Feeding interaction of exotic Oreochromis niloticus (Linnaeus, 1758) versus native Coptodon rendalli (Boulenger, 1896) in the upper Kabompo River, northwest of Zambia.

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Abstract

Evaluating the feeding interaction of fishes is fundamental in understanding the impacts of introduced species on the community structure and ecosystem function of native species. In the Zambian Rivers, studies have shown that native species has been impacted upon by exotic Oreochromis niloticus, but few studies have investigated feeding interactions between exotic Oreochromis niloticus which is omnivorous and aquaculture preferred herbivorous native species (Coptodon rendalli) in the natural distribution. We analysed the stomach contents of 368 specimens of the fishes to examine the feeding interactions between O. niloticus and C. rendalli in the upper Kabompo River, northwest of Zambia. Both species were grouped into size classes of <50, 51-100 and 101-150 mm total length (TL). However, in the size classes 51-100 mm and 151-100 mm O. niloticus had a larger dietary niche because of its generalist diet than the native species, whose diet mainly comprised of diatoms and algae. There was no significant ontogenetic diet shift for both species, except for O. niloticus in size class 101-150 mm, whose diet consisted mainly of zooplanktons and micro fauna. The results showed an interspecific competition in their size classes, except for 101-150 mm size class, that indicated low dietary overlap. This poses major impacts on food web structure and may explain population decreases of some native species in the upper Kabompo River. Future studies are required to further understand feeding interaction between the exotic and other native fishes in the Kabompo River and other rivers across African where the species coexist.

1. INTRODUCTION

Introduction of the exotic species have become a major threat to many native species and further affecting community structuring and ecosystem functioning globally (Agostinho et al., 2015; Jere et al., 2021; Zengaya et al., 2020). Exotic species in the fresh waters can cause serious disruption in the community assemblage of native species through competition of food resources (Jere et al., 2021; Zengaya et al., 2020). Thus, examining the invasion of exotic species in understanding their impacts on native fish species is critical in fisheries management and conservation biology of lotic environments, which are seen to have dynamic environmental changes along a fluvial gradient (Bwanika et al., 2004; Eloranta et al, 2015; Figueredo & Giani, 2005; Kıran kaya & Ekmekçi, 2013).

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 at 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 North-western Province of Zambia (AES, 2014; Bok & Bills, 2012; Jere et al, 2021).

Tropic interactions between introduced and native species are suggested as one of the processes responsible for structuring populations and, consequently, communities (Figueredo & Giani, 2005; Kıran kaya & Ekmekçi,

2013). For example, in the Kafue River many populations of the native cichlids currently are threatened by the introduction of exotic *O. niloticus* and this has resulted in competition in the food resources leading to the decline in population of native species (Bbole at al., 2014). In addition, 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. Dietary segregation of food resources is one of the main drivers in the assemblage of fish communities in nearly all aquatic habitats (Bwanika et al., 2004; Canonico et al., 2005; Eloranta et al., 2015). Therefore, increasing resource availability reduces competition since resources are no longer limiting, and if resource diversity and availability increases, species will better partition resources (Agostinho et al., 2015; Kırankaya & Ekmekçi, 2013; Miller & Crowl, 2006; Pilger et al., 2010). 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, in the northern most of North America where exotic Lake trout is generalist feeder and overlapping the natural distribution of the native Arctic charr through dietary competition, this seems to have displaced the native species from several habitats (Ke et al., 2008; Kırankaya & Ekmekçi, 2013; Philippsen et al., 2015). Such negative impacts on the population of native species may become more common if other effects such as climate change and other anthropogenic activates that may limit availability of food resources (Agostinho et al., 2015; Figueredo & Giani, 2005; Scheffer et al., 2006; Zengeya et al., 2015).

Competition in the food resources in natural environment is one way in exotic species impact native fish species. Therefore, our study used stomach content analysis to evaluated the feeding interaction of exotic *O. niloticus* and most abundant and aquaculture preferred native fish species *Coptodon rendalli* (Boulenger, 1896) in the upper Kabompo River, Zambia from 2019 to 2020. *Oreochromis niloticus* is an omnivorous species and exhibiting a generalist feeding behaviour, while *C. rendalli* is an herbivorous species (Kenzo & Mazingaliwa, 2002; Zengeya et al., 2015), but both species in early stages of their growing periods they show similar foraging behaviour in lower size classes (Zengeya et al., 2015). However, as they grow further in size *Oreochromis niloticus* species assumed to show somewhat more generalist feeding behaviour than *C. rendalli*, this renders a greater feeding competition between them (Marshall, 2011; Zengeya et al., 2020). The aim of this study was to investigate the feeding interaction between *O. niloticus* and *C. rendalli* in different size classes both local and regional level in natural distribution to understand the food web structuring and help to clarify the impact of exotic species on native species. Although several studies have investigated the diet of each species separately, no studies have investigated resource segregation and overlap in the size classes of their natural distribution, which may vary with presence or absence of an exotic species due to possible competitions. We hypothesised that *O. niloticus* and *C. rendalli* in upper Kabompo River should show significant overlap in their feeding, thus competing for similar food resources in their size classes. To determine this, we used Stomach Content Analysis (SCA) from fish samples collected in sampling points of the upper Kabompo River, northwest of Zambia. We expect both species to occupy different dietary niche in different size classes The results of the study provides new insight regarding coexistence of species in the natural environment and help practitioners and ecologists in Zambia and across the globe to develop strategic management plans for the conservation and management of native species.

2. MATERIALS AND METHODS

2.1 Description of the 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 (Figure 1). 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 upper Kabompo is part of the Kabompo River and is one of the main tributaries of the Zambezi River. It originates at an altitude of approximately 1,500m above mean sea level (amsl) in the highlands which forms the watershed between the Zambezi and Congo rivers. It flows in a general south-westerly direction from the highlands through flatter areas immediately before entering the narrow deep valley known as Kabompo Gorge at Wushingi Hills. Within the Kabompo Gorge the river course

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disappears below rocks and boulders (creating a natural barrier during dry season) and flows underground for approximately 1.5km where it reemerges below a major drop-off in the river gorge approximately 40-50m in elevation. The upper Kabompo River channel including floodplain during peak rain season is up to 1km wide in this upper section of the river, and numerous tributaries join the Kabompo River between the river and the villages. The average water temperature is about 25°c across the study area. The study site 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 Sampling design

The study area covered approximately 15 km of the river with a total of 3 sampling points. This sampled section is invaded by *O. niloticus* . At each sampled site a total of three (3) sampling points were selected with a river distance of about 7.2 km apart. Each sampling point had a total of 200 meters stretch covered encompassing all the available five (5) microhabitat type (runs, riffles, vegetative thicket point, open pool (near fisheries landing area) and the tributaries. Sampling of the fish was conducted in the entire 5 selected aforementioned habitat present in each sampling point. Therefore, a total of 3 sampling points with 15 microhabitats were sampled in the sections of the upper Kabompo River from December 2019 to June 2020.

The studies by Bok and Bills (2012) and DoF (2018) showed that the sampling points have a greater similarity in presence of the exotic and native fish species, rainfall pattern, environmental condition and general water flow regime despite the unique natural barrier that separates them. Due to the proximity of the sampling points, it made the two points of the river easer for exploring their dietary preferences.

2.3 Fish sampling

Fish were collected using the a Fisheries Independent (FI) sampling methods with fish gears that include gill netting materials ranging from 2.5 to 8 cm mesh size and 3 m deep and 30 m longs; two double ended fyke nets made from 20 mm stretched multifilament netting with 75 cm D-ends separated by an 8 m leader; an LR-24 electrofisher-Smith-Root with 400 watt electrical output; and a beach seine net of 25 m long, and 3 m deep. Fyke and gill net gears were deployed along the banks of the slow flowing waters where boat access was not restricted by fish weirs or fallen tree and inspected in the morning (6 am) and afternoon (17 pm) for period of 2 months, and displayed for 24 hours. Electric fishing and seining were conducted during daytime over three days per week within each sampling point. 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), however, effort was limited by the amount of suitable habitat for each gear type and restricted to areas where it was deemed safe to operate. Because variations in the feeding based on feed item of the fishes depend on body size and developmental stages; we selected individuals of each species that corresponded to the adult size class interval or rather those in the same size category as both species attain similar growth size. The specimens were then measured (total length [TL] $\pm$ 1.0 mm) and weighed (wet mass $\pm$ 0.1 g). The species selected were the exotic *O. niloticus* (n = 201) and native *C. rendalli* (N=166) for dietary examination. The selection was based on the most abundant fish species caught in the size class (<50, 51-100, 101-150 mm TL) in the river (capture frequency >10%) according to Eloranta et al. (2015).

2.4 Habitat sampling

In situ water quality parameters (temperature, dissolves oxygen, pH, turbidity and conductivity) at each sampling point were collected and recording on a daily basis. A YSI model 85 meter was used to measure the variables except for pH which was measured with a handheld electronic pH meter. Moreover, the upper Kabompo River is a lotic environment with relatively similar conditions and that the sampling points are in close proximity along the fluvial gradient.

2.5 Stomach content analyses

Stomach content analysis (SCA) were performed to examine taxonomic composition and frequency of occurrence of recently ingested food items and subsequently the difference in both the intraspecific and interspecific

differences in diets of native *C. rendalli* and the exotic *O. niloticus* . Stomach emptiness was achieved using vacuity index (VI) to indicate the quantity of unfilled as number of empty stomachs , while the Stomach fullness (SF) that refers to the average number of relatively full stomachs, and both were estimated on a scale of 0 for empty to 4 for fully distended according to Hyslop (1980). A measuring ruler was used to measure the total length of each stomach (accuracy). 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).

The dietary niche breath was estimated using Levin's index (1968), whereas a symmetric niche overlap coefficient of Pianka (1973) was used to estimate individual dietary specialisation within a populations of both the exotic and native species. The Levin's index values near 0 signify specialized diets with almost no overlap, whilst 1 is similar use of food resources or complete overlap. Overlap using symmetric niche breath 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).

2.6 Statistical analyses

Depending on normality and homoscedasticity of data, either *t*.test or Mann-Whitney U -test was used to compare the results of the indices VI, SF, Levin's index and symmetric niche overlap of exotic *O. niloticus* and native *C. rendalli* species (Sokal & Rohlf, 1995). These statistical analyses were performed using R software version 3.6.0 (R Core Team, 2019).

3. RESULTS

A total of 202 exotic *O. niloticus* and 166 native *C. rendalli* were caught in the upper Kabompo River in the range of 20 to 150 mm TL and placed in size classes <50, 51-100, and 101-150 mm during the survey period. The length of the two species in each size class were similar, but number of catches of *O. niloticus* of native *C. rendalli* examined for SCA in the 3 size classes was 48% low from the overall catch (Table 1). Both species were caught in different time period (06:00hrs, 12:00hrs. and 17:00hrs) during the survey and the species were found evenly abundant in all sampling points, except for 06:00hrs that had 68% less catches (Table 1).

The native *C. rendalli* in size class 51-100 mm and 101-151 mm fed on algae, diatoms and detritus (Table 2). The diet for both species in the <50 mm size class consisted mainly of algae, while *O. niloticus* diet shifted in the 51-100 mm size class, with detritus, zooplankton, insects and microfauna becoming the most important food items, indicating a slight ontogenetic diet shift (Table 2). For both species fewer stomachs were empty and food items found were grouped into food items categories. The feeding patterns of *C. rendalli* were discontinuous and cephalus than of exotic *O. niloticus* (Table 2). In general, *O. niloticus* had a more diverse diet than *C. rendalli* resulting from foraging on algae, chlorophytes, diatoms, microfauna, and detritus in all size classes except for size class <50 mm. *Coptodon rendalli* fed selectively on similar food item in different size classes, indicating a no ontogenetic diet shift. The mean number of food items observed in size class <50 mm did not differ significantly among stomachs of the two species, but exotic *O. niloticus* showed a larger volume than that of *C. rendalli* in size class 51-100 mm and 101-150 mm with significant peaks at 17:00hrs and higher feeding intensity at 12:00 hrs.

The mean SF was relatively high in *O. niloticus* than *C. rendalli* in size class <50 mm, 51-100 mm and 101-150 mm (U =129, n =89, p =0012; U =153, n =81, p =0165 and U =144, n =129, p =0283, respectively), while VI was low in the largest size classes (51–100 mm and 101 to 150 mm) (U =338, n =133, p =0.001; U

=319, n =127, p =0128 and U =387,n =141, p =0172, respectively) (Table 3). The Levin's index mean values for *O. niloticus* and *C. rendalli* showed dietary segregation partially in the size classes, except in size class <50 mm (U = 216, n = 91, p = 01397) (Table 3). In the size class 51–100 mm and 101-150 mm, *C. rendalli* showed a significantly higher degree of individual dietary specialization than *O. niloticus* (U =291, n =87,p =0.001 and U= 288, n= 101, p< 0001, respectively) (Table 3). However, a partial dietary segregation was also observed between *O. niloticus* and native *C. rendalli* species, particularly in size class 51-100 mm (U =291,n =87, p =0.001), as *O. nilotius* also consumed other food items such the zooplankton and other micro fauna (Table 3). *Coptodon rendalli* also showed a significantly higher degree of individual dietary specialization compared with *O. niloticus* in size class 101-150 mm. The mean volume of the food items consumed by both species observed in their stomach contents did not significantly differ, *O. niloticus* showed a larger number of the consumed food items than *C. rendalli* (Tables 2 and 3).

Dietary overlap between exotic *O. niloticus* and *C. rendalli* was significantly high in size classes <50 mm and 51-100 mm (niche breath coefficient 0.637and 0.667, respectively) (Table 4). Both species in the <50 mm size class consumed mainly diatoms and algae, while *O. niloticus* alone in the 51-100 mm and 101-150 mm size classes consumed mostly zooplankton, chlorophytes, and algae, dominated by Microcystis, Gonium, and Phacus, with significantly low dietary overlaps (niche breath coefficient 0.422and 0.223, respectively) (Table 4). *Oreochromis niloticus* is predominantly omnivorous, but its diet consisted of zooplankton, microfauna and insects in 101-150 mm size class, and there significantly low dietary overlap with *C. rendalli* diet comprised mainly as diatom, cyanophytes, chlorophytes and macrophytes (niche breath coefficient 0.118)(Table 4).

4. DISCUSSION

Although the food resources of *O. niloticus* were quite specific and similar (algae, diatoms, zooplankton, and detritus), but algae and diatoms were the most important items in the diet of native *C. rendalli* species. Both species in the size class <50 and 51-100 mm fed mainly on the similar food resources. The principal difference between the diets of exotic Nile tilapia and the native species was the size class 101-150 mm in which particular food items came to be more important, since the native utilized algae as a broader food category in different size classes. 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 101-150 mm size class than *C. rendalli* . 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 results give congruent feeding preferences for both in different size classes in the upper Kabompo River. For both species, similarity in feeding item was evident in the size classes <50 mm, except for size class 51-100 mm which showed a partial niche segregation. *Oreochromis niloticus* evidently had a more diverse and broader food resource niche than native *C. rendalli* species. This was observed by dominating fish communities of *O. niloticus* having been observed to have a wide trophic niche feeding zooplankton and detritus (Kırankaya & Ekmekçi, 2013; Werner & Gilliam, 1984; Winemiller, 1989; Mason et al., 2008; Zengeya et al., 2015). This was evident in our study as *O. niloticus* was seen have wider feeding spectrum than native *C. rendalli* . However, competitive interactions and dietary overlap with natives such as *O. macro chir* 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 (Marshall, 2011; Trewavas, 1983; 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

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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 101-150 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 *C. rendalli* exhibited high trophic niche overlap in <50 mm size class. 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 *Coptodon rendalli* where caught in relatively similar abundant of the aforementioned size class 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 this native species is among 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 highly abundant as recorded during this study. *Oreochromis niloticus* is a native pelagic herbivore which feeds mainly on detritus, zooplanktons, small invertebrates (in size classes 51-100 and 101-150 mm), and algae (in size class <50 mm), suggested a potential dietary niche overlap with *C. rendalli* (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 in <50 mm size class for *C. rendalli*. *Oreochromis niloticus* and *Coptodon rendalli* in the 51-100 mm size class showed partial segregation in their diets (Minshull, 1969; Junor, 1969; Kenzo & Mazingaliwa, 2002; Zengeya et al., 2015). In contrast, the high dietary niche overlap was observed for both species in <50 mm size class 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 cascading effects in the 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 further trophic cascading effect on ecosystem functioning (Marshall, 2005; AES, 2014; Zengeya et al., 2020).

The narrow dietary niche of native species observed in 51-100 mm size class suggests that a small change in food resource abundance could generate a big shift in dietary intraspecific competition of native species in the population sizes. This narrow dietary niche could contribute to population decreases of native species, particularly, *C. rendalli*, which showed a relatively high degree of dietary overlap with *O. niloticus*. This may be because the system has been changing rapidly over the last few years due to anthropogenic 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

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is dietary niche overlap among natives, suggesting shared resource use and potential competition. However, as indicated by wide dietary niches in <50 mm class size, *O. niloticus* species is 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. Such vulnerably contributed by presence of exotic species may create intraspecific competition within size classes of the species and interspecific competition of the species, leading to habitat displacement and possible extinction of native species.

In conclusion, partial dietary segregation observed in size class of *O. niloticus* and *C. rendalli* confirm the coexistence and interspecific competition between them in the upper Kabombo River. Further studies are required to investigate food web structure that may help to explain population decreases of some native species due to invasion in the upper Kabompo River and other rivers across African where the species coexist.

5. ACKNOWLEDGMENT

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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8. REFERENCES

A. E. S (Aquatic Ecosystem Service). (2014). Fish and fisheries assessment for the Kabompo Hydro Electric Project. Pre- and post-wet season baseline surveys (summer 2013 and winter 2014). Deliverable 2104/3. Aquatic Ecosystem Services, 4 Parry Street, Grahamstown, South Africa.

Agostinho, A.A., Suzuki, H.I., Fugi, R., Alves, D.C., Tonella, L.H., & Espindola LA (2015). Ecological and life history traits of *Hemiodus orthonops* in the invasion process: looking for clues at home. Hydrobiologia 746: 415-430

Bbole, I., Katongo, C., Deines, A.M., Shumba, O., & Lodge, D. (2014). Hybridization between non-indigenous Oreochromis niloticus and native Oreochromis species in the lower Kafue River and its potential impacts on the fishery. *Journal Ecology and Natural Environment* , 6, 215-225.

Bok, A., & Bills, R. (2012). Baseline specialist study: Ichthyology and aquatic fauna assessment for the Trident Copper, Nickel mining project, North West Province, Zambia. Coastal and Environmental Services, Grahamstown, South Africa.

Brendonck, L., Maes, J., Rommens, W., & Dekeza, N. (2003) The impact of water hyacinth *(Eichhornia crassipes)* in a eutrophic subtropical impoundment (Lake Chivero, Zimbabwe). II. Species diversity. Archiv fur Hydrobiologie 158:389-405

Bwanika, G.N., Makanga, B., Kizito, Y., Chapman, L.J., & Balirwa, J. (2004). Observations on the biology of the Nile tilapia, *Oreochromis niloticus* (L.) in two Ugandan crater lakes. African Journal of Ecology 42:9 3-101.

Canonico, G.C., Arthington, A., McCrary, J.F., & Thieme, M.L. (2005). The effects of introduced tilapias on native biodiversity. Aquat Conserv 15: 463-483.

D. o. F. (Department of Fisheries). (2018). Provincial annual report. Department of Fisheries, Northwestern province, Registry.Solwezi. Zambia.

Eloranta, A.P., Nieminen, P., & Kahilainen, K.K. (2015). Trophic interactions between introduced lake trout *(Salvelinus namay cush)* and native Arctic charr *(S. alpinus)* in a large Fennoscandian subarctic lake. Ecology and Freshwater Fish 24: 181-192

F.A.O (Food and Agriculture Organization). (2012). The world fisheries and aquaculture, 2012. FAO, Rome

Figueredo, C.C., & Giani, A. (2005). Ecological interactions between Nile tilapia *(Oreochromis niloticus* , L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). Freshwater Biology 50: 1391-1403.

Gozlan, R.E., Britton, J.R., Cowx, I., & Copp, G.H. (2010). Current knowledge on non-native freshwater fish introductions. Journal of Fish Biology 76, 751–786.

Helfman GS, Collette BB, Facey D (1997). The diversity of fishes. Blackwell Sciences, Boston, MA

Hyslop, E.J. (1980). Stomach contents analysis—a review of methods and their application. Journal of Fisheries Biology 17:4 11-429.

Jere, A., Jere, W.W.L., Mtethiwa, A., & Kassam, D. (2021). Impact of *Oreochromis niloticus* (Linnaeus, 1758) (Pisces: Cichlidae) invasion on taxonomic and functional diversity of native fish species in the upper Kabompo River, northwest of Zambia. *Ecology and Evolution* , 11, 12845-12857. DOI: 10.1002/ece3.8031.

Jere, A., Jere, W.W.L., Mtethiwa, A., & Kassam, D. (2021). Breeding pattern of *Oreochromis niloticus* (Linnaeus, 1758) versus native congeneric species, *Oreochromis macrochir* (Boulinger, 1912) in the upper Kabompo River, northwest of Zambia. *Ecology and Evolution* , 11, 12345-12857. DOI: 10.1002/ece3.8377.

Junor, F.J.R. (1969). *Tilapia melanopleura* Dum, in an artificial lakes and dams in Rhodesia with special reference to its undesirable effects. Rhodesian Journal of Agricultural Research 7:6 1-69.

Ke, Z., Xie, P., & Gou, L. (2008). *In situ* study on effect of food com- petition on diet shift and growth of silver and bighead carps in large biomanipulation fish pens in Meiliang Bay, Lake Taihu. Journal of Applied Ichthyology 24: 263-268

Kenzo, U., & Mazingaliwa, K. (2002). Field guide to Zambian fishes, plankton and aquaculture. Japan International Cooperation Agency, Kitwe.

Kırankaya, Ş.G.,& Ekmekçi, F.G. (2013) Life-history traits of the invasive population of Prussian carp, *Carassius gibelio* (Ac ti no pterigi: Cypriniformes: Cyprinidae), from Gelin güllü Reservoir, Yozgat, Turkey. Acta Ichthyol Piscat 43: 31-40

Langton, R.W. (1982). Diet overlap between the Atlantic cod *Gadus morhua* , silver hake, *Merluccius bilinearias* and fifteen other northwest Atlantic fin fish. Fish Bull 80:7 45-759

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomological Soc Am 15(3):237–240 Lowe-McConnell RH (1987) Ecological studies in tropical fish communities. Cambridge University Press, Cambridge

Marshall, B.E. (2005). The impact of eutrophication on Lake Chiveross, Zimbabwe: a tropical African reservoir. In: Reddy MV (ed) Restoration and management of tropical eutro phic lakes. Science Publishers, Enfield, NH, p 6–13

Marshall, B.E. (2011). Fishes of the Zambezi River. In: Marshall B (ed) The fishes of Zimbabwe and their biology, Vol 3. Royal Museum for Central Africa/Musee Royalde l'Afrique Centrale, pp 97–145

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Mason, N.W.H., Irz, P., Lanoiselee, C., Mouillot, D., & Arguillier, C. (2008). Evidence that niche specialization explains species-energy relationships in lake fish communities. J Anim Ecol 77: 285-296.

Miller, S.A., & Crowl, T.A. (2006). Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. Freshw Biol 51:8 5-94

Minshull, J. L. (1969). An introduction to the food web of Lake Sibaya, northern Zululand. Limnological Society of South Africa Newsletter 13:20-25

Moriarty, C.M., & Moriarty, D.J.W. (1973). Quantitative estimation of the daily ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda. Journal of Zoology 171: 5-23

Philippsen, J.S., Hauser M., & Benedito, E. (2015). Isotopic niches of sympatric native and exotic fish species in a Neotropical floodplain. An Acad Bras 87: 825-833

Pianka, E.R. (1973). The structure of lizard communities. Annu Rev Ecol Syst 4: 53 -74

Pilger, T.J., Gido, K.B., & Propst, D.L. (2010). Diet and trophic niche overlap of native and nonnative fishes in the Gila River, USA: implications for native fish conservation. Ecology of Freshwater Fish 19:3 00-321

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sagar, M. V., Nair, R. J., & Gop, A. (2019). Stomach Content Analysis Techniques in Fishes. ICAR Sponsored Winter School on Recent Adances in Fishery Biology Techniques for Biodiversity Evaluation and Conservation. 1-21. Available at; http://eprints.cmfri.org.in/id/eprint/13315. [Accessed on 2nd June 2020].

Scheffer, M., Geest, J.V., Simmer, K., Jeppesen, E., & others (2006). Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 112:2 27-231

Sokal, R.R., & Rohlf, F.J. (1995). Biometry: the principles and practice of statistics in biological research, 3rd edn. W.H. Freeman, New York, NY

Trewavas, E. (1983). Tilapiine fishes of the genera *Saro thero- don* , *Oreochromis* and *Danikilia* . British Museum (Natural History), London.

Werner, E.E., & Gilliam, J.F. (1984). The ontogenetic niche and species interactions in size-structured populations. Annual Revenue Ecological System 15: 393-425

Winemiller, K.O. (1989). Ontogenetic diets shifts and resources partitioning among piscivorous fishes in the Venezuelan Ilanos. Environmental Biology of Fishes 26:1 77-199

Winemiller, K.O. (1991). Comparative ecology of *Serranochromis* species (Teleostei: Cichlidae) in the upper Zambezi River floodplain. Journal of Fisheries Biology 39: 617-639

Winemiller, K.O. & Kelso-Winemiller, L.C. (2003). Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrologic

cycle. Journal of Fisheries Biology 63: 120-128

Zengeya, T. A., Booth, A. J., & Chimimba, C. T. (2015). Broad Niche Overlap between Invasive Nile Tilapia Oreochromis niloticus and Indigenous Congenerics in Southern Africa: Should we be concerned? 4959–4973. DOI: 10.3390/e17074959.

Zengeya, T. A., Kumschick, S., & Weyl, O. L. F. (2020). An evaluation of the impacts of alien species on biodiversity in South Africa using different assessment methods. In: van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA (eds) Biological invasions in South Africa. *Springer* , Berlin, 487–512. https://doi.org/10.1007/978-3-030-32394-3_17.

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 and analyzed	Time of Capture
Oreochromis niloticus	Nile tilapia	Exotic	124	6:00 AM
			91	12:00 Noon
			63	17:00 PM
Coptodon rendalli	Redbreast tilapia	Native	94	6:00 AM
			109	12:00 Noon
			21	17:00 PM

Table 2 . The diet (% occurrence) of *Oreochromis sparrmanii and Coptodon rendalli* in relation to length, upper Kabompo River.

		Length class (mm)	Length class (mm)	Length class (mm)	Length class (m
		O. niloticus <50 mm	O. niloticus 51-100mm	O. niloticus 101-150mm	C. rendalli <50 mm
N		9	3	8	10
B		0.7	0.6	0.1	0.6
Food item group	Specific food item				
Cyanophyceae	*Chroococcus*				
	Merismopedia	27.8		0.5	5.9
	Microcystis	66.7	90		17.7
	Oscillatoria	50	40	20	76.5
	Spirulina	50			14.6
	Anabaena				
Chlorophyceae	*Ankistrodesmus*		20	43	17.7
	Asterococcus	44.4	60		
	Closterium	11.1			5.9
	Cosmarium	50	20		41.2
	Filamentous algae	72	60	3.4	100
	Gonium	83.3	70		11.8
	Tetrastrum		20		
Diatomophyceae	*Amphora*				
	Cycotella	100	80	5	47.6
	Cymbella	38.9	20		57.1
	Gomophonema	72	40		71.4
	Gyrosigma	5.6			28.6
	Melosira	88.9	70	1.3	29.4
	Navicula	94.4	90		5.9
Dinophyceae	*Pinnularia*	77.8	50		5.9
Rotifers	*Synedra*	55.6	20		
	Brachionus	38.9	20		35.3
Rhizopoda	*Centropyxis*	27.8	20		35.5
Plant detritus		77.8	50	0.5	100
Microfauna	*Insexts*		4	78	

Table 3 . 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 (± = Standard Deviation) and VI=vacuity index

Stomach Content Analysis (SCA)	Oreochromis niloticus	Oreochromis niloticus	Oreochromis niloticus	Coptodon
	Number of fish(n)	Size class (mm. TL)	Mean±SD	Number
Stomach fullness	46	<50	1.9 ± 1.4	48
	65	51-100	3.0 ± 0.9	79
	90	101-150	3.5 ± 0.5	39
Vacuity index	46	<50	7.2	48
	65	51-100	31	79
	90	101-150	51.4	39
Levin's index	46	<50	1.4 ± 1.4	48
	65	51-100	2.0 ± 0.3	79
	90	101-150	2.5 ± 1.5	39

Table 4 . Mean values of the dietary overlap of *O. niloticus* and *C. rendalli* species in size classes in upper Kabompo River. The values are Pianka's (1973) symmetrical measure of niche breath. Breadth coefficients with significant values (>0.60) in bold font.

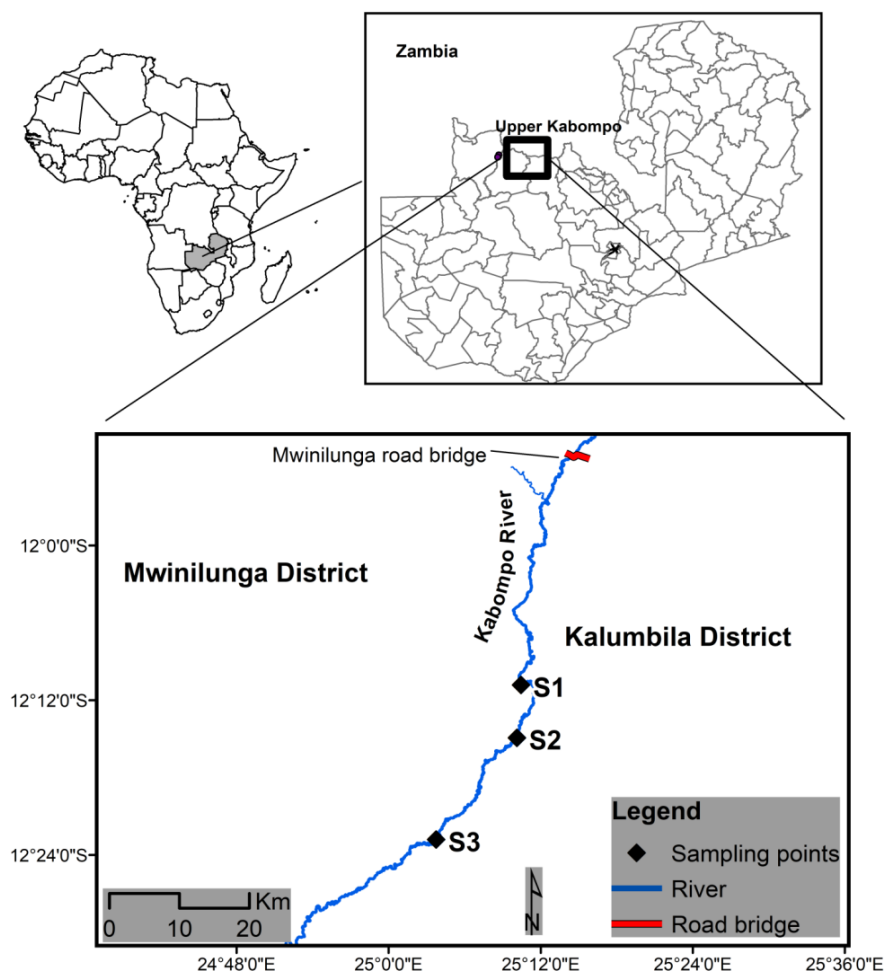| Species		Oreochromis niloticus	Oreochromis niloticus	Oreochromis niloticus
	Size class (mm. TL)	<50	51-100	101-150
Coptodon rendalli	<50	**0.637**	0.328	0.201
	51-100	**0.667**	0.492	0.223
	101-150	0.582	0.422	0.118

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

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