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Resource use by the facultative lepidophage *Roeboides affinis* (Günther, 1868): a comparison of size classes, seasons and environment types related to impoundment

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We report the consumption of scales and other food resources by the facultative lepidophage *Roeboides affinis* in the upper Tocantins River where it was impounded by the Serra da Mesa Hydroelectric Dam. We compared the diet among size classes, between dry and wet seasons, and between sites with distinct water flow characteristics (lotic *vs*. lentic) related to the distance from the dam and phase of reservoir development. As transparency and fish abundance increased after impoundment, we expected a higher consumption of scales in lentic sites. Likewise, habitat contraction, higher transparency and decrease in terrestrial resources availability, would promote a higher consumption of scales. Scales were consumed by 92% of individuals and represented 26% of the total volume of resources ingested by *R. affinis*. Diet composition varied significantly among size classes, with larger individuals consuming more scales and larger items, especially odonatans and ephemeropterans. Scale consumption was not significantly different between dry and wet seasons. *Roeboides affinis* incorporated some food items into the diet as a response to the impoundment, like other species. Scale consumption was higher in lotic sites, refuting our initial hypothesis, what suggests that the lepidophagous habit is related the rheophilic nature of *R. affinis*.

Caracterizamos o consumo de escamas e outros recursos alimentares por *Roeboides affinis*, um lepidófago facultativo, no alto rio Tocantins, na região represada pela Usina Hidrelétrica de Serra da Mesa. A dieta foi avaliada em relação a classes de tamanho, estações chuvosa e seca, e entre locais com características distintas de fluxo d'água (lótico *vs*. lêntico) relacionadas com a distância da barragem e fase de desenvolvimento do reservatório. Com o aumento da abundância de peixes e da transparência da água após o represamento, esperamos um maior consumo de escamas nos locais lênticos. Da mesma forma, na época seca, o habitat menor e mais transparente, além da redução da disponibilidade de itens terrestres, levaria a um maior consumo de escamas. Escamas foram consumidas por 92% dos indivíduos e representaram 26% do volume total de itens ingeridos por *R. affinis*. A composição da dieta variou significativamente entre classes de tamanho, com indivíduos maiores consumindo mais escamas e itens de maior porte, especialmente odonatas e efemerópteros. Não houve diferença no consumo de escamas entre as estações seca e chuvosa. *Roeboides affinis* incorporou itens à sua dieta como resposta ao represamento, a exemplo de outras espécies na bacia do alto rio Tocantins. O consumo de escamas foi maior nas localidades lóticas, contrariando a hipótese inicial e sugerindo que o hábito lepidofágico está ligado à natureza reofílica de *R. affinis*.

Key words: Diet, Hydrological regime, Impoundment, Scale-eating, Tocantins-Araguaya basin.

Introduction

Among the several forms of mutilation, defined as the habit of consuming parts of animals which are still alive, the consumption of scales is perhaps the most usual among fishes. Lepidophagy is a specialized feeding habit that has probably evolved independently several times along the evolutionary history of teleosts (Fryer & Iles, 1972; Gerking, 1994). Scale eaters include four freshwater and seven marine fish families which are not phylogenetically related (Sazima, 1983).

Roberts (1970) was the first to summarize information about the scale-eating habit of South American characiforms. Later, Sazima (1980), in his seminal work on the behavior of Neotropical lepidophagous fishes, categorized several levels of lepidophagy:

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obligatory, facultative, intermediate, and occasional. The evolutionary origin of lepidophagy may have arisen from either social or trophic causes, although these are not mutually exclusive, as suggested by Sazima (1983). Hypotheses related to a trophic origin include scraping of epilithic and epiphytic algae, ectoparasites removal, collection of food in several substrates including dead fish bodies, or predation, *i.e*., occasional ingestion of scales during unsuccessful attacks to smaller fish.

Morphological and behavioral features for scale consumption are more apparent for the Neotropical characids than for other fish also considered as lepidophages. Teeth projected outwards the mouth, such as those displayed by the characins of the genus *Roeboides*, are utilized to remove scales from other fish. *Roeboides* is the only polytypic genus of specialized scale-eaters, being widespread throughout the Neotropics and present in almost all major river basins (Sazima, 1983). The genus *Roeboides* (Characidae; subfamily Characinae) is formed of 21 species distributed in the Neotropical realm, from southern Mexico to La Plata basin, Argentina (Lucena & Menezes, 2003; Lucena, 2003). Lucena (1998) proposed the division of the genus into four monofiletic units. One of them is the *affinis*-group (subclade C in Lucena, 1998), with representatives in the basins of the rivers Amazonas, Orinoco, Paraguay-Paraná, São Francisco, Paranaíba, and Pindaré-Mearim, and also in the drainages of Guiana and Suriname. *Roeboides affinis* (Günther, 1868) is one of the nine species that compose this group, and, within the Brazilian territory, is distributed in the drainages of the rivers Paraguay-Uruguay, lower Paraguay, Amazonas, Orinoco and Tocantins-Araguaia (Lucena, 2007). This species was widely distributed in the upper Tocantins River previously to its impoundment by the Serra da Mesa Hydroelectric Dam (Dez 95 to Oct 96). During the first year after dam closure (Oct 96 to Oct 97) *R. affinis* became abundant in newly formed lentic sites (Iglesias-Rios, 2012), but after the completion of reservoir filling, fewer remaining individuals were restricted to the lotic sites upstream.

Fishes of the genus *Roeboides* are recognized as lepidophages. The degree of specialization on the consumption of scales, however, is reported to vary among species (*e.g*. Novakowski *et al*., 2004) or even within the same species seasonally (*e.g*. Peterson & Winemiller, 1997) or ontogenetically (*e.g*. Peterson & McIntyre, 1998; Novakowski *et al*., 2004). *Roeboides affinis* is considered a facultative lepidophage, and seasonal and ontogenetic variations, with larger individuals consuming more scales, have been recorded by Peterson & McIntyre (1998) in a seasonally flooded savanna in Venezuela.

In the present study we characterize the consumption of scales and other food resources by *Roeboides affinis* in the upper Tocantins River, which was impounded by the Serra da Mesa hydroelectric dam in 1996, and compare it among distinct size classes, and between seasons and sites with distinct characteristics of water flow (lotic *vs*. lentic) related to the distance from the dam and phase of reservoir development.

In the Tocantins River, the augmented flooded area was accompanied by an increase of fish abundance of about 500% after dam closure (Iglesias-Rios, 2012), probably because species were either attracted by the high availability of food resources (*e.g*. Albrecht & Pellegrini-Caramaschi, 2003; Albrecht *et al*., 2009) or were trapped during downstream movements. Individuals of *Roeboides* are active during the day (Sazima, 1980), and, as in lentic environments water transparency is higher, we expect that species that use visual cues to detect prey would be benefited. In the specific case of *R. affinis*, the encounter and consumption of scales would be facilitated by a better visualization and also by the augmented abundance of fishes registered after impoundment. Therefore, the comparison of lentic and lotic sites will enable the evaluation of impoundment effects upon the diet of this species. On the other hand, during the operation period, after filling completion, the fish abundance decreased but remained higher than in the pre-impoundment period (Iglesias-Rios, 2012). Thus, we expect that the percentage of scales consumption by *R. affinis* would vary between these two phases, in lentic sites.

Likewise, during the dry season, besides the higher transparency and fish densities, due to habitat contraction, both in lentic and lotic environments, the availability of allochthonous food resources is usually lower. Thus, we expect that the populations of *R. affinis* rely more on scales during the dry season. Nevertheless, seasonality would have less influence on lentic sites than on lotic sites, because water level oscillations do not follow the natural hydrological cycle but rather depend on the power operation scheme to generate energy. Seasonal changes in the availability of terrestrial sources for the ichthyofauna could be expected to be less pronounced in lentic than in lotic sites, because the volume/area relation is lower, thus the land-water ecotone supposedly has less influence in the reservoir.

Other studies have described the diet of *Roeboides* species in impounded rivers (*e.g*. Mèrona *et al*., 2001; Casatti *et al*., 2003; Novakowski *et al*., 2004), but none has explicitly examined the effects of impoundment upon the diet or scale consumption. We herein describe patterns of resource consumption, focusing on scales, by *Roeboides affinis* in lotic and lentic environments as related to the impoundment of the Tocantins River, without neglecting other potential sources of variation described in previous studies (ontogeny and seasonality), and aim to determine which of these factors are most influential on the patterns observed.

Material and Methods

Study area

The Tocantins River forms in the pre-Cambrian Brazilian Shield and flows for about 2400 km northwards up to Marajó Bay, where it waters into the Atlantic Ocean. In October 1996 the upper stretch of the Tocantins River was impounded by the Serra da Mesa Hydroelectric Dam, flooding an area of approximately 1,700 Km² after filling completion. With a volume of 54,4x10^9 m³ this is the largest reservoir in terms of storage capacity in Brazil (De Fillipo *et al*., 1999), located within the geographical coordinates 14°38'36"S 48°59'14"W and 14°03'57"S 48°29'37"W. A map of the study region can be found at Albrecht

& Pellegrini-Caramaschi (2003). Before the impoundment, the affected portion of the river was a succession of waterfalls, riffles and pools within steep banks, flowing through a hilly terrain covered by Cerrado vegetation. The region has a well-defined hydrological regime, with a rainy season from November to April, and a dry season from May to October.

Fish sampling

Fish collections were carried out as part of an environmental project entitled "Basic Studies on the Icthyofauna of Serra da Mesa Reservoir" (Goiás, central Brazil), which aimed to assess the responses of the ichthyofauna to the impoundment. The project encompassed three periods: pre-impoundment (Dec/1995 to Oct/ 1996), post-impoundment filling (Dec/1996 to Apr/1998) and post-impoundment operation (Jun/1998 to Feb/2000).

Fish were collected bimonthly with standardized sets of gill nets in 15 sites: five sites from the pre-impoundment period within the area that later would become the reservoir plus two sites upstream that remained lotic after impoundment (comprehending a total of 7 lotic sites) and 8 lentic sites within the reservoir area. We pooled data from all lotic sites to compare with all lentic sites, regardless of period, thus using a spatial comparison as a surrogate to investigate the effects of impoundment. On the other hand, temporal comparisons aimed to investigate the effects of the hydrological regime upon the diet of *R. affinis*, thus data for the wet and dry seasons were also pooled regardless of the period related to impoundment.

In the field lab, specimens of all caught species were identified, measured and weighed. Stomachs with content were removed and fixed in 5% formaldehyde for further analyses.

Voucher specimens of *Roeboides affinis* are deposited at Museu Nacional do Rio de Janeiro (MNRJ 15200) and at Laboratório de Ictiologia Sistemática, Universidade Federal do Tocantins, Porto Nacional (UNT 3271 to 3275).

Dietary Analyses

The stomach content of 155 specimens of *Roeboides affinis* was analyzed under a stereoscopic microscope. Food items were identified to the lowest taxonomic category and quantified through the volumetric and frequency of occurrence methods. Volumes of items consumed were quantified on a 1-mm-high transparent dish with a 1 x 1 mm grid beneath, as described in Albrecht & Pellegrini-Caramaschi (2003). For each stomach we also counted the number of scales and determined the percentage of scales related to other items by dividing the volume of scales by the sum of volumes of all food items.

We identified a total of 29 food items, that were grouped into coarser categories in order to avoid a large amount of zeroes in the matrices of relative volumes. Groupings aimed to embark rather ecological than taxonomic features. Thus, some categories might show a hierarchical relationship: for example, odonatans and ephemeropterans could be included within aquatic arthropods or pupae & larvae, but were *a priori* considered as a different category because the larger size of these nymphs could reveal patterns other than could be revealed if these items were merged to other smaller aquatic larvae or also to adult aquatic arthropods. Likewise, fish and scales were also separated, because patterns of lower or higher specialization on scale consumption could be masked.

Standard length of analyzed individuals ranged from 5.0 to 14.1 cm. For dietary comparison among size classes, specimens were assigned to classes of 2-cm intervals.

Data Analyses

A Correspondence Analysis (CA - Lepš & Šmilauer, 2003; Gotelli & Ellison, 2004) was performed to identify patterns of distribution of individuals in the resource use space, using the volumetric percentage matrix. Scores generated for the first axis were compared statistically for different size classes (five classes), seasons (dry *vs*. wet) and environment types (lotic *vs*. lentic). Scores were previously tested for normality (Shapiro-Wilks) and homogeneity of variances (Levene) and were arcsin square-root transformed. As even after transformation data did not meet the requirements for parametric statistics, non-parametric equivalents (Kruskall-Wallis and Mann-Whitney) were employed for comparisons (Zar, 2010).

To directly test for differences in the percentage of scales consumed, comparisons were made considering only this item. As data again did not meet the requirements of normality and homocedasticity even after transformation, we compared scale consumption among size classes with a Kruskall-Wallis test, and both seasons (dry *vs*. wet) and environment types (lotic *vs*. lentic) using Mann-Whitney. Therefore, the interaction among these categorical variables could not be tested (Zar, 2010). Additionally, scale consumption between the filling and operation phases, in lentic sites, was compared through a Mann-Whitney test.

A Spearman rank correlation was used to test for significant correlations between the standard length (L_s) of individuals and the amount of scales consumed (Zar, 2010).

All data analyses were performed in the R program version 2.14.1 (R-Development Core Team, 2012). The Correspondence Analysis (CA) was performed with the Vegan package version 2.0-2 (Oksanen *et al*., 2011).

Results

Scales were consumed by 92% of specimens and represented 26% of the overall diet volume of *Roeboides affinis* in the upper Tocantins River. These results are summarized on Table 1. From this percentage, 31% were cycloid scales, 3% ctenoids and 65% could not be identified due to a high degree of digestion. The number of scales per stomach ranged from 1 to 53, and in half of the stomachs analyzed, scales coalesced into a single mass. Scales shared the stomach content with other food items in 74% of individuals analyzed.

The distribution of *R. affinis* individuals within the diet space is shown on Fig. 1. The eigenvalues obtained for the first and second CA axes were 0.78 and 0.74, respectively.

Table 1. Volumetric percentage (VO%) and frequency of occurrence (FO%) of the food resources consumed by all individuals analyzed of *Roeboides affinis* from 12 sites in the upper Tocantins River, from 1995 to 2000.

	Lotic				Lentic			
	Dry		Wet		Dry		Wet	
Food items	VO (%)	FO (%)	VO (%)	FO (%)	VO (%)	FO (%)	VO (%)	FO (%)
Aquatic arthropods	11.7	36.8	12.2	31.0	14.5	70.6	8.7	60.0
Ephemeroptera nymphs	8.1	10.5	9.7	9.5	15.3	35.3	0.6	18.3
Fish	9.1	-	4.5	-	1.0	29.4	11.3	16.7
Microcrustaceans	-	31.6	-	21.4	9.4	20.6	9.8	3.3
Odonata nymphs	48.4	15.8	11.5	19.0	5.0	20.6	4.4	16.7
OM+S	1.6	52.6	-	19.0	1.9	23.5	6.5	15.0
Pupae & Larvae	7.3	5.3	6.3	2.4	27.3	14.7	26.7	15.0
Scales	12.3	47.4	50.2	66.7	16.4	41.2	19.1	65.0
Terrestrial arthropods	0.8	5.3	2.5	14.3	4.8	2.9	10.8	23.3
Vegetal debris	0.8	10.5	3.1	16.7	4.3	17.6	2.0	20.0
Total number of individuals	19		42		34		60	

The graphical representation of the CA differentiates four groups based on statistical comparisons of the scores on axis 1: Diet composition varied significantly between lentic and lotic sites (U = 1735; p< 0.001) and among size classes (H = 17.41; df = 4; p = 0.001). The first three classes (5.0 to 8.9 cm) were different from the two larger classes (9.0 to 14.1 cm); thus we grouped this five categories into only two distinct groups thereafter (Group 1 and Group 2, respectively). No significant differences in diet composition were found between dry and wet seasons (U = 3105.5; p = 0.13).

Extreme positive scores on axis 1 were associated to the consumption of Odonata and Ephemeroptera nymphs (Table 2), ordaining most larger-sized individuals (Group 2) from lotic sites on the lower right corner of the graph. Scales were consumed by most individuals of all groups, thus had intermediate scores. Smaller-bodied individuals (Group 1) had the broadest diet, especially in the lentic environment, showing the most widespread distribution within the diet space (Fig. 1). Negative scores on axis 1 were associated to arthropods, both terrestrial and aquatic, which were consumed mainly by smaller-bodied individuals of both lentic and lotic sites.

On axis 2, positive scores were associated to the consumption of terrestrial arthropods, fish and MO+S, whereas negative scores, to aquatic arthropods. Individuals from lotic sites were ordained mainly within the lower quadrant of the graph (Fig. 1). Statistical comparisons of axis 2 scores yielded differences between dry and wet seasons (U = 1692.5; p< 0.001).

When scale consumption was analyzed separated from other food resources, significant differences between lentic and lotic sites were found (U = 706: p = 0.01), with individuals from the latter consuming more scales. On the contrary, comparisons between seasons (U = 678.5; p = 0.22) or among size classes (H = 0.67; df = 4; p = 0.95) did not yield significant differences. The comparison between the post-impoundment phases in the lentic sites (filling *vs*. operation) was marginally significant (U = 17; p = 0.0727). Box-plots with median values are shown on the panel (Figs. 2 a-d).

As the distribution of smaller-sized individuals (Group 1) was skewed by lentic sites, we ran the same analysis including only those individuals to check if differences were related rather to size class than to environment type. As this comparison remained significant, with Group-1 individuals in lotic sites consuming more scales than Group-1 individuals from lentic sites (U = 142,5; p = 0,03036), differences can be attributed to environment type rather than an artifact of biased samples.

No correlation was demonstrated between the standard length and the amount of scales consumed by individuals of *R. affinis* (r = 0.015; p = 0.88).

Discussion

Roeboides affinis was confirmed as a facultative lepidophagous fish in the upper Tocantins River. Most individuals consumed scales, but its volumetric contribution was relatively low and variable according to the factors herein examined (size, season and water flow characteristics). As expected, larger individuals tended to consume more scales, albeit not proportionally, *i.e.*, no correlation was found between the size of individuals and scale consumption. A larger consumption of scales was also found in lotic sites, even by smaller individuals, contradicting our initial expectations. Likewise, more scales were consumed during the flood season, albeit not significantly. Patterns of overall resource consumption also differed between lotic and lentic sites and between size classes.

Scales might be present within the stomach content of fishes for several reasons, such as remains of a fish swallowed whole or in chunks, removal from live or dead fish, or because they were picked from the bottom. Thus, it is not always straightforward to determine the origin of scales present in stomach contents (Goulding *et al*., 1988). On the other hand, behavioral studies alone might also lead to equivocal conclusions (*e.g*. Lima *et al*., 2012). Species belonging to several trophic guilds were reported to consume scales in the upper Tocantins River (Albrecht, 2005). Examples are the omnivores *Leporinus friderici* (Bloch, 1794) (Albrecht & Caramaschi, 2003) and *L. taeniofasciatus* Britski, 1997 (Albrecht & Pellegrini-Caramaschi, 2003), which probably picked scales from the bottom substrate as part of dead animals, and, naturally, the fin-nipper piranhas *Serrasalmus*

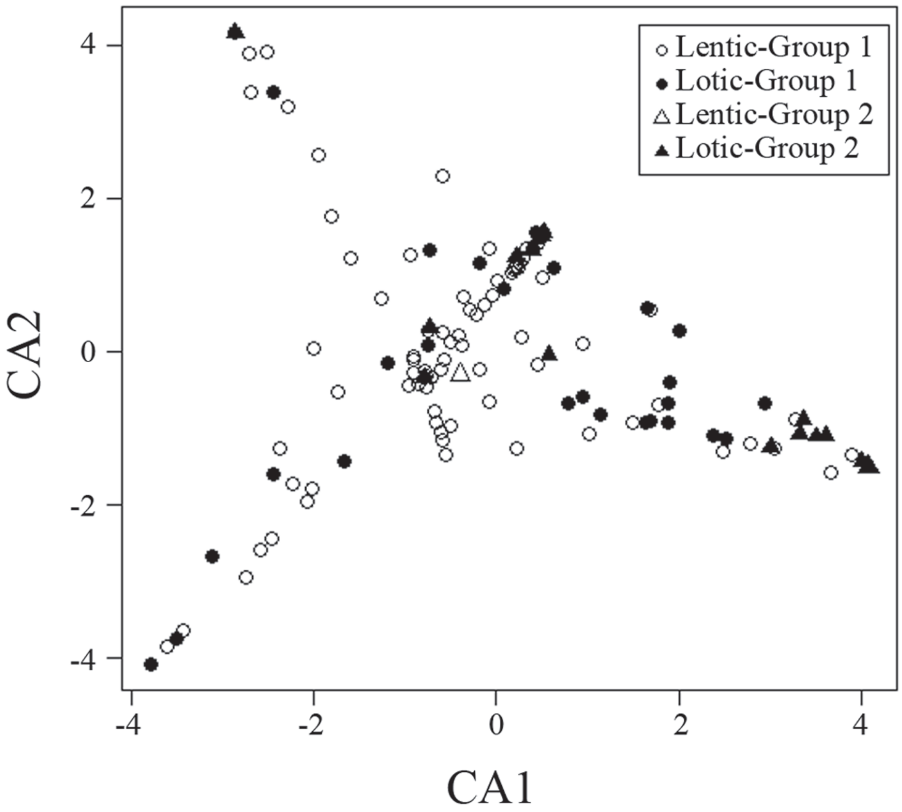

Fig. 1. CA ordination of 155 individuals of *Roeboides affinis* of two groups formed by five size classes (Group1, n = 33, and Group 2, n = 22) according to the consumption of food items (volumetric proportions) in the upper Tocantins River in two environment types (Lotic, n = 61, *vs*. Lentic, n = 94) related to its impoundment by the Serra da Mesa Hydroelectric Dam, from 1995 to 2000.

rhombeus (Linnaeus, 1766) and *S. eigenmanni* (Norman, 1929) (Albrecht et al., 2012). Scale consumption was also registered for some species as diverse as siluriforms of the family Trichomycteridae (Goulding *et al*., 1988) and characiforms of the genus *Astyanax* (Vilella *et al*., 2002) in environments as different as the Negro River in the Amazon and an Atlantic Forest stream in subtropical Brazil, respectively.

The reason why many species consume scales remains unclear, but it probably involves energetic value. Energy content per dry mass unit of fish scales is approximately two-thirds of that in the whole fish (Nico & De Morales, 1994). The chemical composition of scales is about 41-84% organic protein, such as collagen and ichthylepidin, and up to 59% is bone, mostly $Ca_3(PO_4)_2$ and $CaCO_3$ (Helfman *et al*., 2009). The mucus could also be an important energy source associated to the consumption of scales (Lewis, 1970). Goulding *et al*. (1988) suggest that in nutrient-poor rivers, such as the Negro River, several fishes consume scales as a complementary nutrient source. On the other hand, Wagner *et al*. (2009) found that two african scale-eater cichlids, although feeding as high as piscivores in the food web, had overall longer intestines. Scales are supposedly more difficult to digest than muscle, thus a longer intestine is needed for appropriate extraction of nutrients and energy from their scale-based diet. Scales are digested as they pass along the digestive canal. In the stomach, scales sometimes are found as a coalescent and scarified mass, like observed for *R. affinis*, and are reduced to a shapeless pulp when excreted.

For lepidophages, target scales are located on the prey flank or at the fin base, and the activity consists in butting,

Table 2. Variables (food items) scores in the first two axes of the CA ordination of individuals of *Roeboides affinis* from 12 sites in the upper Tocantins River, from 1995 to 2000. Scores are organized from the highest to the lowest on axis 1.

	CA1	CA2
Aquatic arthropods	-3.79	-4.09
Ephemeroptera nymphs	1.931	-1.011
Fish	-0.763	0.269
Microcrustaceans	-0.559	-1.399
Odonata nymphs	4.081	-1.509
OM+S	-2.025	0.248
Pupae & larvae	-0.792	-0.343
Scales	0.52	1.54
Terrestrial arthropods	-2.864	4.17
Vegetal debris	-0.367	0.106

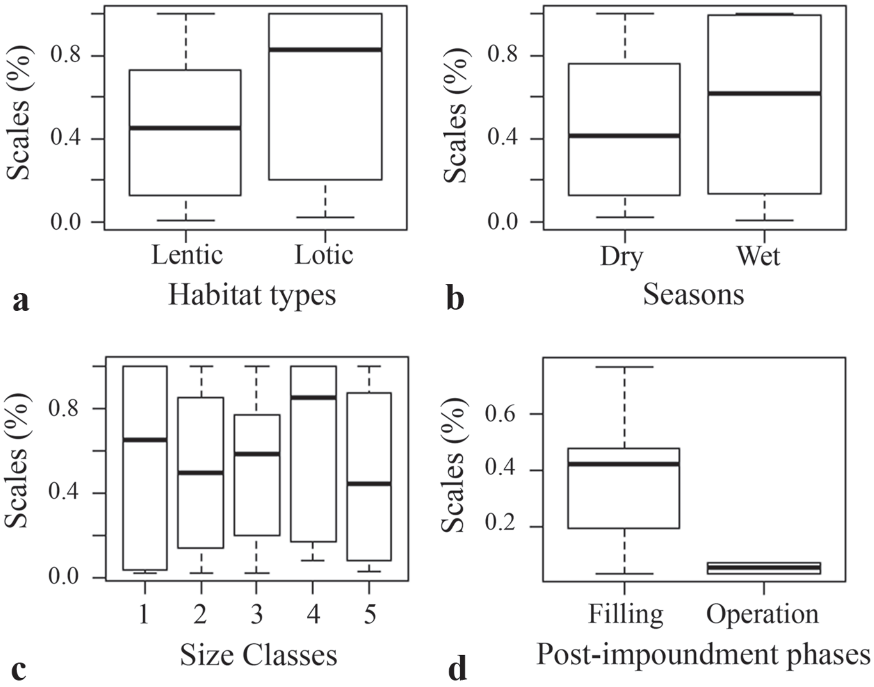

Fig. 2. Medians of percentage volume of scales consumed by *Roeboides affinis* in the upper Tocantins river, from 1995 to 2000, in: (**a**) different environmental types (Lotic, n = 38, *vs*. Lentic, n = 52); (**b**) seasons (Dry, n = 25, *vs*. Wet, n = 68); (**c**) size classes 1 (n = 12), 2 (n = 38), 3 (n = 26), 4 (n = 9) and 5 (n = 5) and (**d**) different post-impoundment phases (Filling, n = 9, *vs*. Operation, n = 2) in lentic sites.

biting or rasping the scales (Sazima, 1983). The prey (or "host") is not injured, as scales are regenerated in a few weeks. Therefore, scales represent an abundant and easily renewable energy source (Nico & Taphorn, 1988). Scales usually stem from several species, different from that of the predator (Gerking, 1994). The variety of sizes, forms and coloration of scales often found within the same stomach of several individuals of *R. affinis* herein analyzed, corroborate this observation.

The stomach of scale-eaters might contain a variety of food items. *Exodon paradoxus* had fish scales filling 88% of stomach contents in sandbank habitats in the Tocantins River drainage (Pereira *et al*., 2007). More than 50% of the stomach contents of the highly specialized *Roeboides prognathus* (Boulenger, 1895) (= *Roeboides affinis*) analyzed by Sazima (1980) contained only scales, whereas the other half had also insects, mainly Trichoptera larvae, and adult Naucoridae and Diptera. *Roeboides thurni* Eigenmann, 1912 (= *Roeboides affinis*) was reported to eat upon fish (58%), terrestrial invertebrates (21%) and aquatic invertebrates (21%) in the lower Tocantins River before its impoundment by the Tucuruí dam (Mèrona *et al*., 2001). Pereira *et al*. (2007) reported a diet based on terrestrial insects (43%) and fishes (42%) for *R. affinis* in sandbank habitats in the middle stretch of the Tocantins River drainage. In the upper Tocantins River, a little more than one fourth of the volumetric percentage was comprised of scales in the diet of all populations of *R. affinis* analyzed. Immature insects (pupae & larvae), Odonata and Ephemeroptera nymphs, other aquatic arthropods and fish were also important items in the overall diet of *R. affinis*.

Novakowski *et al*. (2004) show that morphological features influenced the amount of scales consumed by three *Roeboides* species [*R. paranensis* Pignalberi, 1975 (= *R. descalvadensis*), *R. prognathus* (= *R. affinis*) and *R. microlepis* (Reinhardt, 1851)], in lotic and lentic sites within the area of Manso Reservoir, Mato Grosso (Midwestern Brazil). The ontogenetic development of individuals was accompanied by the migration of teeth outside the mouth, leading to an increase in scale consumption.

Diet shifts as individuals grow larger are a major feature of fish ecology across several feeding guilds (*e.g*. Horn, 1989; Novaes *et al*., 2004; Albrecht *et al*., 2009), and it seems not to be different in fish with specialized feeding habits, such as the lepidophages (*e.g*. Nshombo *et al*., 1985; Peterson & McIntyre, 1998; Novakowski *et al*., 2004). In fact, larger *R. affinis* individuals had a distinct diet in the upper Tocantins River, with a higher consumption of large aquatic nymphs (odonatans and ephemeropterans) and also a higher relative amount of scales. Nevertheless, no correlation was observed between fish size and scale consumption, contrary to what was observed for *R. affinis* in the Venezuelan *llanos* (Peterson & McIntyre, 1998).

Roeboides affinis displayed seasonal differences in its overall diet in the Tocantins River, driven mainly by the relative consumption of terrestrial *vs*. aquatic arthropods, but not by scale consumption. Contrasting results were obtained for *Roeboides dayi* (Steindachner, 1878) and the Asian scale-eater glassfish *Chanda nama* Hamilton, 1822 regarding seasonal comparisons in scale consumption, although both species seem to have benefited from higher fish densities: *R. dayi*, from the augmented fish densities due to habitat contraction in the dry season (Peterson & Winemiller, 1997), while *C. nama* especially from higher densities of juveniles only, because of the higher fish recruitment during the rainy season (Grubh & Winemiller, 2004).

Tropical rivers are prone to great seasonal variations, hence not favoring the evolution of specializations and selecting broader niches, with most fish displaying high feeding plasticity (Lowe-McConnell, 1987). On the other hand, the great variation observed in aquatic habitats and the resources they contain, provides Neotropical fishes with many avenues for interspecific niche diversification through resource specialization (Peterson & Winemiller, 1997). Lepidophagy is considered a highly specialized feeding habit, although scales are probably complemented by other kinds of food (Sazima, 1983), as herein shown for *R. affinis*. Specialization implies an evolved morphological or physiological adaptation to use a specific resource, whereas in a more ecological view, specialization might simply imply the act of consuming a relatively limited fraction of the range of available resources (Bolnick *et al*., 2003).

Roeboides affinis showed variations in the proportional consumption of scales according to environment type. Populations from the remaining lotic sites upstream consumed more scales than those from the reservoir, contrary to what was hypothesized. The highly augmented fish abundance after impoundment accompanied the expansion of the water body (Iglesias-Rios, 2012), so possibly fish density was not proportionally much higher than before. Contrary to what was previously expected, transparency could have exerted a negative influence on the predatory capacity of *R. affinis*. Scale eating implies that prey might be larger than the predator, so the latter needs to cope with the high mobility and possible counterattack by its prey (Sazima, 1983). Furthermore, since lepidophagy does not kill the prey, prey fishes might learn to avoid predators. Therefore, a higher transparency could have jeopardized attack strategies by *R. affinis* rather than eased encounter of prey. Also, individuals found in lentic sites were smaller than those from lotic sites. The colonization of the reservoir area by younger individuals was demonstrated also for other species in the upper Tocantins River (*e.g. Brycon gouldingi* Lima, 2004 and *B. falcatus* Müller & Troschel, 1844), which grew and gained weight within the reservoir area during the heterotrophic phase (Albrecht *et al*., 2009), i.e., a phase of high productivity that typically occurs soon after impoundment as a result of the incorporation of allochthonous materials, liberation of nutrients from the soil, and decomposition of the flooded vegetation (Margalef, 1983; Petrere & Ribeiro, 1994).

Notwithstanding, if *R. affinis* did not respond to impoundment by increasing the consumption of scales as previously hypothesized, other changes in overall diet were detected. Planktonic microcrustaceans and terrestrial arthropods were more important in the diet of *R. affinis* in the reservoir. This response was also shown by the invertivorous catfish *Auchenipterus nuchalis* (Spix & Agassiz, 1829) and other fish species (Albrecht *et al*., 2012). *Roeboides affinis* has shown to be a facultative lepidophage in the Tocantins River, with a differentiated consumption of scales depending especially on ontogeny and water flow characteristics. We suggest that the lepidophagic activity of this species is related to its rheophilic features, *i.e*., it involves specialized senses and behavior that have developed in the fast current waters of the embanked Tocantins River. Contrary to the scale-eating specialization among Perissodini cichlids, hypothesized to have arisen in deep water habitats in the African Great Lakes (Takahashi *et al*., 2007; Koblmüller *et al*., 2007), the origin of lepidophagy among the characids might have occurred in lotic waters. More comprehensive comparative studies within a phylogenetic framework upon the diet of scale eater characids could probably shed light on the evolution of this specialized feeding habit in the Neotropical region.

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Literature Cited

Albrecht, M. P. 2005. Estrutura trófica da ictiofauna do rio Tocantins na região sob influência da usina hidrelétrica Serra da Mesa, Brasil Central. Unpublished Ph.D. Dissertation, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 194p.

Albrecht, M. P. & E. P. Caramaschi. 2003. Feeding ecology of *Leporinus friderici* (Teleostei: Anostomidae) in the upper Tocantins River, Central Brazil, before and after installation of a hydroelectric plant. Studies on Neotropical Fauna and Environment, 38: 33-40.

Albrecht, M. P., E. P. Caramaschi & M. H. Horn. 2009. Population responses of two omnivorous fish species to impoundment of a Brazilian tropical river. Hidrobiologia, 627: 181-193.

Albrecht, M. P. & E. Pellegrini-Caramaschi. 2003. Feeding ecology of *Leporinus taeniofasciatus* (Characiformes: Anostomidae) before and after installation of a hydroelectric plant in the upper rio Tocantins, Brazil. Neotropical Ichthyology, 1: 53-60.

Albrecht, M. P., C. Brazil-Souza, J. R. Pereira, D. C. O. Rosa, R. Iglesias-Rios & E. P. Caramaschi. 2012. Uso de recursos alimentares e estrutura trófica da ictiofauna antes e depois do represamento. Pp. 167-210. In: Mazzoni, R., E. P. Caramaschi & R. Iglesias-Rios (Eds.). Usina Hidrelétrica de Serra da Mesa: 15 anos de estudos da ictiofauna do Alto Tocantis. Rio de Janeiro: FURNAS.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey & M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist, 161: 1-28.

Casatti, L., H. F. Mendes & M. Ferreira. 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana reservoir, Paranapanema river, Southeastern Brazil. Brazilian Journal of Biology, 63: 213-222.

De Filippo, R., E. L. Gomes, J. Lenz-César, C. B. P. Soares & C. F. S. Menezes. 1999. As alterações da qualidade da água durante o enchimento do reservatório de UHE Serra da Mesa - GO. Pp. 323-345. In: Henry, R. (Ed.). Ecologia de reservatórios: estrutura, função e aspectos sociais. FAPESP/Fundibio: Botucatu.

Fryer, G. & T. D. Iles. 1972. The Cichld fishes of the great lakes of Africa. Edinburgh: Oliver & Boyd.

Gerking, S. D. 1994. Feeding ecology of fish. San Diego, Academic Press.

Gotelli, N. J. & A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Sunderland, Massachusetts, USA.

Goulding, M., M. Leal Carvalho & E.G. Ferreira. 1988. Rio Negro: rich life in poor water. The Hague: SPB Academic Publishing.

Grubh, A. R. & K. O. Winemiller. 2004. Ontogeny of Scale Feeding in the Asian Glassfish, *Chanda nama* (Ambassidae). Copeia, 2004: 903-907.

Helfman, G. S., B. B. Collette, E. D. Facey & B. W. Bowen. 2009. The diversity of fishes: biology, evolution and ecology. Oxford: Backwell Science.

Horn, M. H. 1989. Biology of marine herbivorous fishes. Oceanography and Marine Biology Annual Review, 27: 167-272.

Iglesias-Rios, R. 2012. Estrutura das comunidades de peixes antes e depois do represamento. Pp. 287-337. In: Mazzoni, R., E. P. Caramaschi & R. Iglesias-Rios (Eds.). Usina Hidrelétrica de Serra da Mesa: 15 anos de estudos da ictiofauna do Alto Tocantins. Rio de Janeiro: FURNAS.

Koblmüller, S., B. Egger, C. Sturmbauer, K. M. Sefc. 2007. Evolutionary history of Lake Tanganyika's scale-eating cichlid fishes. Molecular Phylogenetics and Evolution, 44: 1295-1305.

Lepš, J. & P. Šmilauer. 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge, UK.

Lewis R.W. 1970. Fish cutaneous mucus: a new source of skin surface lipids. Lipids, 5: 947-949.

Lima, M. R. L., E. Bessa, D. Krinski & L. N. Carvalho. 2012. Mutilating predation in the Cheirodontinae *Odontostilbe pequira* (Characiformes: Characidae). Neotropical Ichthyology, 10: 361-368.

Lowe-McConnel, R. H., 1987. Ecological studies in tropical fish communities. Cambridge University Press: Cambridge.

Lucena, C. A. S. 1998. Relações filogenéticas e definição do gênero *Roeboides*, Günther (Ostariophysi; Characiformes; Characidae). Comunicações do Museu de Ciências e Tecnologia da PUCRS, Série Zoologia, 11: 19-59.

Lucena, C. A. S. 2003. Revisão taxonômica e relações filogenéticas das espécies de *Roeboides* grupo-*microlepis* (Ostariophysi, Characiformes, Characidae). Iheringia, 93: 283-308.

Lucena, C. A. S. 2007. Revisão taxonômica das espécies do gênero *Roeboides* grupo-*affinis* (Ostariophysi, Characiformes, Characidae). Iheringia, 97: 117-136.

Lucena, C. A. S. & N. A. Menezes. 2003. Subfamily Characinae (Characins, Tetras). Pp. 200-208. In: Reis, R. E., S. O. Kullander & C. J. Ferraris (Eds.). Check list of the freshwater fishes of South and Central America. EDIPUCRS, Porto Alegre.

Margalef, R. 1983. Limnología. Barcelona*:* Ed. Omega.

Mérona, B., G. M. dos Santos & R. G. de Almeida. 2001. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Environmental Biology of Fishes, 60: 375-392.

Nico, L. G. & M. de Morales. 1994. Nutrient content of piranha (Characidae, Serrasalminae) prey items. Copeia, 1994: 524-528.

Nico, L. G. & D. C. Taphorn. 1988. Food habits of piranhas in the low llanos of Venezuela. Biotropica, 20: 311-321.

Novaes, J. L. C., E. P. Caramaschi & K. O. Winemiller. 2004. Feeding of *Cichla monoculus* Spix, 1829 (Teleostei: Cichlidae) during and after reservoir formation in the Tocantins River, Central Brazil. Acta Limnologica Brasiliensia, 16: 41-49.

Novakowski, G. C., R. Fugi & N. S. Hahn. 2004. Diet and dental development of three species of *Roeboides* (Characiformes: Characidae). Neotropical Ichthyology, 2: 157-162.

Nshombo, M., Y. Yanagisawa & M. Nagoshi. 1985. Scale-eating in *Perissodus microlepis* (Cichlidae) and change of its food habits with growth. Japanese Journal of Ichthyology, 32: 66-73.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens & H. Wagner. 2011. Vegan: Community Ecology Package. R package version 2.0-2. Available from: http://CRAN.R-project.org/package = vegan/ (27 June 2012).

Pereira, P. R., C. S. Agostinho, R. J. Oliveira & E. E. Marques. 2007. Trophic guilds of fishes in sandbank habitats of a Neotropical river. Neotropical Ichthyology, 5: 399-404.

Peterson, C. C. & K. O. Winemiller. 1997. Ontogenetic diet shifts and scale-eating in *Roeboides dayi*, a Neotropical characid. Environmental Biology of Fishes, 49: 111-118.

Peterson, C. P. & P. McIntyre.1998. Ontogenetic diet shifts in *Roeboides affinis* with morphological comparisons. Environmental Biology of Fishes, 53: 105-110.

Petrere, J. R. M. & M. C. L. B. Ribeiro. 1994. The impact of a large tropical hydroelectric dam: the case of Tucuruí in the middle river Tocantins. Acta Limnologica Brasiliensia 5: 123-133.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org/ (27 June 2012).

Roberts, T.R. 1970. Scale-eating American characoid fishes, with special reference to *Probolodus heterostomus*. Proceedings of the California Academy of Sciences. 38: 383-390.

Sazima, I. 1980. Estudo comparativo de algumas espécies de peixes lepidófagos (Osteichthyes) (A comparative study of some scale-eating fishes). Unpublished Ph.D. Dissertation, Universidade de São Paulo, São Paulo. 264p.

Sazima, I. 1983. Scale-eating in characoids and other fishes. Environmental Biology of Fishes, 9: 87-101.

Sazima, I. & F. A. Machado. 1982. Hábitos e comportamentos de *Roeboides prognathus*, um peixes lepidófago (Osteichthyes, Characoidei). Boletim de Zoologia da Universidade de São Paulo, 7: 37-56.

Takahashi, R., K. Watanabe, M. Nishida & M. Hori. 2007. Evolution of feeding specialization in Tanganyikan scale-eating cichlids: a molecular phylogenetic approach. BMC Evolutionary Biology, 7:195. Open Access. doi:10.1186/1471-2148-7-195

Vilella, F. S., F. G. Becker & S. M. Harts. 2002. Diet of *Astyanax* species (Teleostei: Characidae) in an Atlantic Forest River in Southern Brazil. Brazilian Archives of Biology and Technology, 45: 223-232.

Wagner, C. E., P. B. McIntyre, K. S. Buels, D. M. Gilbert & D. M. Michel. 2009. Diet predicts intestine length in Lake Tanganyika's cichlid shes. Functional Ecology, 23: 1122-1131.

Zar J. H. 2010. Bioestatistical Analysis. 5th ed. Prentice-Hall, New Jersey.

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