Influence of feeding plasticity on the fitness of small Neotropical characids

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ABSTRACT. This study investigated the diet of four characids [Hyphessobrycon eques (Steindachner, 1882), Odontostilbe pequira (Steindachner, 1882), Psellogrammus kennedyi (Eigenmann, 1903) and Serrapinnus calliurus (Boulenger, 1900)] coexisting in two lagoons and checked for possible spatial differences and the influence on population fitness. The main goal was check if these species show better fitness according to the nutritional value of the food resource consumed. In this way, it is expected that the species show improved nutritional conditions (evidenced by the relative condition factor) when foraging for items of animal origin, and the reverse is expected when consuming items of plant origin and detritus. Sampling was conducted in August 2011. The diet was evaluated by analyzing contents and calculating the relative condition factor for each sampled individual, obtaining a mean value for each population. Species exhibited high food plasticity; H. eques and P. kennedyi altered most their diets from a lagoon to another. Despite these variations, the condition factor showed no significant spatial variation for any species. The results indicated that these species have physiological adaptations that allow them to obtain the maximum energy from food, even if it has low nutritional value, or that fish can compensate for the consumption of low nutritional food by increasing the consumption rate. Thus, regardless of the type of resources consumed, these have met the metabolic needs of the fish in the studied lagoons.

KEYWORDS. Fishes, diet, condition factor, Pantanal, lagoons.

Palavras-chave. Peixes, dieta, fator de condição, Pantanal, lagoas.

Fish use a wide array of food resources available in the environment (Schneider et al., 2011) and are known to occupy all trophic levels, more than any other vertebrate group (Wootton, 1990). Members of the family Characidae have all types of feeding habits and can change them depending on the environment and spatial and seasonal fluctuations (e.g. Barreto & Aranha, 2006; Pellicce & Agostinho, 2006; Dias & Fialho, 2009; Tófoli et al., 2010; Alves et al., 2011; Manha et al., 2012; Wolff et al., 2013). This behavior is known as trophic flexibility or plasticity (Wootton, 1990; Lowe-McConnell, 1999) that allows different species to coexist by reducing the interspecific competition (Brown, 1995). However, due to this ability, many fish can change their diets in the presence of potential competitors and/or predators and even under shortage of preferred food and, forced to consume low nutritional value food.

The optimal foraging models predict that animals will always choose higher energy foods with a minimum of effort,
so that the cost/benefit relationship is balanced (Stephens & Krebs, 1986; Gerking, 1994). However, optimal food items may not be available in nature, making the diet a result from the interaction between food preference and food availability in the environment (Wootton, 1990). Factors such as size, morphology and prey behavior influence this cost-benefit relationship (Stephens & Krebs, 1986). Thus, the consumption of non-preferred and lower energetic food items can change the fitness of the population (Cruz-Rivera & Hay, 2000).

In this way, investigating the diet and feeding tactics of fish species provide important information about the population structure (Hahn et al., 1997; Barreto & Aranha, 2006; Specziár & Erós, 2014). Furthermore, these results combined with the condition factor, which indicates the degree of well-being and reflects the recent feeding conditions (Le Cren, 1951; Vazzoler, 1996), point out whether feeding plasticity is disadvantageous, especially when considering spatial variation in the diet of a population. Bowen et al. (1995), also mentioning other authors, argue that invertebrate prey are high in both protein and energy while plant tissues are lower in energy, since most species use lower energy carbohydrates for both structural elements and energy storage. These differences in protein and energy contents are ecologically significant inasmuch as consumer growth rate is expected to be directly proportional to nutrient level both within and among the ranges for food categories. Ferreira et al. (2012), also comment that the consumption of aquatic insects being energetically advantageous in comparison to detritus.

The characids Hypessobrycon eques (Steindachner, 1882), Odontostilbe pequira (Steindachner, 1882), Psellogrammus kennedyi (Eigenmann, 1903) and Serranipinnus calliurus (Boulenger, 1900) occur simultaneously in lagoons associated with the Miranda River, Pantanal of Mato Grosso do Sul State, and commonly show variations in their diets (e.g. Carvalho & Del-Claro, 2004; Crippa et al., 2009; Ximenes et al., 2011; Alves et al., 2011). Because these species co-occur and show high feeding plasticity, they represent a good model to investigate how changes in food quality (low and high energy) maintain these populations.

Although the plasticity in fish diet is relatively well known, its influence on the fitness of the populations remains poorly understood. Given the above, through the analysis of stomach contents, we investigated possible spatial variations in the diet of each of these species, considering two similar lagoons. In addition, we calculated the condition factor to determine whether changes in diet reflect on the welfare of fish and consequently the fitness of these populations. The main goal was check if these species have better nutritional status according to the energy content of the food consumed (Bowen et al., 1995). Thus, it is expected that the species have improved nutritional conditions when foraging for items of animal origin and the reverse is expected when consuming items of plant origin and detritus.

**MATERIAL AND METHODS**

**Study area.** The Miranda River is located in the Pantanal of Mato Grosso do Sul State, starts in the Maracaju mountain and partially drains limestone areas of the Bodoquena mountain. The drainage area has 47,000 km² (EMBRAPA, 1991). This tributary is localized downstream of the city of Miranda and receives the waters of the Salobra River. From that point, the floodplain is spatially extended to the right, running through several meanders and undergoing extensive ranges of forests, crossing the Pantanal, receiving reflux water and other tributaries, as the Vermelho River, which contribute with water through small channels in the events of large floods (EMBRAPA, 1991).

Two sampling sites were established in two lagoons called A (19°35'00.4"S and 056°59'22.1"W) and B (19°32'09.7"S and 057°03'03.3"W), belonging to the Miranda River floodplain (Fig. 1). Samplings were conducted in the low water period, in which there is low connectivity of the lagoons with the main river.

**Sampling and data analysis.** Fish were collected in August 2011, using trawls nets 20 meter long (1 cm mesh size between opposite knots), fixed in 10% formalin and identified according to Britski et al. (2007). Each specimen was measured (standard length, cm), weighed (total weight, g), and gutted; stomachs containing food were fixed in 4% formaldehyde. Voucher specimens of fish species caught and used in this study are deposited in the fish collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia/UEM) (H. eques: NUP 12609; O. pequira: NUP 12644; P. kennedyi: NUP 12608; S. calliurus: NUP 12647).

Stomach content was analyzed under stereo and optical microscopes. Food items were identified to the lowest taxonomic level using specific literature.

The quality and quantity of food consumed by fish was evaluated by the volumetric (%V) and occurrence (%O) methods (Hyslop, 1980). The values for each food item were combined in the Feeding Index (%IAi) (Kawakami & Vazzoler, 1980) using the formula: IAi = %Fi * %Pi / (%Fi + %Pi) * 100, where: i = food item; F = occurrence frequency (%) of the item i in the diet; V = volumetric frequency (%) of the item i in the diet.

The occurrence frequency (%Fi) was calculated by recording the number of fish in which each item occurred, obtaining the percentage in relation to the total stomachs with food. For the volumetric frequency, the volume of each item was obtained by the percentage in relation to the total value of every stomach contents. The volume was obtained through gridded dish, where the volume was obtained in mm³ and later transformed into ml (Hellawel & Abel, 1971).

To check for significant difference in the diet of fish between the lagoons, a Multi-Response Permutation Procedure (MRPP) was used. This is a non-parametric multivariate method used to test for differences between predefined groups (Zimmerman et al., 1985). The original matrix was transformed into a dissimilarity matrix by the Bray-Curtis method, and the significance of the null
hypothesis was tested by a randomization procedure with 1000 permutations. The analyses were run using the statistical software PC-Ord® 4.0 (McCune & Mefford, 1999).

Values of total weight (Wt) and standard length (Ls) of each individual were fitted to the Wt/Ls curve (Wt = a Lt b), and the values of the regression coefficients a and b was estimated. These coefficients were used to calculate the expected values of weight (We) using the equation: We = aLt b. Then, we calculated the relative condition factor (Kn) for each individual, which corresponds to the ratio between observed and expected weight for a given length (Kn = Wt/We) (Le Cren, 1951). We used the nonparametric Mann-Whitney U test at 5% level to test the differences in the values of the relative condition factor for each species in the sampled lagoons. Analyses were performed in Statistica 7.1® (Statsoft, 2005).

RESULTS

The analysis of 370 stomach contents of Hyphessobrycon eques, Odontostilbe pequira, Psellogrammus kennedyi and Serrapinnus calliurus indicated that these species consumed mainly food of autochthonous origin. Diets consisted mainly of benthic organisms and detritus, regardless of the lagoon. Was observed a very low consumption of terrestrial invertebrates (Fig. 2).

Comparing each population considering the lagoon, differences were found in the main food consumed (> 50% IAi), however, these changes were more evident for H. eques and P. kennedyi. The first consumed detritus and scales in the lagoon A and chironomids in the lagoon B, while the second species consumed filamentous algae (Zygnemataceae) in the lagoon A and chironomids in the lagoon B (Tab. I). Odontostilbe pequira and S. calliurus consumed primarily algae and detritus in both lagoons, demonstrating slight spatial changes in their diets (Tab. I).

The diet of the species was modified according to the environment considered. Such differences were indicated by the multi-response permutation procedure (MRPP) (H. eques: A = 0.224; p < 0.005 - O. pequira: A = 0.170; p < 0.005 - P. kennedyi: A = 0.112; p < 0.005 - S. calliurus: A = 0.153; p < 0.005).

Values of the relative condition factor were not significantly different (p> 0.05) between the lagoons (Tab. II).

DISCUSSION

The four species studied are small-sized fish ranging from 4.0 to 6.0 cm in the adult stage, what characterizes them as foragers. They are ecologically important species, representing a link in food chains and a part of the diet of intermediate and top predators (Corrêa et al., 2009).
fishes, feed, in general, in an opportunistic (or generalistic) way (Pelicice & Agostinho, 2006). They show no clear morphological adaptation for food intake (Crippa et al., 2009).

In this study, the species have consumed primarily food of autochthonous origin (benthic), which can be related to the low water period at which the sampling was made, when little allochthonous material enters the system, and the
water level is extremely low. Crippa et al. (2009) examined small characideans in the Upper Paraná River floodplain and report that the year at which the fish were collected was characterized as dry, which might have contributed to the small importance of terrestrial invertebrates for the diet of the fish species studied.

Spatial variations in diet were more evident when the species altered their feeding habits according to the lagoon. Hence, H. eques and P. kennedyi were detritivorous/invertivorous and algivorous/invertivorous in the lagoons A and B, respectively. Despite this observation, H. eques also consumed fish scales in the lagoon A, almost at the same proportion as detritus, a very nutritious food (Peterson & Winemiller, 1997) and abundant in the bottom, comparable to chironomids, consumed in the lagoon B. Thus, from an energetic point of view, this dietary change does not justify changes in nutritional status of this species, because, anyway, the population consumed a food high in both protein and energy, according to Bowden et al. (1995). Other studies on H. eques also registered the preference for food of animal origin (Casatti et al., 2003; Pelicce & Agostinho, 2006; Crippa et al., 2009). On the other hand, for P. kennedyi that changed the diet from filamentous algae to chironomids, items with large difference in energy content (Bowden et al., 1995), the nutritional status was one of the best among the species studied. In this case, it can be inferred that the species has physiological adaptations that allow to obtain the maximum energy from food, even if it has low nutritional value, such as plant tissues, or that fish can compensate for the consumption of low nutritional food by increasing the consumption rate (Bowden et al., 1995). Such variation in diet quality and frequency of feeding exists particularly for generalists fishes, which are able to exploit a wide range of resources (Yeager et al., 2014). This compensatory feeding strategy has been demonstrated for many taxa when environmental conditions limit the availability of high quality forage (Taillon et al., 2006; Yeager et al., 2014). Apparently, P. kennedyi seems to have the same strategy in other environments, since Ximenes et al. (2011) classified the species as herbivorous in ten marginal lagoons of the Cuiabá River, MG, while Resende et al. (2000), considered it as zooplanktivorous in the Miranda River floodplain, MS.

Odontostilbe pequiura and S. calliurus did not change their main food between the lagoons; they always consumed a mixture of detritus and unicellular and filamentous algae. The first species was considered benthivorous, and the second, omnivorous by Ximenes et al. (2011) and algivorous by Alves et al. (2011). Despite the low nutritional value of the food, these species showed no differences in the condition factor, showing close values, regardless of the lagoon. The reason attributed to P. kennedyi may be applied to these two species.

In short, the occurrence of spatial variations in the diet caused no changes in the relative condition factor, suggesting that the species analyzed were not affected by possible changes in the supply of resources between lagoons. According Futuyma & Moreno, (1988) species able to consume lower-quality resources when these vary greatly through time or space, may allow fitness to be maintained. Although aquatic invertebrates have high protein and energy content, algae represented the most nutritious source among primary producers in freshwater environments. They have high levels of protein and energy besides secondary metabolites that can act as antioxidants, and antibiotics (Yurkowski & Tabachek, 1979; Bowden et al., 1995; Mišurcová et al., 2010). Also, an experiment pointed out that an increase in the ingestion rate compensates for the consumption of reduced energy items (Bowden et al., 1995). Algae and detritus are especially abundant food in floodplain environments, which requires little energy for search and consumption, whereas aquatic invertebrates, despite their abundance, are items that require more energy for search. Thus, the similar values of the condition factor, regardless of the food source, are related to a balance between food availability and energy expenditure for consumption. Therefore, regardless of the resource consumed, these have met the metabolic needs of the fish in the studied lagoons, with positive effects on the fitness of these populations. However, this study showed effects of short-time between diet and body condition. Future research should consider systematic collection of long-term and stable isotopic analysis to understand the role of feeding plasticity on body condition in fish populations.

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