

# Diet overlap and feeding preference of *Oreochromis niloticus* (Linnaeus, 1758) versus two native cichlids of the upper Kabompo River, northwest of Zambia.

Arthertone Jere<sup>1</sup>

<sup>1</sup>Lilongwe University of Agriculture and Natural Resources Faculty of Natural Resources

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## Abstract

Evaluating the food and feeding habits of fish is fundamental in fisheries and conservation biology research. In this study, the diet of exotic *Oreochromis niloticus* was compared with the 2 most abundant and aquaculture preferred native cichlids of native species (*Oreochromis macrochir* and *Coptodon rendalli*) in the upper Kabompo River, Zambia. We hypothesized that exotic and native cichlids would show no dietary niche overlap. We analyzed the stomach contents of 114 specimens of the fishes sampled. Fishes were grouped into 3 major feeding groups: microphages, macrophages and carnivores, and omnivores. They were also grouped into size classes of <50, 51-100, 101-150, and 151-302 mm total length (TL). *O. niloticus* had a larger dietary niche than two native species (71% and 22%, respectively). The dietary niche overlap between *O. niloticus* and native *C. rendalli* species in size classes <50 was significant ( $F(2, 45) = 0.084, p < 0.05$ ). Dietary niche overlap between the native *O. macrochir* species in size class <50 mm was low ( $F(2, 33) = 2.13, p > 0.05$ ), while as in size classes 51-100 mm and 101-150 mm was high ( $F(2, 35) = 0.27, p < 0.05$ ) for *C. rendalli*. There was no clear evidence of ontogenetic diet shift of native cichlids, with the exception of *O. macrochir*, which showed ontogenetic diet shifts within the 51-100 mm size class. The dietary overlap results indicate interspecific competition between exotic *O. niloticus* and native *O. macrochir*, which may have major impacts on food web structure in the upper Kabompo River and may explain population decreases of some native species.

## 1. INTRODUCTION

Exotic species have become a major threat to many native species and whole ecosystems over the world (Agostinho et al., 2015; Jere et al., 2021; Zengaya et al., 2020). Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is the most widely distributed exotic fish species in Sub Saharan Africa. In Zambia, it was introduced in the late 1980's by Department of Fisheries for research and development in aquaculture (Bbole et al., 2014; DoF, 2018; FAO, 2012). However, the introduction of *O. niloticus* poses a major threat to native fishes as it is known to cause trophic cascades with potential impacts on the entire fish community, particularly in highly diverse regions such as the Northwestern Province of Zambia (AES, 2014; Bok & Bills, 2012; Jere et al., 2021).

Partitioning of resources between coexisting species has been suggested as one of the processes responsible for structuring populations and, consequently, communities (Figueredo & Giani, 2005; Kiran kaya & Ekmekçi, 2013). Studies conducted by Gozlan et al. (2010) showed that, in contrast to terrestrial organisms which partition resources mainly through habitat segregation, for assemblages of fishes and other aquatic animals trophic separation is more important. Partitioning of food resources is the main factor in the development of fish communities in nearly all aquatic habitats (Bwanika et al., 2004; Canonico et al., 2005; Eloranta et al., 2015).

The degree of trophic adaptability of certain fish species may limit feeding preferences when confronted with environmental changes. Changes in resource availability may influence changes in the assemblage of fish

species in a community (Miller & Crowl, 2006; Kirankaya & Ekmekçi, 2013). For instance, direct competition for food resources between exotic and native species may result in diet shifts and affect native species' fitness (Eloranta et al, 2015). In certain cases, native species can also be affected indirectly by exotic species. For example, cichlids may influence a trophic cascade by either decreasing or increasing the availability of nutrients such as phosphorus and nitrogen, which may promote plankton blooms and lead to fluctuation in the dissolved oxygen content of water (Ke et al., 2008; Kirankaya & Ekmekçi, 2013). Furthermore, Nile tilapia in some cases may increase turbidity through sediment resuspension (Zengeya et al., 2015). These suspended solids in water have the capacity to reduce macrophyte survival, which may result in a shortening of the trophic pathways of native species (Scheffer et al., 2006; Agostinho et al., 2015). Moreover, studies by other investigators have appropriate and practical approaches to assessing possible impacts of exotic species on native fishes (Figueredo & Giani, 2005; Zengeya et al., 2015).

The use of stomach content analysis (SCA) to infer feeding strategies and habits of native and exotic fish species within a food web is an effective tool in the conservation of native populations (Pilger et al., 2010). For example, stomach content analysis of *Serrasalmus marginatus* and *S. maculatus* in the upper Parana River in Mexico revealed high trophic niche overlap between the species, which both consume fish fragments, detritus and plankton (Agostinho et al., 2015; Philippsen et al., 2015). SCA is useful for understanding the functional role of organisms in a food chain and is an important tool for elucidating trophic differences between phylogenetically related fishes (Keet et al., 2008). The results of SCA can be used to define trophic niches (Agostinho et al., 2015), and have become an important predictor of the impacts of invasive alien species (Pilger et al., 2010; Agostinho et al., 2015).

This study evaluated the dietary preferences of exotic *O. niloticus* and 2 most abundant and aquaculture preferred native fish species (*Oreochromis macrochir* and *Coptodon rendalli*) in the upper Kabompo River, Zambia. A Known population of exotic *O. niloticus* is established in the study area, and decreases in populations of native species (*O. macrochir* and *C. rendalli*) have been reported (AES 2014; DoF 2018; Jere et al., 2021). Understanding the dietary preferences of these species may help explain these decreases and clarify how exotic species impact native species. *O. niloticus* and native species have generally similar feeding behavior (Kenzo & Mazingaliwa, 2002; Zengeya et al., 2015), although *O. niloticus* are assumed to show somewhat more generalist foraging behaviour, feeding on a greater diversity of food items than native species (Marshall, 2011; Zengeya et al., 2020). Thus, we hypothesized that *O. niloticus* and native species in upper Kabompo River would show no dietary niche overlap with the two major native species. We used SCA to test our hypothesis, the results of which should provide new insight regarding coexistence of species in the environment and help to develop strategic management plans for the conservation and management of native species in the upper Kabompo River.

## 2. MATERIAL AND METHODS

### 2.1 Description of study site

The study was undertaken in the upper Kabompo River, located on the border of Kalumbila and Mwinilunga districts in Zambia. Kalumbila District includes major mining towns in the Northwestern Province. The study area lies approximately 60 km from the source of the Kabompo River (12.1845°S, 25.1765°E to 12.3691°S, 25.0442°E). The water surface area is approximately 1473 km<sup>2</sup>, with numerous fish landing sites. The study site (Figure 1) was chosen because of its frequent fishing activity and high fish diversity. The fishery (covering all the native species caught in this study) is also of economic importance to local communities as a livelihood and a source of brood fish for the Aquaculture Breeding Programme.

### 2.2 Data collection and analysis

The study area covered approximately 15 km of the river with a total of 3 sampling points 7.2 km apart. At each sampling point, a 200 m stretch of river was sampled, encompassing all 5 available microhabitat types (runs, riffles, vegetative thickets, open pools (near fisheries landing area) and the tributaries) of the river. Surveys were conducted for a period of 1 month in the hot, dry season (December 2019) and 1 month in the hot, wet season (January-February 2020). The sample periods were chosen because temperatures

are conducive to abundant food resources at these times (AES 2014). Fish were collected using fishery independent methods with gill nets 3 m deep and 30 m long, mesh size ranging from 1 to 3.5 inch; Fyke nets 3 m deep and 30 m long; an electrofisher; and a beach seine net 3 m deep and 25 m long. The specimens were identified immediately after capture according to Kenzo & Mazingaliwa (2002). The specimens were then measured (total length [TL]  $\pm$  1.0 mm) and weighed (wet mass  $\pm$  0.1 g).

A total of 3 species were selected for SCA, based on the most abundant fish species caught in the river (capture frequency >10%) according to Eloranta et al. (2015). The species selected were the exotic *O. niloticus* (n = 201) and two natives; *O. macrochir* (n = 110) and *C. rendalli* (N=56). The fishes caught from five aforementioned distinct habitats at different times of the day (6 a.m., 12 afternoon and 5 p.m. to comprehensively understand effective feeding period of the day) (Table 1). Indices used for diet interpretation included; vacuity index (VI) is the quantity of unfilled as number of empty stomachs and the gut fullness (GF) is average number of relatively full stomachs investigated on scale of 0 for empty to 4 for fully distended with food and lastly the diet diversity was evaluated according to Hyslop (1980). The frequency of occurrence method was used to determine the percentage of stomachs containing a particular food item relative to the total number of stomachs containing food (Hyslop 1980). The fish were first grouped into 3 major feeding groups: microphages, macrophages and carnivores, and omnivores, and then later grouped into lower taxonomic or functional categories for quantitative comparisons. Diet categories were chlorophytes, cyanophytes, diatoms, microfauna (zooplankton, insects and protozoa), fish, macrophytes, detritus, and unidentified items. The area occupied by each food item in the stomach of a specimen was transformed into a percentage of each food category. Numerical analysis was not used to categorize broader food items because (1) lumping resource states often inflates niche overlap values, and (2) broader categories generally represent one or more renewable resources (Winemiller 1989).

Dietary overlap between *O. niloticus* and the native species was calculated using the symmetric niche overlap coefficient of Pianka (1973), in which values are constrained between near 0 (specialized diets with almost no overlap) and 1 (similar use of food resources or complete overlap). Overlap was categorized as low (0.0-0.29), moderate (0.30-0.59), or high (0.6-1.00), with high overlap indicating biological significance (Langton 1982). The dietary niche width was estimated using Levins' (1969) standardized index of niche breadth, in which values near 0 indicate a specialized diet, and values near 1 signify generalist diets.

To understand dietary preference, analysis of the diets of *O. niloticus* and native fish species in the upper Kabompo River was conducted to understand pattern of dietary overlap. To achieve this, results of the indices (vacuity, stomach fullness and Levin's standardized niche breath) were collated via spreadsheets using Microsoft Excel 2007 (summation, percentage and mean functions). Further, principal component analysis (PCA) was performed to identify the patterns in dietary similarity between *O. niloticus* and the two native fish species. Scatter plots from the first factors (component with absolute values equals to or greater than 0.6) were used to visualize the variation in diets among species. Principal component analysis uses matrix algebra to model a correlation matrix as a set of orthogonal (perpendicular) axes. The PCA axis (dietary gradient) corresponds to an eigenvector. Thus, eigenvalues describes the variance accounted for by the corresponding axis. The first principal components indicated the largest percentage of total variation that can be modeled by the algorithm (Sagar et al., 2019). Thereafter, an analysis of variance (ANOVA) was then conducted on mean values from the dietary indices to detect significant difference at 0.05 significance level (Sokal & Rohlf, 1995). These statistical analyses were performed using R software version 3.6.0 (R Core Team, 2019).

### 3. RESULTS

Analysis of 114 stomachs of exotic and native fish species ranging in TL from 21 to 302 mm showed that they employed similar feeding habits. The largest species, *O. niloticus* and *O. macrochir*, were found in all 4 class sizes. Smaller catches of species *C. rendalli* and *O. macrochir* were found in size classes <50, 51-100, and 101-150 mm. *O. niloticus* and larger native species (*O. macrochir*) did not significantly differ ( $F = (2, 44) 0.48, p > 0.05$ ) in size class. *O. niloticus* and smaller native species (*C. rendalli*) were significantly

different in size class <51 mm ( $F(2, 51) = 0.27, p < 0.05$ ) (Table 1).

Therefore, the two native species showed a significantly higher degree of individual dietary specialization than *O. niloticus* ( $F(2, 35) = 0.084, p < 0.05$ ) (Figure 3). The mean number of food items observed did not differ significantly among stomachs of native species, but exotic *O. niloticus* showed a larger volume and number of *C. rendalli* presented significant peaks ( $F = 5.31$ , food items than native species in size class <50 mm  $p < 0.05$ , at 5 pm) of higher feeding intensity at 12:00 h ( $F = 0.63, p > 0.05$ ). For juveniles of both exotic *O. niloticus* between the smaller and the larger species, fewer *O. niloticus* stomachs were empty and fewer insect food and native species (*O. macrochir* and *C. rendalli* grouped according to larger food items class sizes), feeding patterns were discontinuous and cephalus than of exotic *O. niloticus* (Figure. 2). significantly different ( $F(2,35) = 2.71, p < 0.05$  and  $F = 11.62$ , Dietary overlap among the native species was  $p < 0.05$ , respectively), with a distinct peak at 12:00 h varied and significantly low ( $F(2,27) = 2.13, p > 0.05$ ) in size when the stomachs were fullest (Tables 1).

Analysis of dietary preferences of exotic and native species showed that mean SF was relatively high in *O. niloticus*, *O. macrochir* and *C. rendalli* (between  $3.0 \pm 0.9$  and  $4.0 \pm 0.1$ ), while VI was low in the largest size class (151–302 mm) and high in size classes <150 mm (Table 2). The results showed that adult exotic *O. niloticus* fed continually ( $F(2,18) = 0.34, p > 0.05$ ), while adults of native *O. macrochir* and *C. rendalli*, and smaller species (in size class <51 mm) of *C. rendalli*, fed on algae, diatoms and detritus (Figure. 2). The diet for fish in the <50 mm size class consisted mainly of algae, while diet shifted in the 51-100 mm size class, with fish and microfauna becoming the most important food items (Figure 2). In general, *O. niloticus* had a more diverse diet than native fishes resulting from foraging on algae, chlorophytes, diatoms, microfauna, and detritus in all size classes, while native species fed selectively on different food items in different size classes, indicating a slight ontogenetic diet shift.

Dietary overlap between exotic *O. niloticus* and natives was significantly high ( $F(2, 25) = 0.08; p < 0.05$ ) for size class <50 mm (Table 3). *Oreochromis niloticus* in the <50 mm size class consumed mainly diatoms and algae, while individuals in the 101-150 mm and 151- 302 mm size classes consumed mostly zooplankton, chlorophytes, and algae, dominated by Micro cyst is, Gonium, and Phacus. There were some significantly low dietary overlaps among smaller native species at <50 and 101–150 mm size classes, except for *O. macrochir*, among which significantly high diet overlap was observed (niche breath coefficients 0.625, 0.691, and 0.782, respectively) (Table 3). *Coptodon rendalli* is predominantly herbivorous, but its diet consisted of zooplankton and insects in the 151-302 mm size class, and there was a low dietary overlap with *O. niloticus* for fish 151–302 mm in length (niche breath coefficient 0.211).

Similarly, results for the first principal component axis indicated a high positive correlation with food items such as microfauna, others and fish, and a high negative correlation with cyanophytes, chlorophytes and macrophytes (Table 4). This axis presents 53.2% of the variation explained from omnivorous species (*O. niloticus* and *O. macrochir*). The second principal component axis showed a strong positive correlation with diatoms, microfauna and zooplanktons, and a strong negative correlation with others and fish (Figure 4). This axis presents 18.3% of the variation explained from omnivorous fish species of *O. niloticus* and *O. macrochir*. *Oreochromis niloticus* and native *O. macrochir* grouped closely in dietary space as defined by PCA axes 1 and 2, and did not significantly differ ( $F(2,33) = 0.36, p > 0.05$ ) in their diet using ANOVA test, indicating dietary overlap (Figure 4. and Table 4).

A weak association was observed between *O. niloticus* and native *C. rendalli* fish species in the diets (Table 5). The first principal component axis has strong positive correlations with food items such as diatom, cyanophytes, chlorophytes and macrophytes. This axis presents 50.7% of the variation explained herbivorous *C. rendalli* and omnivorous *O. niloticus* (Figure 5 and Table 5). The second principal component axis showed a strong negative correlation with microfauna, other and zooplanktons. This axis presents 15.8% of the variation explained *O. niloticus* and native *C. rendalli*. *Oreochromis niloticus* and native *C. rendalli* grouped closely in dietary space as defined by PCA axes 1 and 2, was significantly different ( $F(2,45) = 2.28, p < 0.05$ ) in their diet, indicating no dietary overlap.

#### 4. DISCUSSION

Although the food resources of *O. niloticus* and native species were quite specific and similar (algae, diatoms, zooplankton, and detritus), algae and diatoms were the most important items in the diet of native species; individuals in the size class <50 mm fed mainly on these resources. The principal difference between the diets of exotic Nile tilapia and the native species was the size above which a particular item came to be more important, since natives utilize algae as food over a longer period of time. Our results also indicated that *O. niloticus* were more generalist with respect to diet composition and the abundance of food items, and relied more heavily on zooplankton and chlorophytes in the >151 mm size class than native species. This more generalist foraging on microphages, macrophages, microfauna, and detritus probably explains the high abundance of *O. niloticus* relative to native species in the river.

Contrary to our main hypothesis, the stomach content analysis data provided no evidence of niche segregation between native species and exotic *O. niloticus* in the upper Kabompo River. *O. niloticus* evidently used more diverse food resource than native species. When dominating fish communities, *O. niloticus* have been observed to have a wide trophic niche but generally prefer zooplankton and detritus (Werner & Gilliam, 1984; Winemiller, 1989; Mason et al., 2008; Kirankaya & Ekmekçi, 2013; Zengeya et al., 2015). However, competitive interactions and dietary overlap with natives such as *O. macrochir* may force *O. niloticus* to occupy a wider trophic niche (Kenzo & Mazingaliwa, 2002; Marshall, 2011; Zengeya et al., 2015). Hence, the observed narrow niche use of native species may partly result from increased competition for food resources following the invasion of *O. niloticus*. In Lake Chivero, exotic *O. niloticus* and natives presented a low dietary overlap and wide niche areas, while omnivores had a high trophic niche overlap where food sources were limited (Junor, 1969; Marshall, 2011). However, *O. niloticus* feeds on larger quantities of food than native species in Lake Victoria (Trewavas, 1983; Marshall, 2011; Zengeya et al., 2015). Inclusion of more detritus and the algae *Microcystis*, *Gonium*, and *Phacus* in the diet of *O. niloticus* may also indicate differences in foraging tactics relative to native species.

Our results from SCA suggested that the wide dietary niche of *O. niloticus* is largely due to marked size class differences in niche use. Some size classes of *O. niloticus* had exceptionally wide or narrow trophic niches, indicating low or high levels of interspecific competition in diets, respectively, and high individual variation in feeding habitats (Werner & Gilliam, 1984; Zengeya et al., 2015). The small number but high quantity of food items consumed by *O. niloticus* in the 151-302 mm size class is probably due to specialized foraging on abundant food sources in certain habitats, whereas the relative importance of food items consumed by most native species and also some *O. niloticus* in the <101 mm size classes probably indicates a diet dominated by algae chlorophytes and diatoms. The selection of these food items at size class 151–302 mm of the species is likely associated with their high abundance in the upper Kabompo River, as reported for a nearby section of the river outside the sampled area (Bok & Bills, 2012; AES, 2014).

Previous studies suggest that dietary niche overlap between species can be interpreted as evidence of multiple shared food sources (Helfman et al., 1997; Pilger et al., 2010) and therefore as an indicator of potential competition (Eloranta et al., 2015). The exotic species *O. niloticus* and the native species *T. sparrmannii* exhibited high trophic niche overlap. However, their wider trophic niche area suggests that the *O. niloticus* are opportunistic and can change to overcome possible competition in trophic position or diet composition, and may explain the coexistence of these 2 species (Lowe-McConnell, 1987; Winemiller, 1991, Winemiller & Kelso-Winemiller, 2003; Agostinho et al., 2015). In contrast, all native species in our study had narrower dietary niches. For example, although cichlids might include many species, individual species demonstrate a narrow dietary niche area, suggesting that these species are specialists.

*Orochromis macrochir* and *C. rendalli* less abundant of smaller size class caught during the study. The species are of similar size classes, feeding mainly on filamentous algae, benthic invertebrates, and diatoms (Kenzo & Mazingaliwa 2002). Thus, the dietary niche of these species may overlap with that of *O. niloticus* at the base of the trophic web. Nowadays these native species are 3 of the less abundant species in the upper Kabompo River (DoF 2018). In contrast, the *O. niloticus* population has greatly increased in the last decade, and abundant Nile tilapia was recorded during this study. *C. rendalli* is a native pelagic herbivore which

feeds mainly on fish, invertebrates (in size classes >51 mm), and algae (in size class <50 mm), suggested a potential dietary niche overlap with *O. niloticus* in the smallest size class (Kenzo & Mazingaliwa 2002, Marshall 2011, Zengeya et al., 2015).

Niche differentiation can explain how species co-exist in an ecosystem, but empirical support has been sparse (Mason et al., 2008; Zengeya et al., 2015). However, niche specialization has been regarded as a common phenomenon in fish community assemblages (Pilger et al., 2010; Eloranta et al., 2015). In the upper Kabompo River, there seems to be dietary niche specialization among native species, supported by their relatively low trophic niche overlap. The only substantial overlaps among native species were observed between *O. macrochir* and *C. rendalli*.

*O. macrochir* and *C. rendalli* in the 51-100 mm size class, which are ecologically similar (Minshull, 1969; Junor, 1969; Kenzo & Mazingaliwa, 2002; Zengeya et al., 2015). In contrast, the high dietary niche overlap between the native species in all size classes and *O. niloticus* suggests potential competition for food resources (Brendonck et al., 2003; Marshall, 2011; Zengeya et al., 2015). The presence of *O. niloticus* can also affect populations of native species indirectly. In many studies, invasion by *O. niloticus* has been related to a decrease in numbers of aquatic plants and phytoplankton biomass, and a reduction in macroinvertebrate and macrophyte populations (Moriarty & Moriarty, 1973; Marshall, 2011). For example, in the Olifants River in the Western Cape Province of South Africa, Nile tilapia became the dominant species within a few years of introduction and eliminated macrophytes within a few years of establishment, coinciding with significant declines in previously abundant native species within the community. As a result, natives are now confined to smaller tributaries and headwaters (Zengeya et al., 2015). Furthermore, the presence of *O. niloticus* can lead to trophic cascades (Marshall, 2005; AES, 2014; Zengeya et al., 2020).

The narrow dietary niche of native species suggests that a small change in food resource abundance could generate a big shift in native species population sizes. This narrow dietary niche could contribute to population decreases of native species, particularly, *O. macrochir* and *C. rendalli*, which showed a relatively high degree of dietary overlap with *O. niloticus*, in contrast to our hypothesis. This may be because the system has been changing rapidly over the last few years due to mining activities in the surrounding area, as predicted by a 2010 biological monitoring study (Bok & Bills, 2012; DoF, 2018). Mining activities may affect fish habitat condition and affect populations of native fishes. Another factor is dietary niche overlap among natives, suggesting shared resource use and potential competition. However, as indicated by wide dietary niches, both *O. niloticus* and native species are able to switch food sources depending on the abundance of these sources, while native species that feed only on a small range of food sources are more vulnerable to changes in resource abundance.

There is a need for detailed studies on the biology of all native fish species in the upper Kabompo River and also data from the dry cold season, when food resources are limited in the river. This will help to increase our understanding of the impacts of *O. niloticus* on native fish communities.

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## 6. AUTHORS' CONTRIBUTIONS AND CONFLICT OF INTEREST

Arthertone Jere-Lead in data collection, data analysis, writing and manuscript editing, Dr Wilson W. L. Jere - Lead and supervisor in research design, data analysis and editing; Dr Austin Mtethiwa-Lead and supervisor in writing and editing; Professor Daud Kassam-Lead and supervisor in writing and manuscript editing.

## 7. DATA ACCESSIBILITY

The data that has been used in this study is available and the Dryad data repository will be used to archive

the data. The authors cited in this document have acknowledged that data should be stored in the Dryad data repository at <https://doi.org/10.5061/dryad.sj3tx9661>.

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**Table 1**. Abundance of the fishes caught and time of capture in upper Kabompo River, December 2019-February 2020 survey.

Species	Common names	Status	Individuals caught	Time of Capture
<i>Oreochromis niloticus</i>	Nile tilapia	Exotic	14	6:00 AM
			161	12:00 AM
			40	5:00 PM
<i>Oreochromis macrochir</i>	Greenhead tilapia	Native	5	6:00 AM
			10	12:00 AM
			95	5:00 PM
<i>Coptodon rendalli</i>	Redbreast tilapia	Native	9	6:00 AM
			44	12:00 AM
			3	5:00 PM

**Table 2**. Mean stomach fullness and % Vacuity index of stomachs of the fish collected by total length class in upper Kabompo River, December 2019- February 2020. N = total number of stomachs examined, SF = mean stomach fullness ( $\pm$  = Standard Deviation) and VI=vacuity index.

Species	Size class (mm.TL)	N	SF	VI (%)
<i>Oreochromis niloticus</i>	151-302	2	3.8 $\pm$ 0.4	13
	101-150	5	3.5 $\pm$ 0.5	7.4
	51-100 <50	9 4	3.0 $\pm$ 0.9 1.9 $\pm$ 1.4	31 51.4

Species	Size class (mm.TL)	N	SF	VI (%)
<i>Oreochromis macrochir</i>	151-302 101-150	4 2 9 5	$3.7 \pm 0.5$ $2.6 \pm 1.2$	41.2 20.8 16 51.4
<i>Coptodon rendalli</i>	51-100 <50		$1.5 \pm 1.0$ $2.9 \pm 1.1$	
	101-150	6	$3.5 \pm 0.6$	16.7
	51-100	4	$3.6 \pm 0.5$	21.4
	<50	10	$2.5 \pm 1.2$	21.5

**Table 3.** Mean values of the dietary overlap of exotic and native species in size classes (<50 mm TL: upper left panels and 51-100 mm and 101-150mm TL: lower right panels) in upper Kabompo River, December 2019- February 2020. The values are Pianka's (1973) symmetrical measure of niche. Breadth coefficients with significant values (>0.60) in bold font. Dash (-) = not comparable.

Status	Species	<i>C. rendalli</i>	<i>O. macrochir</i>	<i>O. niloticus</i>
Exotic	<i>O. niloticus</i>	<b>0.625</b>	<b>0.691</b>	-
Native	<i>O. macrochir</i>	0.551	-	<b>0.782</b>
Native	<i>C. rendalli</i>	-	0.211	0.465

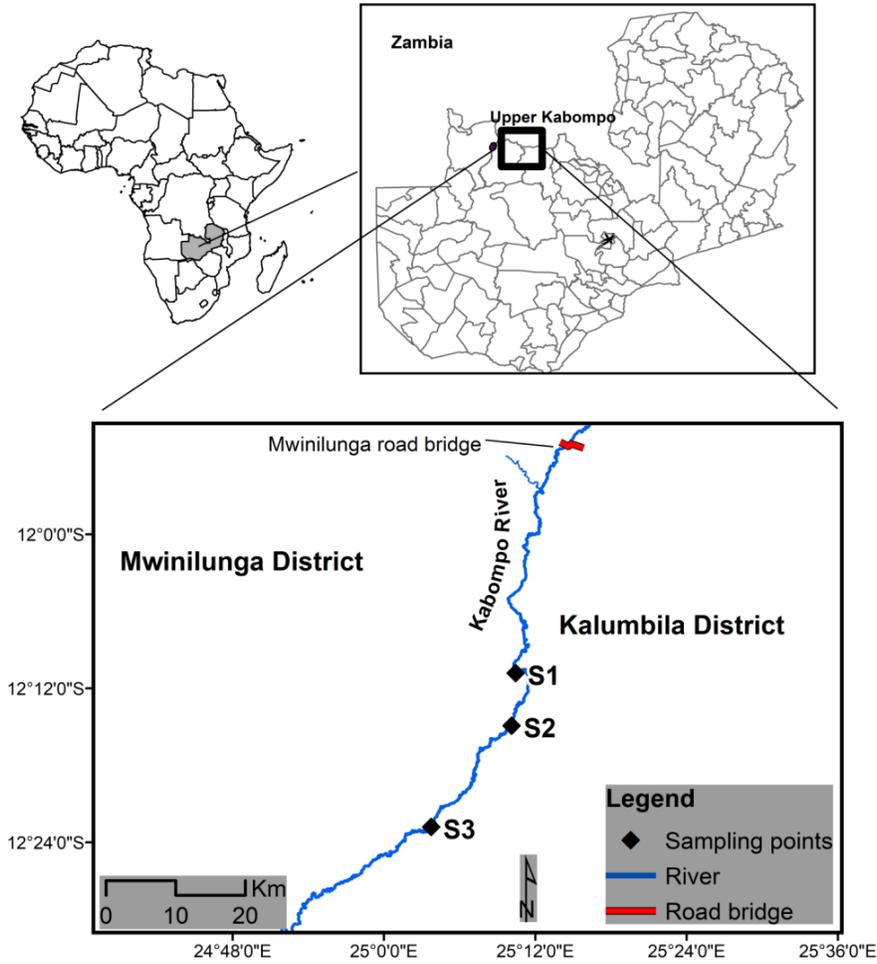
**Tables 4.** Loadings from principal components analysis of *O. niloticus* and *O. macrochir* fish species based on dietary characters in the upper Kabompo River.

Food Item	PCA axis	
	1	2
Eigenvalue	4.259	1.461
Percent of variance explained	53.242	71.503
Cyanophytes	0.630	-0.137
Chlorophytes	0.094	0.856
Diatoms	0.807	0.297
Macrophytes	0.836	-0.117
Microfauna	0.898	0.198
Detritus	0.891	-0.173
Others	0.919	-0.056
Zooplanktons	-0.239	-0.731
Fish	0.000	0.000

**Table 5.** Loadings from principal components analysis of *O. niloticus* and *C. rendalli* fish species based on dietary characters in the upper Kabompo River.

Food Item	PCA axis	
	1	2
Eigenvalue	4.058	50.226
Percent of variance explained	1.261	66.485
Cyanophytes	0.778	-0.002
Chlorophytes	0.039	-0.249
Diatoms	-0.854	0.082
Macrophytes	-0.874	0.164

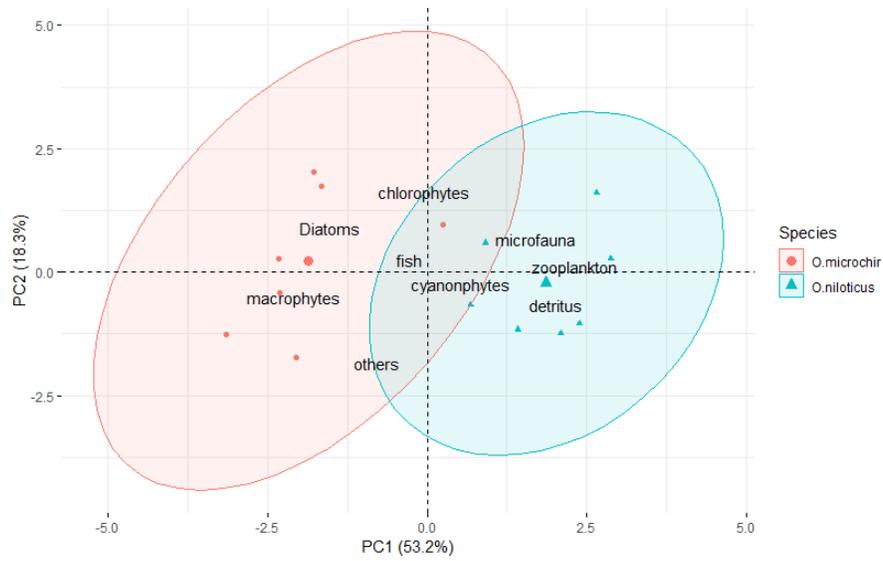
Food Item	PCA axis	PCA axis
Microfauna	0.874	0.082
Detritus	0.676	0.551
Others	0.858	-0.233
Zooplanktons	-0.022	0.894
Fish	0.000	0.000



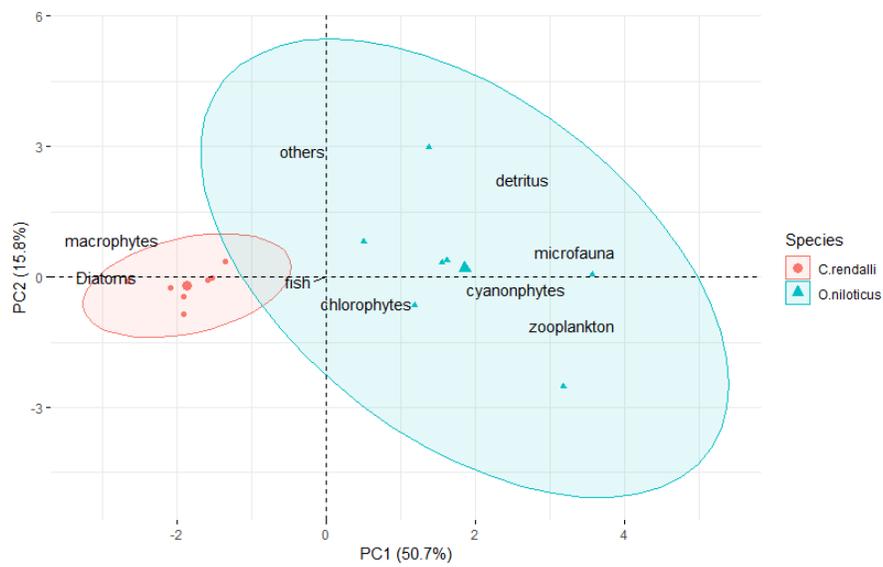
**Figure 1.** Map of the study area - upper Kabompo River

[CHART][CHART][CHART]

**Figure 2 .** A comparison of the the diets (% volume) of exotic and native fish species in the upper Kabompo River. December 2019 – February 2020. Microfuna= Insects, Zooplankton and protozoa.



**Figure 3.** PCA ordination of *O. niloticus* and native *O. macrochir* fish species based on dietary characters in the upper Kabompo River.



**Figure 4.** PCA ordination of *O. niloticus* and native *C. rendalli* fish species based on dietary characters in the upper Kabompo River.