74	1.8937	**0.005**
+Sub_Leaf litter	1	292.48	2.1446	**0.010**
+Sub_Sand	1	293.36	1.2984	0.160

Step: LgAbn10 ~ Habitat + Current + Depth

	Df	AIC	F	Pr(>F)
+Algae	1	290.87	1.9659	**0.005**
+Sub_Leaf litter	1	290.88	1.9572	**0.025**

+Sub_Sand	1	291.73	1.1486	0.280

Step: LgAbn10 ~ Habitat + Current + Depth + Algae				
	Df	AIC	F	Pr(>F)
+Sub_Leaf litter	1	290.83	1.9192	**0.030**
+Sub_Sand	1	291.60	1.1897	0.215

Step: LgAbn10 ~ Habitat + Current + Depth + Algae + Sub_Leaf litter				
	Df	AIC	F	Pr(>F)
+ Sub_Sand	1	291.59	1.1501	0.315