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ADVANCES IN CICHLID RESEARCH III

The diverse prey spectrum of the Tanganyikan scale-eater *Perissodus microlepis* (Boulenger, 1898)

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Abstract Feeding upon the scales of other fish—lepidophagy—is a highly specialized foraging strategy in fish. Scale-eating is rare in teleosts, yet has evolved several times in East African cichlids, the most famous case being the Perissodini clade in Lake Tanganyika. Here, we examined the prey spectrum of the scale-eater *Perissodus microlepis* (Boulenger, 1898) via morphological assessment and targeted sequencing (barcoding) of ingested scales. We found that the size of the ingested scales, but not their number, correlates with the body size of scale-eaters. Sequencing of a segment of the mitochondrial ND2 gene in more than 300 scales revealed that *P. microlepis* feed upon a broad spectrum of prey species. In total, we detected 39 different prey species, reflecting the cichlid community in the rocky littoral zone of Lake Tanganyika. The most common prey were the algae-eaters *Petrochromis polyodon*, *Pe. ephippium*, *Eretmodus cyanostictus*, *Tropheus moorii*, and *Simochromis diagramma*, which make up more than half of the diet. The diversity of scales found within scale-eaters and the overall broad prey spectrum suggest that *P. microlepis* is an opportunistic feeder. Mouth-handedness and body color hue of the scale-eaters do not seem to have an influence on prey choice.

Keywords Cichlidae · Lake Tanganyika · Adaptive radiation · Barcoding · Lepidophagy

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Introduction

Lake Tanganyika, the oldest of the African Great Lakes, is home to a particularly diverse freshwater fauna with a great degree of endemism, including the morphologically, ecologically and genetically most diverse assemblage of cichlid fishes in Africa (Fryer & Iles, 1972; Salzburger et al., 2002, 2014). Within a period of about 10 million years, more than 200

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cichlid species have evolved in Lake Tanganyika, occupying a broad range of ecological niches (Koblmüller et al., 2008; Muschick et al., 2012; Meyer et al., 2017). Taxonomically, the Tanganyikan cichlid species have been grouped into 12–16 tribes, i.e., the taxonomic rank between the subfamily and genus level (Poll, 1986; Takahashi, 2003). The Tanganyikan cichlid tribes differ with respect to species numbers (one species in, e.g., Boulengerochromini to roughly 100 species in Lamprologini), breeding mode (mouthbrooding vs. substrate spawning), as well as the range of foraging strategies (see e.g., Koblmüller et al., 2008). One of the most peculiar feeding modes in cichlids from Lake Tanganyika is the scale-eating behavior of several members of the Perissodini tribe (Marlier & Leloup, 1954; Takahashi et al., 2007).

The strategy to forage on scales of other fishes ('lepidophagy') is known from a few species in a few fish families only (Sazima, 1983; Martin & Wainwright, 2013; Kolman et al., 2018). In Lake Tanganyika, however, there are six Perissodini species that more or less exclusively feed upon scales of other fish (Takahashi et al., 2007, 2016). To this end, scale-eaters ambush their prey from the rear, suddenly attack and bite out a single or a few scales together with epidermis from the flanks of their victims. Scale-eaters are a common component of the littoral fish communities in Lake Tanganyika (Hori et al., 1993) and show a number of adaptations with regard to their specific way of feeding including hook-like teeth, asymmetry of the mouth opening as well as aggressive mimicry (Liem & Stewart, 1976; Hori, 1993; Hori & Watanabe, 2000; Takahashi et al., 2007; Boileau et al., 2015). In particular the mouth dimorphism of scale-eaters has received considerable scientific attention, following Hori's initial report of negative frequency-dependent selection in *Perissodus microlepis* (Boulenger, 1898) (Hori, 1993; Indermaur et al., 2018; see below).

Perissodus microlepis (Fig. 1) is the most common of the Tanganyikan scale-eaters; it has a lake-wide distribution and occurs across all habitat types to a depth of up to 70 m (Takahashi et al., 2007; Konings, 2015). Two discrete morphs with respect to mouth morphology were recognized in *P. microlepis*, one with a mouth opening to the right side ('right morph'), and one to the left side ('left morph') (Hori, 1993). The mouth polymorphism in *P. microlepis* has long been implicated with a lateralized feeding behavior,

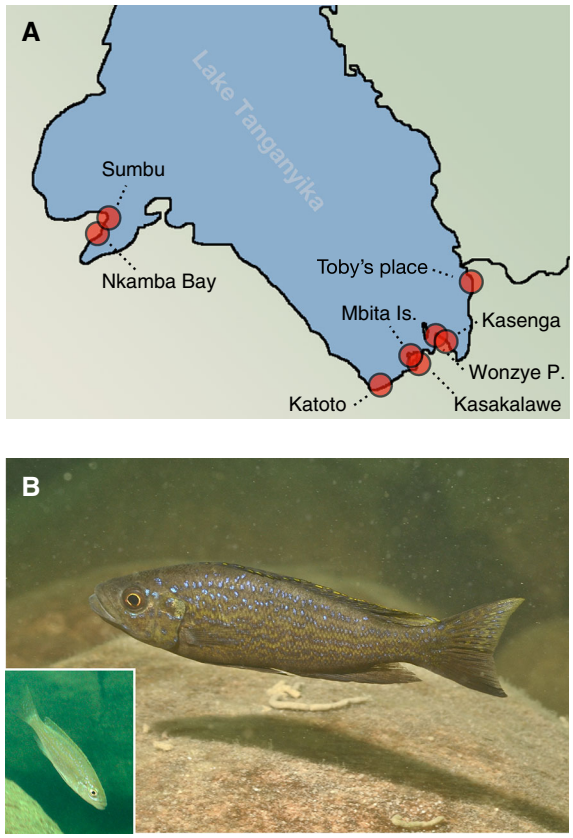

Fig. 1 Sampling location and study species. **A** Map of the southern part of Lake Tanganyika with the eight sampling locations. **B** *Perissodus microlepis* (dark morph; inset: light morph)

whereby the right morph attacks the left flank of prey fish and vice versa (Hori, 1993). This has later been confirmed experimentally (Van Dooren et al., 2010; Lee et al., 2012; Takeuchi et al., 2012; Takeuchi and Oda, 2017). More recently, it has been suggested that the angle of mouth opening is continuously distributed in *P. microlepis* instead of having two discrete modes (Kusche et al., 2012), whereas an analysis of lower-jaw bones by Takeuchi et al. (2016) revealed a bimodal distribution of mouth orientation. In addition to the polymorphism in mouth orientation, there is also a difference in body coloration in *P. microlepis*. Nshombo (1994) reported the existence of four different color morphs in *P. microlepis*, and found that these color morphs exhibit different attack strategies. Hori & Watanabe (2000), on the other hand, suggested that a local morph of *P. microlepis* found in the South of Lake Tanganyika characterized

by a yellow anal fin has adopted an aggressive mimicry strategy to feed upon Cyprichromini.

In this study, we examined the prey spectrum of the Tanganyikan scale-eater *Perissodus microlepis* using a DNA-barcoding approach. It has previously been suggested, based on direct observations in the field, that *P. microlepis* is an opportunistic feeder attacking a broad range of fish species (Nshombo et al., 1985; Hori et al., 1993); it has further been found that juvenile scale-eaters feed on copepods and become more and more specialized with age (Takeuchi et al., 2016). Similarly, in the scale-eater *Plecodus straeleni*, a diverse range of prey species has been found, in this case using a molecular approach to taxonomically assign ingested scales (Boileau et al., 2015). Here, we adopted the strategy of Boileau et al. (2015) and sequenced a fragment of the mitochondrial NADH Dehydrogenase Subunit II (ND2) gene in hundreds of scales extracted from the intestinal tracts of more than 100 specimens of *P. microlepis* collected in the South of Lake Tanganyika, following scale counts and the morphological classification of all scales. We then tested if the prey species spectrum correlated with mouth orientation (left vs. right) or body color hue (dark vs. light) of the scale-eaters.

Methods

Sampling

In total, we collected 203 adult specimens of *Perissodus microlepis* in the southern part of Lake Tanganyika in February and March 2010 under permits issued by the Lake Tanganyika Research Unit, the Department of Fisheries, Food and Agriculture, Republic of Zambia; and the Department of Immigration, Republic of Zambia. Fish were collected at eight sampling sites by means of gill-nets on SCUBA in a depth between 5 and 20 m (see Fig. 1A, Table 1, and Supplementary Table 1 for details). Specimens were photographed, weighed, sexed via inspecting their gonads, and measured for standard (SL) and total length (TL); we also determined, whenever possible, the mouth orientation (left vs. right) as well as body color hue (dark vs. light) on fresh specimens. The intestinal tract of each specimen was removed in the field and preserved in 96% ethanol; specimens were then individually labeled and preserved in 96% ethanol. Samples were transported to the Zoological Institute of the University of Basel for further analyses.

Table 1 Sampling information (see Supplementary Table 1 for details on the specimens)

Location	GPS coordinates		*N*
	South	East	
Kasakalawe	8.78098	31.08062	17
Kasenga	8.71525	31.14187	20
Katoto	8.80611	31.02666	20
Mbita Island	8.75323	31.08457	37
Nkamba Bay	8.5508	30.56622	30
Sumbu	8.55053	30.56622	5
Toby's Place	8.62323	31.20045	68
Wonzye Point	8.72519	31.13338	6

Scale morphological analysis and counting

The intestinal tracts of all collected specimens of *P. microlepis* were inspected in detail in the laboratory, using a Leica MZ75 stereomicroscope. Eighty-four intestinal tracts were empty or their stomach and gut contents were too digested to allow further assignment, leaving us with a total of 119 intestinal tracts for further inspections. Of these, 117 intestinal tracts contained exclusively fish scales, whereas in one stomach we found, in addition to scales, a fish eye and in another one a fish embryo. The scales recovered from these 119 intestinal tracts were photographed with a Leica DFC310 FX digital camera mounted on to a Leica M205FA stereomicroscope; scales were counted and sorted according to size (into four different quartiles, XS, S, M, and L), general morphology (ctenoid vs. cycloid), and pigmentation, following the criteria described in Kuusipalo (1998). Scales were then rinsed with ethanol and collected in separate 2 ml microcentrifuge tubes filled with 96% ethanol for molecular analyses via DNA barcoding.

DNA barcoding of scales

For DNA barcoding of scales recovered from the intestinal tracts of *P. microlepis*, we followed a modified version of the protocol described in Boileau et al. (2015). In short, we extracted DNA from

individual scales applying a phenol–chloroform-isoamyl alcohol precipitation following digestion in 180 µl 2× CTAB Buffer and 7.5 µl Proteinase *K* (10 mg/ml) overnight at 37°C and 300 rpm on an Eppendorf® Thermomixer compact. DNA quality was determined with a NanoDrop ND-1000 spectrophotometer (ThermoFisher Scientific).

For PCR amplification of a 407-bp-long section of the mitochondrial NADH Dehydrogenase Subunit II (ND2) gene, a standard marker in East African cichlid fish (e.g., Kocher et al., 1995; Salzburger et al., 2002, 2005), we used the primers ND2-327 (5′-CCC TCT TCA TGC TTG ACT CC-3′) and ND2-733 (5′-GGG GTG TGA GAG CTG TTA GG-3′) (Boileau et al., 2015). To avoid amplification of *P. microlepis* endogenous DNA, we added blocking oligonucleotides Perplex-488-blocH (5′-ctg GCC CTT GTT GGG GGC TGA ttt-3′) and Perplex-617-blocL (5′-aaa CAT AAT GAA GTA GGT AAG AAG GGT ctc-3′). These blocking oligonucleotides were designed to specifically anneal within the ND2 genes of several Tanganyikan scale-eaters of the tribe Perissodini including *P. microlepis* and *Plecodus straeleni* (Boileau et al., 2015) to inhibit the amplification of ND2 from those species. PCR was performed with the enzyme AmpliTaq (Applied Biosystems) on a Veriti® 96-well Thermal Cycler (Applied Biosystems) following the protocol described in Boileau et al. (2015); PCR products were then purified with ExoSAP-IT® (Affymetrix) and Sanger-sequenced on an ABI 3130*xl* genetic analyzer using the BigDye® 3.1 kit (Applied Biosystems). The sequences have been deposited on GenBank under the accession numbers MH275093–MH275427.

Sequence analysis and taxonomic assignments

Due to the close relatedness of the potential prey taxa, we used a combination of BLAST searches and phylogenetic analyses to assign the ND2 sequences derived from individual scales recovered from the intestinal tracts of *P. microlepis* to particular prey species (see Boileau et al., 2015). In a first step, individual sequences were inspected by eye with the software CodonCode Aligner v.3.7.1.1 (CodonCode Corporation). BLAST searches (BLASTN) were performed with BLAST + version 2.2.31 against GenBank's nucleotide collection (nr/nt) database (version December 2017) on the sciCORE computer cluster of the University of Basel. For phylogenetic analyses, the obtained sequences were assembled to a reference set containing sequence information of 180 species of cichlid fishes from Lake Tanganyika (Boileau et al., 2015; Meyer et al., 2015) using CodonCode Aligner. Maximum likelihood based phylogenetic analyses were performed with a heuristic search in Paup* 4.0a, build 159 (Swofford, 2002), applying the GTR+G+I model of molecular evolution and using the model parameters estimated from the data. The sequences obtained from ingested scales were assigned to a particular cichlid species whenever the best BLAST hit (according to BLAST score and *E*-value) was identical to the taxon with which the unknown sequence clustered in the phylogenetic tree. In cases where the best BLAST hit was shared between several sequences belonging to more than one species (usually a consequence of the short length of the query sequence), we used the phylogenetic clustering for taxonomic assignment. Sequences that could not be unequivocally assigned to a species according to this strategy were excluded from further analyses.

Statistical analyses

All statistical analyses were performed in R version 3.4.0. El Capitan build (7338) (R Development Core Team, 2008). In a first step, we used the scale-count information to test, via an ANCOVA in the R package Vegan version 2.4-5 (Oksanen et al., 2017), whether the number of scales in the intestinal tracts of scale-eaters is dependent on body size (analyzing SL and TL separately) and sex. In a second step, we used the size-class information of the ingested scales (XS, S, M, L) to test whether scale size correlates with the body size of the scale-eaters, again applying an ANCOVA and analyzing SL and TL separately. We then used the taxonomic assignment of the ingested scales based on DNA barcoding together with the information on mouth orientation (left vs. right) and body color hue (dark vs. light) of the scale-eaters, as well as on sampling location, to test whether there are differences in the prey spectrum with respect to mouth orientation, body color hue or sampling location. The latter test was performed as there is evidence for genetic structuring within *P. microlepis* in the South of Lake Tanganyika (Koblmüller et al., 2009). We used permutational multivariate analysis of variance on

distance matrices, as implemented in the adonis function of the R-package VEGAN. Distance matrices were generated from binary presence/absence data using the function vegdist with Raup-Crick dissimilarity index.

Results

In total, we recovered 10,749 scales in the intestinal tracts of 119 *P. microlepis* specimens (SL distribution of *P. microlepis* 53–115 mm; mean = 75.07 ± 9.65 mm). The number of scales per intestinal tract varied from 1 to 342 (median = 81; mean = 88.1 ± 70.1), which is in the range of what has been reported previously (Takeuchi et al., 2016). Based on morphological grounds (according to Kuusipalo, 1998), we classified the recovered scaled into 53 different scale types, without knowing their taxonomic identity at this stage. The number of scale types per intestinal tract varied from 1 to 16 (median = 5; mean = 5.9 ± 3.2).

On the basis of the scale counts per intestinal tract, we found that the number of scales ingested by a scale-eater did not depend on its body size (ANCOVA; *P*-value = 0.2378). However, we found that the size of the ingested scales correlated with the body size of the scale-eaters (*P*-value < 0.001). Note that no difference in standard or total length was found between male and female scale-eaters in our dataset (Wilcoxon test, SL: *P*-value = 0.6208, TL: *P*-value = 0.9416), so that we did not treat the sexes differentially in this analysis.

The DNA of 384 scales could successfully be amplified, of which 333 samples could successfully be sequenced. Despite the use of blocking primers, 107 sequences obtained from ingested scales matched *Perissodus* reference sequences, rendering it impossible to distinguish between endogenous contamination and potential prey on the basis of the data at hand. These sequences were consequently excluded from further analyses. Another twelve sequences were too short to allow the unambiguous taxonomic assignment to a single reference and were also excluded from further analyses. Thus, a total of 214 scales could be assigned to a particular prey species (in 194 cases based on both BLAST searches and phylogenetic analyses; see Supplementary Table 2).

Among the 214 scales from 88 intestinal tracts of *P. microlepis*, we identified a total of 39 prey species belonging to 8 different cichlid tribes (Fig. 2). According to our analyses, the five most common prey species of *P. microlepis* were *Petrochromis polyodon* (*N* = 37), *Pe. ephippium* (26), *Eretmodus cyanostictus* (20), *Tropheus moorii* (20) and *Simochromis diagramma* (15). These five species, which accounted for more than 50% of the scales found in the intestinal tracts of *P. microlepis*, are all herbivorous. The most commonly found prey species, *Pe. polyodon*, was also the only one detected at all of the eight sampling sites. At the tribal level, the by far most common prey of *P. microlepis* belonged to Tropheini/Haplochromini (*N* = 136; 12 different prey species) followed by the most species-rich tribe in Lake Tanganyika, Lamprologini (*N* = 25, 14 species), the Ectodini (*N* = 20; 6 species) and Eretmodini (*N* = 20; 1 species). Members of the Cyprichromini (*N* = 6; 2 species), Boulengerochromini (*N* = 2; 1 species), Limnochromini (*N* = 2; 1 species), and other Perissodini (*N* = 2; 2 species) were apparently infrequently attacked by *P. microlepis*.

The prey choice of individuals appeared to not be significantly correlated with body color (partial R^2: 0.006, *P* = 0.83), mouth orientation (partial R^2: 0.013, *P* = 0.50), or sampling location (partial R^2: 0.112, *P* = 0.14).

Discussion

In this study, we examined the prey spectrum of the Tanganyikan scale-eater *Perissodus microlepis*. To this end, we first counted and characterized the scales retrieved from the intestinal tracts of more than one hundred individuals of *P. microlepis* collected at eight sites in the southern part of Lake Tanganyika and then determined the sequence of a fragment of the mitochondrial ND2 gene of hundreds of individual scales to permit their taxonomic assignment to specific prey species.

The morphological examination of ingested scales as well as the molecular characterization of a subset of those revealed that the Tanganyikan scale-eater *P. microlepis* feeds upon a broad spectrum of prey species, as already reported by Nshombo et al. (1985) based on field observations. When applying the criteria established for Lake Malawi cichlids (Kuusipalo, 1998), we identified 53 different scale types among the 10,749 scales examined based on

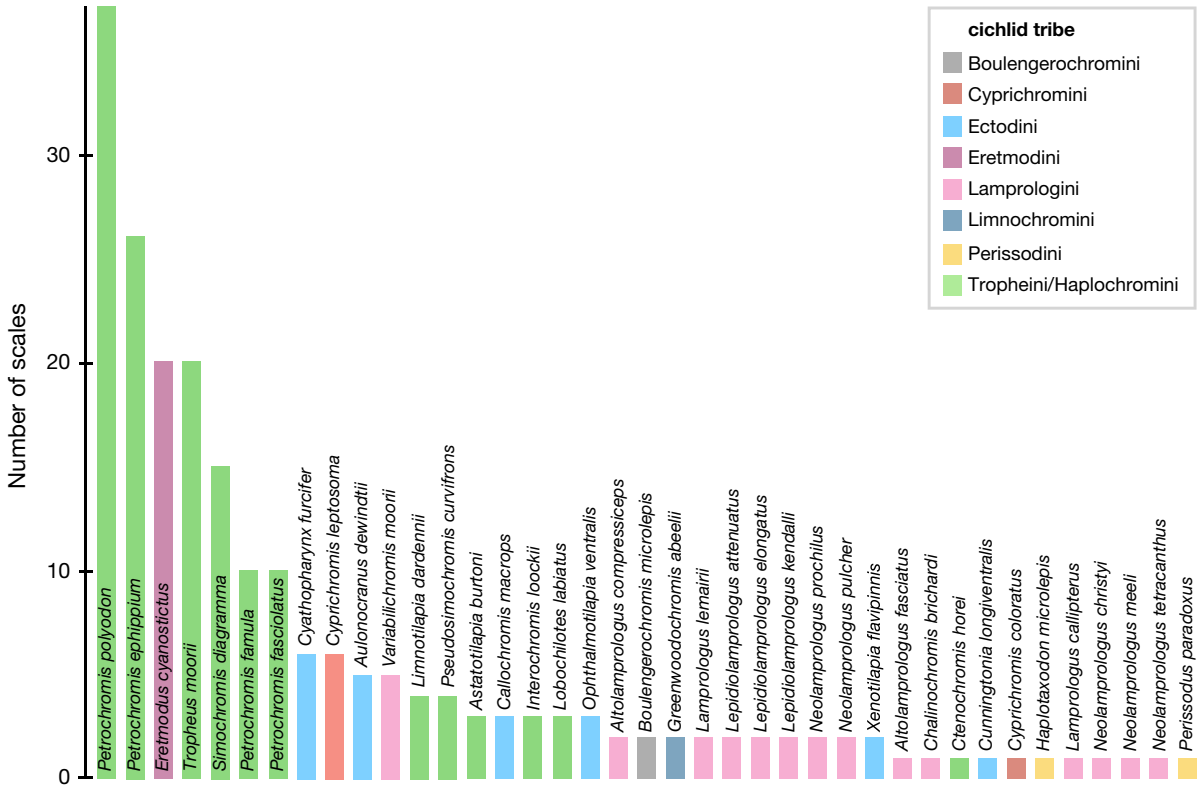

Fig. 2 The prey spectrum of the scale-eater *Perissodus microlepis* in the southern part of Lake Tanganyika. The bars indicate the number of scales extracted from the intestinal tracts of scale-eaters that were assigned to one of 39 different prey species by means of a molecular barcoding approach. The bars are color coded according to the tribe to which the respective species belongs

morphological grounds. The grouping of scales into scale types is not expected to directly correspond to prey species, since several types of scales differing in size and morphology can be found on a single Tanganyikan cichlid (Lippitsch, 1990, 1993). However, this high number already suggests a relatively broad prey spectrum. This was confirmed by the molecular characterization of ingested scales, which led to the identification of 39 different prey species belonging to 8 different cichlid tribes (Fig. 2).

The by far most common prey species belonged to the Tropheini, followed by Lamprologini, Ectodini and Eretmodini, whereas members of other tribes were only infrequently attacked. The prey spectrum of *P. microlepis*, thus, more or less reflects the community composition of cichlids in the rocky littoral zone of Lake Tanganyika (Hori et al., 1993; Muschick et al., 2012; Konings, 2015), where *P. microlepis* is most common. Interestingly, the prey spectrum of *P. microlepis* is rather similar to the one reported previously for another Tanganyikan scale-eater, *Plecodus straeleni* (Boileau et al., 2015). (Note, however, that in the present study, we did not perform additional PCR experiments that would permit detecting mastacembelid eels, which account for 23% of the scales in the intestinal tracts of *Pl. straeleni*.) An apparent difference between the prey spectra of *P. microlepis* and *Pl. straeleni* is that *P. microlepis* is more frequently feeding on *Eretmodus cyanostictus*, which usually occurs in relatively shallow waters (< 10 m). This somewhat reflects the distribution of the two scale-eating species in question: While overlapping in large parts of their depth distribution, *P. microlepis* is also common in shallow waters, where *Pl. straeleni* is rarely observed (Takeuchi et al., 2010).

Our analyses characterize the Tanganyikan scale-eater *P. microlepis* as a rather opportunistic feeder—both at the level of species and the level of individuals—with a broad spectrum of potential prey species. Furthermore, the fact that up to 16 different scale types

were present in a single intestinal tract and that neither the mouth orientation (left vs. right) nor the body color hue (light vs. dark) or the sampling location correlated with prey species, indicate that individual scale-eaters do not seem to be specialized toward a particular prey species. However, we found that the intestinal tracts of larger scale-eaters contain, on average, larger scales, which indicates that adult *P. microlepis* preferentially attack different size classes of prey species according to their own body size. No correlation was found between body size and the number of ingested scales. This is different to the findings of Takeuchi et al. (2016) who showed that the intestinal tracts of larger and more lateralized scale-eaters contained more scales. Note, however, that they inspected scales over a much larger range of body lengths including juveniles that feed on copepods, whereas we here focused on adult specimen only.

Both traits, mouth orientation and body color, could potentially influence the prey choice of *P. microlepis* individuals. Body color correlates with the preference for microhabitats (Nshombo, 1994), which presumably differ in their composition of potential prey. Such habitat preferences of color morphs also occur in other predatory cichlid species in Lake Tanganyika (Kohda and Hori, 1993). Mouth-handedness of *P. microlepis* has been shown to be under negative frequency-dependent selection (Hori, 1993). In a population of scale-eaters with an unbalanced frequency of the two morphs, the more frequent morph will soon be at a disadvantage as prey fish will guard more on the side they are attacked on more often, decreasing the success rate for that morph.

Overall, our study once more demonstrates that molecular barcoding of ingested material is a powerful tool to obtain information on prey composition in general (Symondson, 2002) and for scale-eating cichlids in particular (Boileau et al., 2015). It also shows that this approach is highly sensitive to local faunal differences. For example, we only detected scales of *Lepidiolamprologus kendalli* in the intestinal tracts of *P. microlepis* collected from the western shoreline of Lake Tanganyika, corresponding to the localities where *L. kendalli* occurs (see Konings, 2015). Likewise, we detected scales of the haplochromine *Astatotilapia burtoni* at a location for which we had previous evidence of its occurrence (Pauquet et al., 2018).

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