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Trophic niche differentiation in the African elephant fish community (Mormyridae) from the Sanaga River in Cameroon

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Abstract:

The elephant fishes (Mormyridae) are a diverse family of African freshwater fishes primarily inhabiting tropical and subtropical riverine habitats with a general preference for invertebrate prey. Despite the coexistence of multiple species within these habitats, specific details regarding their trophic specializations remain unclear. In this study, we investigated the trophic ecology and potential trophic resource partitioning of eleven mormyrid fish species from the Sanaga River system (Cameroon) using the stable isotopes of carbon and nitrogen of muscles and trophic prey samples. Albeit mormyrids typically display an invertebrate-based diet, we found variations in isotope signals among some species, and in some cases also across different seasons. Species with elongated snout tend to show higher carbon and nitrogen isotope signals compared to those without snout protrusion, suggesting a potential role of snout shape in their trophic ecology. Notably, three species, *Marcusenisus mento*, *M. sanagaensis* and *Paramormyrops batesii* have a lower trophic position than all the other mormyrid species (*Campylomormyrus phantasticus*, *Hippopotamyrus castor*, *Mormyrops anguilloides*, *M. caballus*, *Mormyrus tapirus*, *M.* sp. "short snout", *M.* sp. "long snout" and *Petrocephalus christyi*). Furthermore, significant differences in isotopic signatures were observed among three closely related species of the *Mormyrus* genus, highlighting ecological niche diversification. This again may be linked to variations in snout protrusion length in these three species (two of them undescribed). Additionally, we detected seasonal impacts on $\delta^{13}C$ values, and to a lesser extent on $\delta^{15}N$, particularly in the comparison of peak wet and dry season samples with those from the transition phase between seasons. Possible explanations for these differences include species migration and/or anthropogenic agricultural activities. Our study provides valuable insight into the trophic ecology of this understudied group of tropical fishes by leveraging stable isotope analysis. We present evidence of niche-partitioning within the species community, and our data could be relevant for future studies on stomach content surveys, (micro)habitat preference, behavioral observations or life-history investigations of mormyrid fishes in this region.

Keywords: mormyrids, stable isotopes, trophic position, trophic ecology, seasonal impact

1. Introduction

Elephant fishes, Mormyridae, exclusively occur in freshwater habitats of Africa, and they are well known for their additional sensory system, the electroreception. Currently there are 228 described species (FRICKE et al., 2023) and their diversification is often associated with evolution of species-specific electric organ discharges (EODs) serving both for electrolocation in turbid waters, as well as for conspecific communication (SULLIVAN et al., 2002; CARLSON et al., 2011). For some species radiations (a rapid increase in number of species from a common ancestor), it was indeed shown that sexual selection plays a bigger role than natural selection (ARNEGARD et al., 2010). Apart from their sensory systems, little is known about the general life history of mormyrids. There is seasonality in the presence of some species in the main river upstream and downstream the falls, as well as in the side tributaries, and migration seems to play a role in some of these mormyrids, as known also from other river systems (OKEDI, 1965; BLAKE, 1977, VAN DER WAAL, 1996). Flooding and seasonality influence food availability in limnetic systems in general but especially in riverine environments and were sometimes proven to play a role in the shifts of diets and consequently trophic position of aquatic animals (e.g., NASIMA et al., 2020; MCMEANS et al., 2019). Studies on ecological aspects like movement patterns, reproductive behavior and feeding strategies are scarce but the few studies conducted were able to illuminate interesting behavioral traits like pack hunting in *Mormyrops anguilloides* in Lake Malawi (ARNEGARD & CARLSON, 2005) or the sound production of *Pollimyrus isidori* mediating their courtship (CRAWFORD, JACOB & BENÉCH, 1997). Feulner et al. (2007) investigated the diversification of mormyrids of the genus *Campylomormyrus* and found divergent morphological traits like the shape of the snout protrusions associated with different trophic specializations. However, this hypothesis was not further investigated as most studies found mormyrids to be mainly invertivorous (WINEMILLER & ADITE, 1997; ADJIBADE et al., 2019; PEEL et al., 2019). A known exception to this is the species *Mormyrops anguilloides* (LINNAEUS, 1758) of which larger individuals and adults were reported to be piscivorous (BAILEY, 1994; SKELTON, 2001). Trophic preferences were studied by KOUAMÉLAN et al. (2006) who examined the stomach contents of three different mormyrid species from the artificial lake Ayame, Ivory coast, and in fact identified different main prey items between the two genera, namely chaoborid larvae for *Petrocephalus bovei* and chironomid larvae for both *Marcusenius* species.

The method of stable isotope analysis is a powerful tool to illuminate trophic ecology aspects, especially if combined with findings of stomach content analyses. Heavier stable isotopes of carbon (^{13}C), nitrogen (^{15}N) or sulfur (commonly ^{34}S) can be detected by stable isotope mass spectrometry and accumulate differently in the organisms compared to the common isotope: the lighter isotopes form weaker bonds than the heavier ones as well as tend to react faster (JARDINE et al., 2003). The ratios of the heavier-to-lighter isotopes of

carbon, nitrogen and sulfur can be compared between prey items and consumers within a food network. This method allows to quantify energy flow in the ecosystem and thus makes it possible to reconstruct food webs or to determine changes of energy flow between species, populations or even on an individual level (MCCONNAUGHY & MCROY 1979; RAU et al. 1983; MINAGAWA & WADA, 1984; JARDINE et al., 2003; LAYMAN et al., 2012). Both aspects are needed to gain a better understanding of habitat and species interactions in order to ensure conservation of the ecosystems and its functions.

In this study, stable isotope analysis is used on multiple species of Mormyridae from the Sanaga River, to test for differences in trophic resource usage. As such, the findings on the trophic ecologies of different species could further explain their successful co-occurrence in the same habitat. Cameroonian freshwater fish diversity is still understudied and here we focus on the mormyrid fish fauna of the Sanaga River system, until recently one of the less regulated rivers in Africa. Our focus lays on the differences in trophic ecology among multiple mormyrid species, collected at different seasons in a Guinean equatorial climate zone (OLIVRY, 1986; AMOUGOU et al., 2015), namely a main wet season (from August until November) and a main dry season (from December to March) plus a transition between the dry and the wet season (from April until July), sometimes divided as a shorter wet season lasting from April until June and a shorter dry season (from July until early August) (BITJA NYOM & PARISELLE, 2015). We analyzed fish samples from multiple localities on the main Sanaga River around the Nachtigal falls, as well as in some nearby tributaries.

2. Material and Methods

2.1. Sampling

The study site for this work was the Sanaga River in Cameroon, which is the country's largest river and has a length of over 918 kilometers (DUBREUIL et al., 1975). The hydrological study of this river made it possible to divide it into three large contiguous segments which are: Upper Sanaga, Middle Sanaga and Lower Sanaga (BITJA NYOM et al., 2020). This study took place in the middle part of the Sanaga and the sampled localities were located along the main stream in the proximity of the cascades of Nachtigal complemented by few inflow stream locations (tributaries) (see Map in Figure 1). The water is characterized to be turbid and murky in the main stream whereas naturally less so in the side streams. The fish were caught using gillnets of different mesh sizes. Gillnets have been set in the evening between 5 p.m. and 6 p.m. at several places and visited between 7 a.m. and 8 a.m. the next day and continuously as well as in the late afternoon. After euthanizing the fish with a lethal amount of MS-222, photographs and measurements were taken, and fin clips collected for DNA analyses. Afterwards, a 1 to 2 centimeter piece of lateral muscle

was dissected out from the fish's body in an area between the ventral and the caudal fin in proximity to the lateral line. Over the years of 2017 and 2018 muscle tissue from eleven species (*Campylomormyrus phantasticus* (PELLEGRIN, 1927), *Hippopotamyrus castor* PAPPENHEIM, 1906, *Marcusenius mento* (BOULENGER, 1890), *Marcusenius sanagaensis* BODEN, TEUGELS & HOPKINS, 1997, *Mormyrops anguilloides* (LINNAEUS, 1758), *Mormyrops caballus* PELLEGRIN, 1927, *Mormyrus tapirus* PAPPENHEIM, 1905, *Mormyrus* sp. "short snout", *Mormyrus* sp. "long snout", *Paramormyrops batesii* (BOULENGER, 1906) and *Petrocephalus christyi* BOULENGER, 1920) were obtained. However, the number of individuals per species vary and the representation of each season is not always complete and at times unequally distributed (Table 1).

In total we collected 288 samples from 288 individuals of 11 species. All samples were transfered in 96% ethanol and stored in a freezer at -20 degrees. We complemented our muscle sampling by adding trophic samples consisting of the individual items from the stomachs of nine individuals (two *Mormyrops caballus*, one *Mormyrops anguilloides*, two *Hippopotamyrus castor*, two *Mormyrus tapirus* and one *Mormyrus* sp. "short snout"), as well as of benthic samples. The latter were obtained by collecting plant material and invertebrates from the river bed area, the riverbank and the water column of the Sanaga River and a tributary, namely from Nachtigal falls and the Wala river. The main reason for this collection was to get an overall idea of the potential prey resources and a reference isotope background. The organisms from these environmental samples were identified taxonomically under a binocular microscope to the highest level possible, from sometimes only class (Gastropoda), mostly the order (e.g. Ephemeroptera) and seldom to family level (Coleoptera, Hydrophilidae and Coleoptera, Elmidae) with the help of pictures taken from stomach content material and two invertebrate identification guides (MOISAN J. *et al.*, 2010; MARY, N., 2017). The water plant material was not further identified, and the various plants were mixed to achieve an amount of over 2 mg and labelled accordingly as the group called "plant". The isotope values generated by both, the stomach content material and the benthic material, are jointly represented when later referring to the values of the "trophic samples", unless otherwise specified.

2.2. Sample processing

The muscle tissue samples were transferred to 2ml Eppendorf tubes and were dried for 48 hours at 60 °C or at 45 °C for 72 hours over the weekend in a drying oven. If bone structures were present in the sample, they were carefully removed with a clean forceps. Then samples were ground with two beads, one placed at the bottom and one at the top, at the frequency 25/s for 20 seconds or at 30/s for 30 seconds in case of a bigger piece using a ball mill (MM400, Retsch, Germany). After taking the beads out, one millilitre of ethanol was added, and sample has been shaken until homogenous. The samples were then centrifuged for 30 seconds at 6000 rpm. About 600 microliters of ethanol were taken out gently with a pipette and a second

drying step was followed at 24 up to 48 hours for 60 °C. In case the sample was not completely transformed into the powder yet, an additional ball grounding was performed at 25/s frequency for 10 seconds and then centrifuged for 30 seconds at 6000 rpm and final drying for 15 minutes and 60 °C. Subsequently, the samples were weighted in tin capsules to achieve 0.5 milligrams ideally while allowing a range of 0.45 to 0.55 mg and folded into tiny cubes using a thin and thick tweezer and put in labelled sample boxes. The trophic samples were processed in the same manner except grounding happened partly manually and sometimes with only one silver ball. Plant material had to achieve a weight of 3 mg. Some trophic samples were too light, e.g., the *Hydracarina* group, and had to be excluded from further analysis (17 samples out of 64). Total carbon and nitrogen amounts as well as the isotopic ratios $\delta^{13}C$ and $\delta^{15}N$ were measured with a Delta V Advantage mass spectrometer coupled to Conflo IV and elemental analyzer Flash 2000 using a Thermal Conductivity detector (all instrumentation by Thermo Fisher Scientific, Bremen, Germany). The carbon and nitrogen isotope ratios are expressed following the delta notation, which is the following: $\delta X = 1000*(Rsample/Rstandard - 1)$, where X stands for ^{13}C or ^{15}N, respectively, and R is the relative amount of carbon or nitrogen isotopes ($R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$). International standards were applied to normalise the isotope ratios: The Vienna Pee Dee Belemnite (VPDB) scale (COPLEN, 1996) and atmospheric N2 was used for the carbon and the nitrogen isotope ratios, respectively. In addition to repeated measurements of a series of international standards (IAEA-CH3, IAEA-CH6, IAEA-600, IAEA-N1, IAEA-N2, IAEA-NO3), a glycine standard was included after every 10th sample to provide calibration for elemental composition as well as serve as a quality control for isotopic measurement. Analytical precision resulted within ± 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

In total 302 muscle sample isotope values were obtained, of these 12 values had an unusual C to N ratio and were thus deemed unreliable. Two *Mormyrops caballus* samples failed during the measuring itself. These 14 samples were excluded from further analyses. Regarding the trophic samples, 14 out of 47 values displayed a too low N value, causing a low instrumental signal and hence had to be excluded from the subsequent analysis.

2.3. Data analysis

Delta 13C ($\delta^{13}C$) and delta 15N ($\delta^{15}N$) values were analysed in R Studio Statistical Software (version 1.4.1717; RStudio Team (2021). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.). The package "tRophicPosition" (QUEZADA-ROMEGIALLI C. *et al*., 2018) was used furthermore to access the trophic position of the investigated species using one baseline of all benthic sourced samples from the trophic samples. The used trophic discrimination factors (TDF) were McCutchan (MCCUTCHAN'S *et al.* 2003) for a fish muscle tissue which means a mean of 2.9 ‰ ± 0.32 se for $\delta^{15}N$ and 1.3 ‰ ± 0.3 se of for $\delta^{13}C$. Tropic position (TP) was estimated using a λ (lambda)

= 2 for using also secondary consumers as baseline as no primary producer was available. The conventional range of trophic levels ranges from 1 (primary producers) to 5 (2 to 4.5 for fishes in freshwater ecosystems) (TRITES, 2001; YOĞURTÇUOĞLU et al., 2020). The plant material collected were several species but had to be pooled together to increase weight and thus has only informative value. The model was run with 4 chains and for 20000 iterations. To access the significance of the differences observed in muscle isotopic signals mean values between different seasons one-way ANOVAs as well as Tukey tests to judge the results of the ANOVA were conducted. Alpha was set to 0.01 and the critical value q was found accordingly in available tables online (see Table 3).

3. Results

3.1. Muscle samples analysis

In total, we analysed 288 samples of 11 species of the mormyrid community in the Sanaga River, and we found that the stable isotope signals partly differ among the species (Figure 2). The *Marcusenius* species and *Paramormyrops batesii* share lower $\delta^{13}C$ and $\delta^{15}N$ values in comparison to all other species. Interestingly, some species from different genera possess similar isotopic signatures like *Hippopotamyrus castor* and *Mormyrus tapirus*, or *Mormyrops caballus* and *Campylomormyrus phantasticus* whereas the species from the same genus are more separated from each other. This is especially obvious in *Mormyrus* sp. "short snout" showing the highest $\delta^{13}C$ carbon values.

3.2. Trophic samples

To infer the baseline stable isotope values, we analysed also trophic samples of possible prey items, i.e. the stomach content of the fish individuals and the collected benthic samples. We analysed the stable isotope values of 16 potential prey groups. Some individual samples had to be pooled together in order to reach the threshold weight needed for the analysis, like the group "Plecoptera", "Trichoptera" and "Ephemeroptera". Of the group "Coleoptera Hydrophilidae" and "Lepidoptera pupa" only one individual was present. The $\delta^{15}N$ values range from 4.9 to 5.0 parts per thousand (‰) and the $\delta^{13}C$ values from -17,5 to -28 parts per thousand. "Gastropoda" has the highest $\delta^{13}C$ values and "coleoptera" the lowest. The plant material, "Zygoptera" and "Hemiptera" display the highest $\delta^{15}N$ values whereas "Plecoptera" and "Coleoptera larvae Elmidae" the lowest. There were only three groups that were simultaneously present in the stomach content based trophic samples and the benthic prey items based trophic samples. These were Anisoptera, Gastropoda and Coleoptera larva Elmidae. With the exception of the latter group the isotopic signatures did only marginally differ or were the same. For further reference please see the two plots in Supplementary Material (Figure S1 showing the benthic-based trophic samples only and S2 displaying only the stomach content-based material). While looking at the combined isotopes plot (Figure 3) where the muscle isotope

values are plotted together with the trophic samples, the higher trophic position (higher delta nitrogen values range) of the mormyrid fishes in contrast to their prey items can be noticed.

3.4. Calculations of trophic position

The analysis performed with the tRophicPosition R package (QUEZADA-ROMEGIALLI C. et al., 2018) using all the benthic samples as one baseline revealed the trophic positions of all mormyrids to range between 3 and 4. In the pairwise comparisons of the species from the same genus, we found that the two species of *Mormyrops* only show a marginal difference between their trophic positions (3.8 and 3.7) (Figure 4A). Similarly, the two species of *Marcusenius* seem to share a similar trophic position (3.612 and 3.545) (Figure 4B). On the other hand though, we found differences among the *Mormyrus* species. Namely, *Mormyrus* sp. "short snout" shows a notable difference from the other two species with a tropic position of 3.912. It differs from the *Mormyrus* sp. "long snout" (Figure 4D; mean TP of 3.605) and from *Mormyrus tapirus* (Figure 4E; mean TP of 3.772), while the pairwise comparison of *Mormyrus tapirus* and *Mormyrus* sp. "long snout" revealed a lesser difference in their trophic position (Figure 4C; mean TP of 3.772 vs. 3.605). Interestingly, when performing statistical analysis (t-tests) on the differences of the stable isotope values, only the *Mormyrus* species comparisons reveal a significance (see Table 2 below). This is in accordance with the nearly congruent trophic positions of the *Mormyrops* and the *Marcusenius* species but also reflects the separation of *Mormyrus* sp. "short snout" from *Mormyrus tapirus* and from *Mormyrus* sp. "long snout" nicely.

3.4. The impact of the season

We collected samples from different seasons, namely during the dry season (February and March), the wet season (August, September, October and November) and some samples originate from the transition phase between these two seasons (in the months of May, June and July). We investigated the influence of the season on the stable isotope values and found no difference when comparing dry and wet season values. We did find differences though between the samples collected during the transition phase and the two main seasons. Albeit the low number of samples from the transition phase (only five species; Figure 5), for four species the differences between the wet vs. transition and/or dry vs. transition phase are statistically significant (Table 2). The one-way analysis of variance (ANOVAs) conducted for all species and the subsequent Tukey-Kramer tests revealed that in two species, *Mormyrus tapirus* and *Marcusenius sanagaensis*, both stable isotopes $\delta^{15}N$ and $\delta^{13}C$ were significantly different between the seasons (pairwise comparisons of wet- transition and dry-transition). In *Campylomormyrus phantasticus* a difference was found as well but to a lesser degree as only the $\delta^{13}C$ dry season values were significantly different from the transition samples. The opposite is true for *Petrocephalus christyi*, where the $\delta^{15}N$ values are different.

However statistical analysis could not be performed for the wet season of the latter as there was only one sample from that season available. The only exception was *Hippopotamyrus castor* where the one-way ANOVA showed the differences not to be significant for either stable isotope. Please see Table 3 for details.

4. Discussion and Conclusions

Trophic niche partitioning in mormyrid fishes:

Our results for trophic ecology based on stable isotope signals of different mormyrid species are in accord with previous evidence of mormyrids feeding mostly on insect larvae (VAN DER WAAL, 1985; WINEMILLER & ADITE, 1997). There are, however, noticeable differences among the species. For instance, the two *Marcusenius* species and *Paramormyrops batesii* have a lower trophic position than the other mormyrids, as revealed by the stable isotope averages analysis and the tRophicposition analysis. These species, hence, share a more similar ecological feeding niche compared to the other species. Interestingly, we also observe that the mean isotopic signal of different species within one genus often differs more than when compared across other genera. This is the case for *Mormyrops caballus* and *Mormyrops anguilloides* with distinct signals in both $\delta^{13}C$ and $\delta^{15}N$ compared to *Campylomormyrus phantasticus* (Figure 2), although the actual effect on the trophic position itself was minor in this case (Figure 4A). More strikingly, we noticed differences among the three species of the *Mormyrus* genus. *Mormyrus tapirus*, and two formally undescribed species, *M.* sp. "long snout", and most remarkably *M.* sp. "short snout" differ in $\delta^{13}C$ and $\delta^{15}N$ signals, and, on top of this, *Mormyrus* sp. "short snout" differs from the other two other *Mormyrus* species in the trophic position analysis (Figure 4). Our findings therefore suggest different trophic specializations for these closely related species. Trophic niche partitioning among closely related species from the same habitat has been commonly observed in African fishes (e.g. NAGELKERKE, 1997; POLÁČIK et al., 2014), while resource partitioning has been a general question in ecology since a long time (HARDIN, 1960; SHOENER, 1974). Stable isotope data have already proven to be helpful to visualize trophic niche partitioning within closely related fish species (WANG et. al, 2022). Differences in trophic preferences can also be observed on the jaw/mouth shape, which is often adapted to its specific purpose. For example, in croakers (WANG et al., 2022) the species with the most unique isotopic signatures (*Johnius belangerii*) also has a unique feeding strategy associated with different jaw shape (ZHANG et al., 2020). In mormyrids from Sanaga, species having snout protrusion tend to show higher $\delta^{13}C$ and/or $\delta^{15}N$ signals when compared to species without elongated snouts (Figure 4D). Notably, the three *Mormyrus* species from the Sanaga express anatomical differences in their trunk shape and jaw and lip morphology. In fact, *Mormyrus* sp. "short snout" has more truncated upper lip protrusion, while *M. tapirus* has longer lower lip. *M.* sp. "long snout" has much longer snout than both *Mormyrus* sp. "short snout" and *M. tapirus* (Figure 2). The overall mouth shape and orientation probably reflect subtle differences in microhabitat and prey preferences in

these species. This seems to be in accord with the hypothesis of Feulner et al. (2007) who suggested possible trophic ecology variations based on morphological variations in the snout protrusions within another genus of mormyrids (*Campylomormyrus*) occurring in the same habitat (lower Congo River) (FEULNER et al., 2007).

Muscle tissues are generally ^{15}N- and ^{13}C-enriched relative to their diets as lighter isotopes vanish quicker than the heavier isotopes in the process of respiration and digestion (HOPKINS III & FERGUSON, 2012). These so-called "discrimination factors" lead organisms on a higher rank in the food chain to display also higher isotopic signatures. Accordingly, we observed all mormyrid species to have higher $\delta^{15}N$ values than the prey/trophic samples corresponding clearly to a higher position in the trophic chain. However, the same is not true for the $\delta^{13}C$ values which generally correspond more to amounts of nutrient in the river flow and the distance from various sources of nutrient export and seemed to have an equal range between mormyrids and invertebrates. An exception is the higher $\delta^{13}C$ value in Gastropoda than in mormyrids but this can be explained due to the presence of shells that were too small to be removed prior to analysis, and are made of particular inorganic carbon and thus lead to a higher (less negative) $\delta^{13}C$ as organic carbons are usually depleted in ^{13}C (Hayes, 2001; Goldberg et al., 2007).

The trophic position analysis is mostly based on the $\delta^{15}N$ values since it has been shown that trophic position is corresponding more to the trophic fractionation of $\delta^{15}N$ than to $\delta^{13}C$ (POST, 2002). The environmental benthic samples were set as a baseline for the analysis since we had a limited amount of available stomach content samples. These base samples represent possible sources of carbon and nitrogen from the environment. Nevertheless, we tested the tRophicPosition analysis for the estimation of trophic position with the use of the stomach content as well (see Supplementary material S3) with very similar results. Yet notably, the difference between *Mormyrus tapirus* and *M.* sp. "short snout" trophic positions became slightly smaller. In general, a primary producer is usually used as a baseline for this analysis, unfortunately it was not available in our study as the collected plant material was so few and only of informative value. However, some authors also claimed that macrophytes, the main primary producers in many aquatic ecosystems, were revealed to contribute less to aquatic food webs than assumed (HAMILTON et al., 1992; BUNN & BOON, 1993; FORSBERG et al., 1993; THORP & DELONG, 1994; THORP et al., 1998; LEWIS et al., 2001) or may have only local effects (GROSBOIS et al., 2017a) (PEEL et al., 2019).-Another drawback is not knowing the correct trophic discrimination factors (the exact isotopic shift between prey and consumer) as the ones available for fish muscle tissues like the chosen McCutchan (MCCUTCHAN'S et al. 2003) with a mean of 2.9 ‰ ± 0.32 se for $\delta^{15}N$ and 1.3 ‰ ± 0.3 se of for $\delta^{13}C$ is an averaged one concluded from the authors themselves after they found varying trophic shifts especially for N depending on diet. Interestingly, McCutchan et al. (2003) found lower ^{15}N trophic shift mean values (around 1.4‰) to be relevant for

consumers feeding exclusively on invertebrates in contrast to consumers on high-protein diets. As the trophic discrepancy for $\delta^{15}N$ is a minimum of 2.5‰ between trophic samples and mormyrid consumers in Figure 3 this could be an argument for a more high-protein diet in some mormyrids. These findings once more stress the relevance of knowing more about the specific diet of each mormyrid species. This could be achieved by combining the results of this study with thorough, long-term stomach content analyses in the future.

Stomach content analysis though, only provides a "snapshot" of an organism's diet prior to the moment of capture (DAVIS et al., 2012; PINNEGAR & POLUNIN, 2000) and has several drawbacks such as the difficulty of identifying digested prey items and the resulting persistence and thus dominance of more robust prey as well as infrequent eating of consumers (TAYLOR, 2016 [doctoral thesis]). Yet, the power of this analysis in combination with stable isotope analysis is often emphasised as the two methods can complement each other (DAVIS et al., 2012; LAYMAN et al., 2012; POLÁČIK et al., 2014; DILLON et al.,2021). Stable isotopes can indeed provide an insight into a consumer's diet for a longer period of time. However, it also has its limitations when the organism(s) and its habitat are not well understood, which makes creating models for Bayesian analysis difficult (see above speaking about the trophic discrimination factors), or other factors such as seasonal changes (migration) or differing turnover rates may impact the results and are not described satisfactorily. Turnover rates are generally tissue-dependent and are indeed slower in muscle tissue or bone collagen (two to three months) than in plasma or blood (few days) (e.g., MADIGAN et al., 2021, POLISCHUK et al., 2001) but there are hints that the turnover rate in one tissue can differ as well depending on the species, fish size and life stage (BOSLEY et al., 2002; GASTON et al., 2004; MADIGAN et al., 2012 and MADIGAN et al., 2021).

Effect of seasonality

Dry and wet seasons in tropical regions can be reflected in fish behaviour, migration, reproduction or food/prey availability. Impact of the season on the stable isotope values has been observed in many fish species (NASHIMA et al., 2020; MCMEANS et al., 2019; TAYLOR, 2016 [doctoral thesis]; WANTZEN et al., 2002) and seasonal variability shown to be especially relevant for partly flooded aquatic systems (TAYLOR et al., 2017; MERRON & MANN, 1995; DE ALMEIDA et al. 1997; WANTZEN et al. 2002; EGGLETON & SCHRAMM, 2004). Thus, we have specifically focused on the stable isotope signatures in different seasons. We sampled mormyrid fish in different periods throughout the year (Table 1 and S1). The habitats of the Sanaga River and tributaries are characterized by seasonal flooding during the wet season and are exposed to a rising water level already in the transition phase of the shorter wet season from April to June.

First, we compared wet season and dry season samples, and we found no difference in the stable isotope signal. Then we also focused on the samples from the transition period and surprisingly we found that these samples show significant differences when compared to the wet and the dry season samples. The different isotope signal is present in four out of five tested species, i.e. in *Mormyrus tapirus*, *Marcusenius sanagaensis*, *Petrocephalus christyi* and *Campylomormyrus phantasticus*, while *Hippopotamyrus castor* did not show any differences throughout seasons. Therefore, the transition period seems to influence the diet of some, but not all mormyrid species. This observation could possibly be explained by species migration over the year and, hence, the individuals sampled in the transition phase may originate from different population than the dry- and wet season samples. At least one of the species, *Marcusenius sanagaensis*, is known to be more residing in the tributaries than in the main stream (personal observations on the study by Njom and others during several years of fieldwork). In general, mormyrids are known to migrate (VAN DER WAAL, 1996; OLOPADE, 2013), mostly in relation with the wet seasons spawning (OKEDI, 1965; BLAKE; 1977) but little is known for the tested species from the Sanaga River. Future studies on migration in mormyrids are needed to further test this hypothesis. An alternative explanation would be in the turnover rates. If we still assume turnover rates to be few months for white muscle tissue like in most other more intensively studied fish species (TAYLOR et al., 2017), it could also mean that there was a change of diet at the very beginning of the dry season and during the dry season in fact. Interestingly, this could be an anthropogenic induced cause as the phytosanitary treatment of the plantations along the tributaries is carried out at the end of the major dry season (NJOM et al., 2022). Thus, an unusually larger terrestrial sources input to the water happens in the dry season and possibly impact the signal of some (but not all) species. Lastly, we can also explain the pattern partially by different sampling locations in the transition period for some species (Table S1). For example, the samples of *Marcusenius sanagaensis* from the Mekono River (a polluted tributary with a pollution impact largely increased during the dry season) are different from the main Sanaga River and this seems to influence the results more than the season in this species (revealed by ANOVAs shown in Table S3). Unfortunately, we have no samples from the Mekono River from the dry and wet season to test this effect but the pollution aspect is interfering here considering that the accessible downstream river part is nearly dried out during the dry season. In *Mormyrus tapirus* season and locality seem to both play a role. The most different samples are from Mpem River but even if these samples are excluded from the dataset, the $\delta^{13}C$ values between wet and transition seasons are still significantly different from each other whereas dry versus transition as well as all $\delta^{15}N$ values are not different from each other anymore (as seen in the Supplementary table S3). Interestingly, the transition samples from the same locality (Mpem River) are not significantly different in *Marcusenius sanagaensis*, which illustrates again various responses among species. This conclusion is also underlined by the fact that the transition sample difference in the $\delta^{13}C$ values of *Campylomormyrus phantasticus* (all samples are from

one locality) as well as the difference in the $\delta^{15}N$ values of *Petrocephalus christyi* could not be pinned down to a locality (excluding the Mpem River samples in *P. christyi* had no effect in the outcome). Thus, not only the seasonality aspect remains but also somehow it acts differently for the respective species.

Furthermore, one study (McMeans et al., 2019) found for example piscivore fishes to have higher $\delta^{15}N$ values in the wet season but still most of their studied fishes showed interestingly high variation in their responses. Some studies showed fish to become more generalized feeders during the wet season (Costa-Pereira et al., 2017; Pool et al. 2017) and there are at the same time hints for increasing trophic position during the dry season (Wantzen et al. 2002), whereas other studies showed diverse foraging strategies with no universal seasonal influence pattern (Novakowski et al. 2008), (McMeans et al., 2019). Most likely, all these factors impact the mormyrid isotopic signals and without further investigation it is hard to tell which of them is the most relevant for the Sanaga River mormyrids. In the future, a comprehensive data set covering most species from most localities and different seasons would provide more insight into the nuances of the trophic ecology of the mormyrid species of the Sanaga River system.

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Author contribution statement:

Conceptualisation: ZM, ARBN. Developing methods: ZM, ARBN, PH, JK Conducting the research: ZM, AI, SDN, PH, GMS. Data analysis: PH, JK, GMS. Data interpretation: ZM, SDN, GMS. Preparation figures and tables: GMS. Writing – initial draft - GMS and ZM, Writing – final revision and approval – all authors.

Data Availability statement:

COI sequences used for the species phylogeny will be/are available on GenBank with accession numbers:-----.Raw data of stable isotope analysis of the mass spectrometer for muscle samples are imbedded in sample overview table in Table S1 in Supporting information and for trophic samples in Table S2.

Conflict of Interest Statement:

The authors declare no conflict of interests.

Supporting Information:

Figure S1: Stable isotope analysis of the trophic samples from the benthic samples

Figure S2: Stable isotope analysis of the trophic samples from the stomach contents

Figure S3: Trophic positions comparisons based on stomach content baseline

Table S1: sample list overview of muscle samples isotope values and details about sampling

Table S2: sample list overview of trophic samples

Table S3: results of single-factor ANOVAs and Tukey-Kramer test (if applicable) for species with transition season samples testing the factor of locality

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Table 1: overview of collected species and their representation. Please note that *Mormyrus* sp. “short snout” and *Mormyrus* sp. “long snout” refer to so far undescribed species and thus have these preliminary names in this study.

species	number of individuals	Season
Campylomormyrus phantasticus	32	dry 2017 and dry, transition, wet 2018
Hippopotamyrus castor	18	dry 2017 and dry, transition, wet 2018
Marcusenius mento	4	wet 2017 and transition 2018
Marcusenius sanagaensis	43	dry, wet 2017 and dry, transition, wet 2018
Mormyrops anguilloides	31	dry, wet 2017 and 2018, one transition sample from 2018
Mormyrops caballus	21	wet, dry 2017 and 2018
Mormyrus tapirus	52	dry, wet 2017 and dry, transition, wet 2018
Mormyrus sp. "long snout"	3	dry 2017
Mormyrus sp. "short snout"	36	dry, wet 2017 and dry, wet 2018
Paramormyrops batesii	4	wet 2017 and dry 2018
Petrocephalus christyi	44	dry 2017 and dry, transition 2018, one wet sample from 2018

Table 2: t-tests performed for delta nitrogen values as well as delta carbon values for species comparisons of the same genus

t-test with different variances	p-value (two-tailed)
δ^{13}C *Mormyrops caballus* vs. *Mormyrops anguilloides*	0.116
δ^{15}N *Mormyrops caballus* vs. *Mormyrops anguilloides*	0.650
δ^{13}C *Marcusenius mento* vs. *Marcusenius sanagaensis*	0.126
δ^{15}N *Marcusenius mento* vs. *Marcusenius sanagaensis*	0.515
δ^{13}C *Mormyrus tapirus* vs. *Mormyrus* sp."short snout"	4.42E-12*
δ^{15}N *Mormyrus tapirus* vs. *Mormyrus* sp."short snout"	0.002*
δ^{13}C *Mormyrus tapirus* vs. *Mormyrus* sp."long snout"	0.04
δ^{15}N *Mormyrus tapirus* vs. *Mormyrus* sp."long snout"	0.002*
δ^{13}C *Mormyrus long "snout"* vs. *Mormyrus* sp."short snout"	1.471E-05*
δ^{15}N *Mormyrus long "snout"* vs. *Mormyrus* sp."short snout"	1.003E-05*

* indicates a significant p-value (p-value < 0.025)

Table 3: results of single-factor ANOVAs and Tukey-Kramer test (if applicable) for all species with transition season samples

single-factor ANOVA	p-value	df	Tukey-Kramer q-stat values	dry vs wet	dry vs transition	wet vs transition	critical value with α=0.01
Mormyrus tapirus $\delta^{13}C$	1.288E-07*	50		2.476	8.353**	9.242**	2.678
Mormyrus tapirus $\delta^{15}N$	0.001*	50		0.677	5.253**	5.233**	2.678
Marcusenius sanagaensis $\delta^{13}C$	0.027*	40		0.669	3.157**	3.861**	2.704
Marcusenius sanagaensis $\delta^{15}N$	0.011*	40		0.382	3.796**	4.268**	2.704
Petrocephalus christyi $\delta^{13}C$ dry vs transition	0.520	19					
Petrocephalus christyi $\delta^{15}N$ dry vs transition	0.011*	19					
Campylomormyrus phantasticus $\delta^{13}C$	0.016*	31		0.378	4.354**	3.53**	2.750
Campylomormyrus phantasticus $\delta^{15}N$	0.654	31					
Hippopotamyrus castor $\delta^{13}C$	0.232	14					
Hippopotamyrus castor $\delta^{15}N$	0.169	14					

*indicates a p-value below 0.05 ; ** indicate q-stat value > critical value

Figure captions:

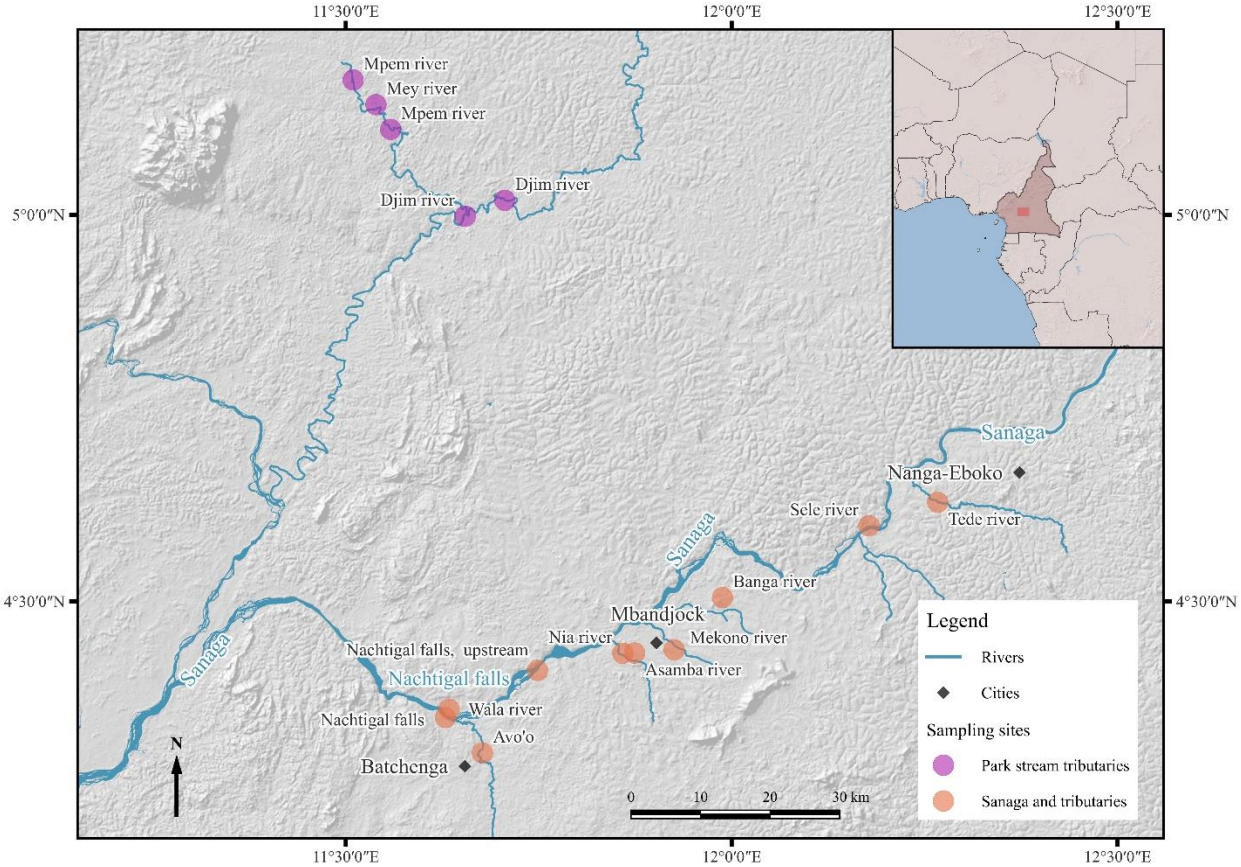

Figure 1: Overview of the study site: Map of the section of the middle Sanaga river close to the Nachtigal Falls (Chutes de Nachtigal) in Cameroon, Africa. The most frequented sampled sites are up- and downstream of Nachtigal falls and are in the vicinity of the town Batchenga (black dot). (Basemap: https://www.esri.com/en-us/maps-we-love/overview, borders: https://www.diva-gis.org/gdata, rivers, streams and places: openstreetmap.org).

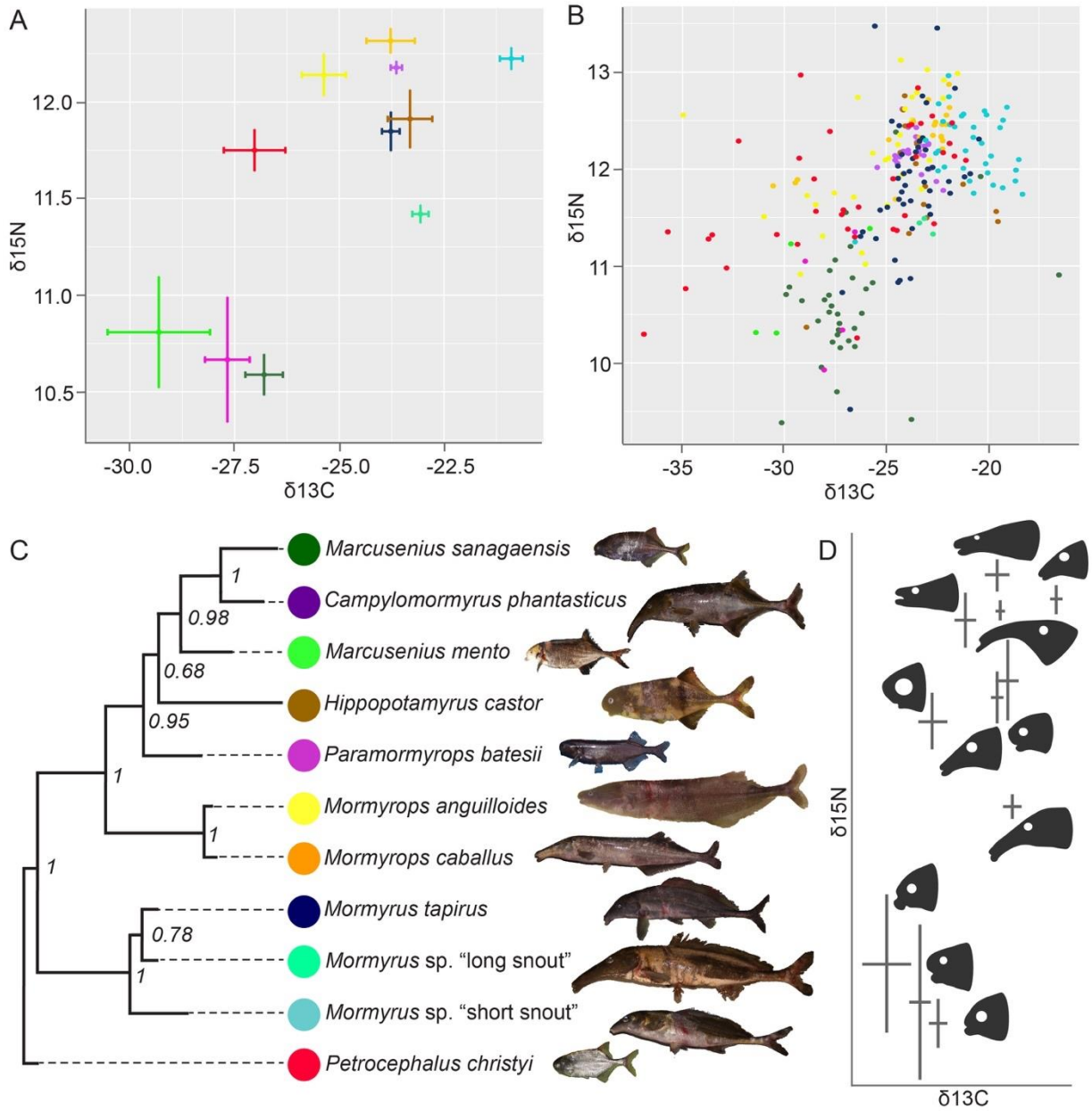

Figure 2: Stable isotope signature of eleven Sanaga river mormyrid species. A) Results of the stable isotope analysis of the muscle samples - mean and standard errors shown. δ^{15} nitrogen values on the y-axis and δ^{13} carbon values on the x-axis; unit in parts per thousand (‰). B) Stable isotopic signatures shown for all individuals. Note that the plots do not include the transition season samples specifically addressed in the text and in Figure 5. Note the different scale of plot A and B. C) Phylogenetic relationships of the studied mormyrid species based on the COI sequences and reconstructed by Bayesian inference. The colour code corresponds to the species in the plots above. D) Head shape of different species projected on the results of

the stable isotope analysis (plot A) to visualize that species with snout protrusion tend to exhibit higher values in δ^{13} C and/or δ^{15} N.

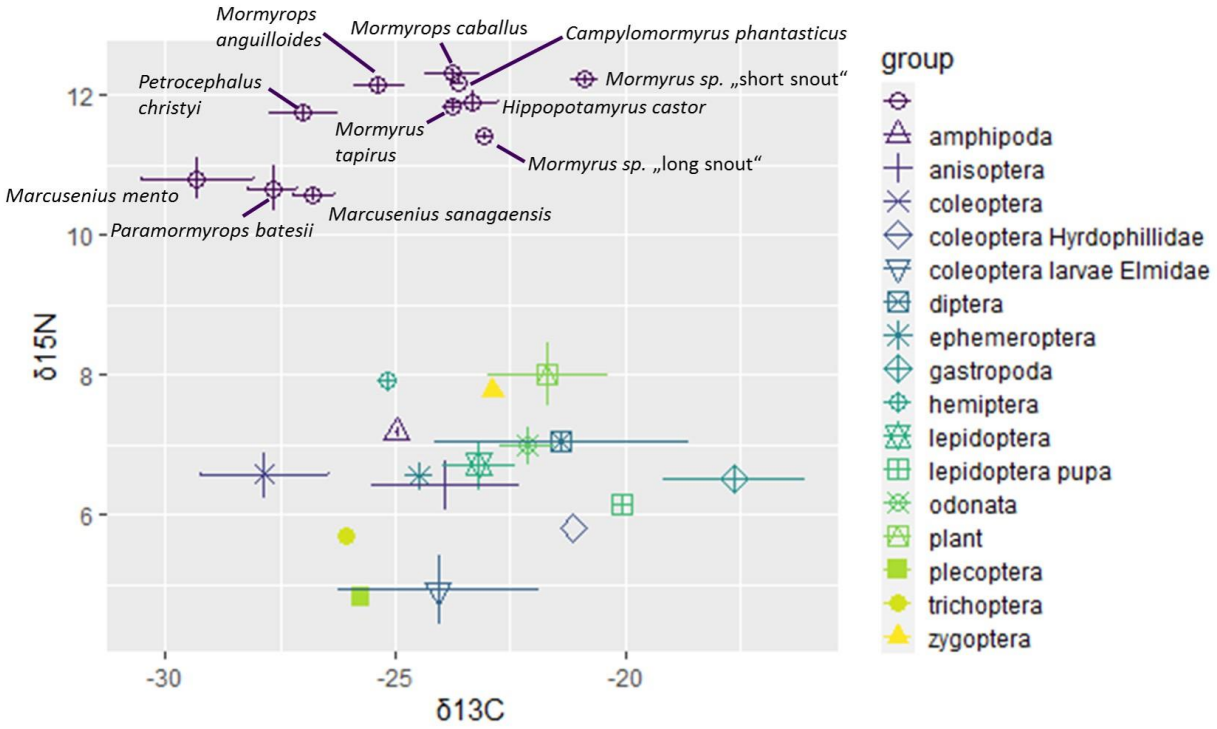

Figure 3: combined isotopes plot showing both the muscle isotope means and standard errors together with the trophic samples values. δ^{15} nitrogen values on the y-axis and δ^{13} carbon values on the x-axis; unit in parts per thousand (‰).

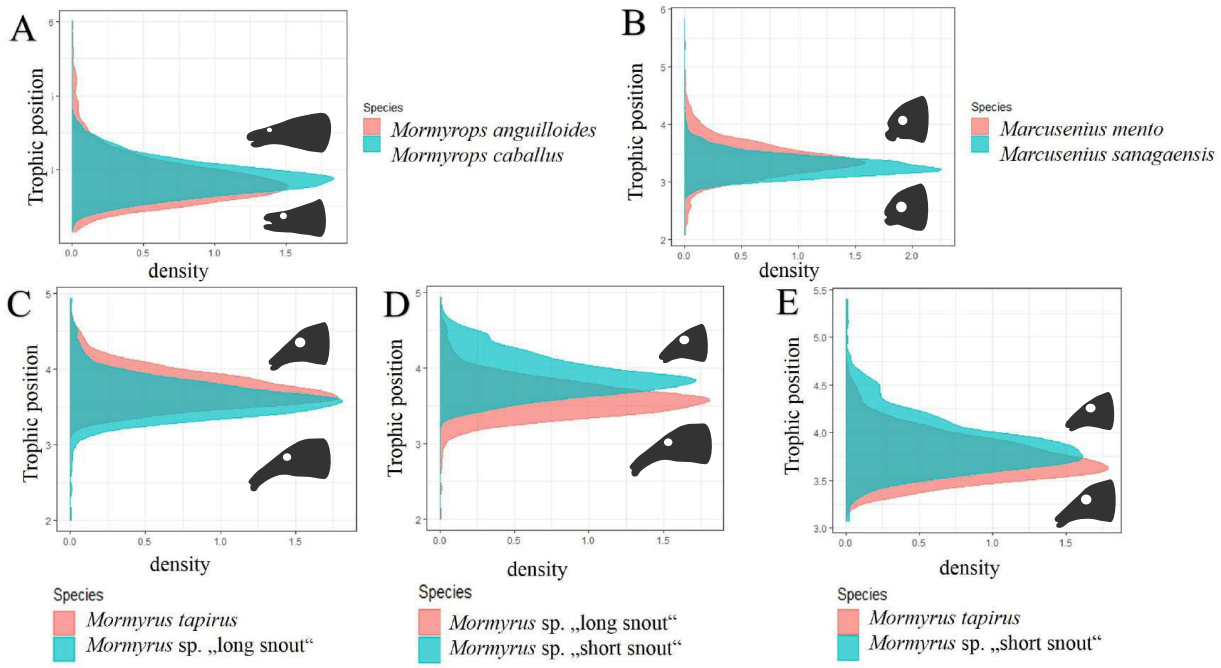

Figure 4: **TP (Trophic Position) plots comparing TPs between two species within one genus.** A) *Mormyrops anguilloides* vs. *Mormyrops caballus*, B) *Marcusenius sanagaensis* vs. *Marcusenius mento*. C)-E) Three species of *Mormyrus* show larger differences among themselves, and in this case species with shorter protrusion tend to have a higher trophic position. C) *Mormyrus tapirus* vs. *Mormyrus* sp. “short snout”, D) *Mormyrus* sp. “long snout” vs. *Mormyrus* sp. “short snout”, E) *Mormyrus tapirus* vs. *Mormyrus* sp. “long snout”. The baseline was generated from all benthic-sourced samples from the trophic samples.

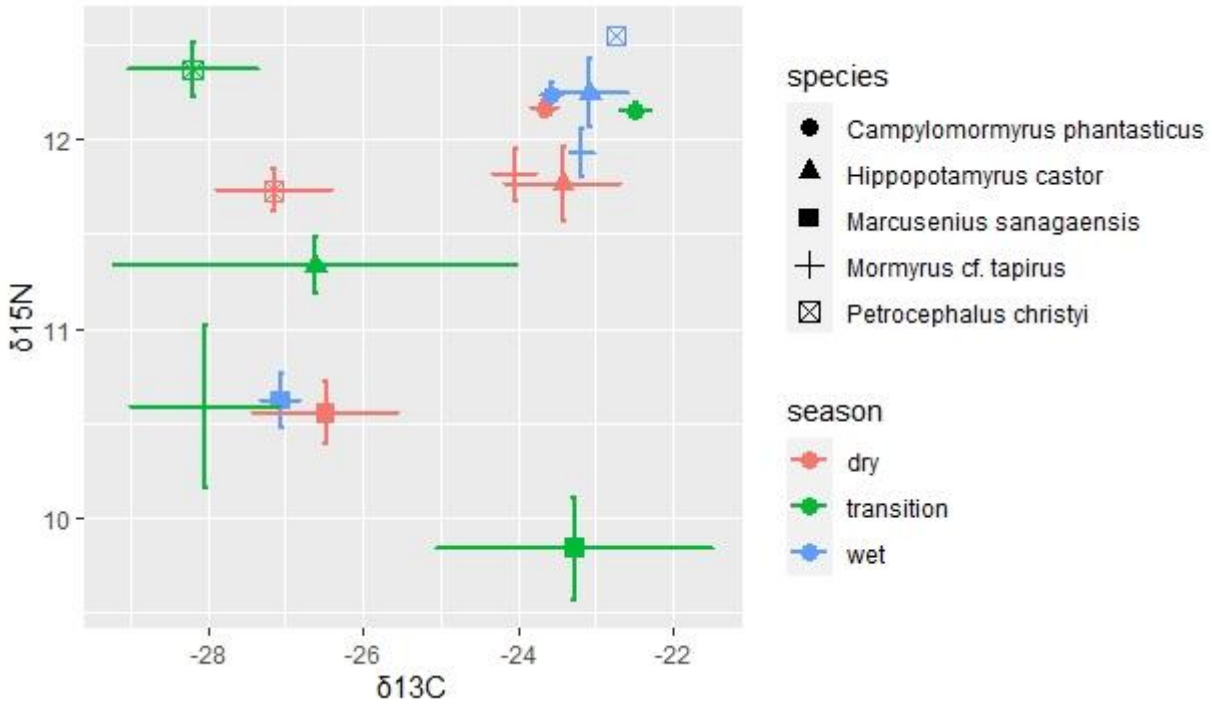

Figure 5: season impact plot of stable isotopes: plotted means and standard errors of five mormyrid species separated by wet (blue-coloured), dry (red-coloured) and transition (green-coloured) season. δ^{15} nitrogen values on the y-axis and δ^{13} carbon values on the x-axis; unit in parts per thousand (‰). Note that the *Petrocephalus christyi* wet sample is only one sample and thus no standard errors are available. The dry season is encompassing the months of February and March, the wet season the months August, September, October and November and the transition season the months of May, June and July.