Ontogenetic diet shifts of *Oreochromis niloticus* and *Tilapia rendalli* of the Barra Bonita reservoir (Tietê river, São Paulo State, Brazil)

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ABSTRACT. The Nile Tilapia, *Oreochromis niloticus*, and the Congo Tilapia, *Tilapia rendalli*, are important members of the African cichlids, and have been introduced to many Brazilian lakes and reservoirs. These species exhibit a large feeding flexibility and may modify their habits during their growth. In the Barra Bonita reservoir, these species are well adapted, representing more than 80% of fish. This study aimed to analyze ontogenetic variation with regard to the diet of these species in this important reservoir. Samples were taken monthly, from March 2007 to February 2008, in Anhembi, São Paulo State. Both species were analyzed by grouping individuals according to size classes. The coexistence of these species was observed in this environment, to which fish were introduced, as well as discreet differences in diet, being that *Oreochromis niloticus* was considered as an detritivorous, since the detritus was constant in the diet of almost all size classes, and presents some changes in its diet according to the different size classes. While *T. rendalli* may was defined as herbivorous, and the contribution of food resources to the diet of *T. rendalli* seems to be different from that of *O. niloticus* along the size classes.

Keywords: cichlids, coexistence, dam, fish feeding, Paraná river basin.

Mudanças ontogenéticas na dieta de *Oreochromis niloticus* and *Tilapia rendalli* da represa de Barra Bonita (rio Tietê, Estado de São Paulo, Brasil)

RESUMO. A Tilápia do Nilo, *Oreochromis niloticus*, e a Tilapia do Congo, *Tilapia rendalli*, são importantes membros do grupo dos ciclídeos africanos, e têm sido introduzidas em diversos lagos e reservatórios brasileiros. Estas espécies exibem uma grande flexibilidade em suas dietas e podem modificar seus hábitos alimentares durante o crescimento. No reservatório de Barra Bonita, estas espécies estão bem adaptadas, representando mais de 80% da pesca. Este estudo teve como objetivo analisar a variação ontogenética na dieta destas duas espécies neste importante reservatório. Foram realizadas amostras mensais, de Março de 2007 a Fevereiro de 2008, no município de Anhembi, Estado de São Paulo. Ambas as espécies foram analisadas agrupando os indivíduos de acordo com a classe de tamanho. Foi possível observar a coexistência e uma discreta diferença na dieta das duas espécies neste ambiente, sendo que *Oreochromis niloticus* foi considerada como detritívora, pois o detrito foi constante na dieta na maioria das classes de tamanho e apresentou algumas mudanças na dieta nas diferentes classes de tamanho. Já *T. rendalli* foi considerada herbívora, e houve diferença quanto à contribuição dos recursos alimentares na dieta ao longo das classes de tamanho comparando as duas espécies.

Palavras-chave: ciclídeos, coexistência, barragem, alimentação, Bacia de rio Paraná.

Introduction

In tropical regions, despite the existence of specialized fish in some types of food, fish species generally reveal great feeding plasticity (LOWE-MCCONNELL, 1999), which complicates the understanding of specific trophic patterns. This plasticity is constituted by an interaction of quality/quantity of the food available in the environment and the degree of morphological and behavioral limitations displayed by species, the latter being enabled by ontogenetic variations (GASPAR DA LUZ et al., 2001).

The ontogenetic changes in fish diets are common Wootton (1990), as demonstrated in many fish groups (AGOSTINHO et al., 2003; DELARIVA et al., 2007; GARCIA-BERTHOU, 2002; NOVAES et al., 2004). Several studies emphasize the seasonal and ontogenetic variation in the diet of tilapiines in African Lakes, Asia and in some Brazilian reservoirs (BWANIKA et al., 2004; 2006; HAHN et al., 2002; MESCHIATTI; ARCIFA, 2002).

The cichlid fishes are scientifically important in studies regarding genetics, evolution, behavior and physiology (NELSON, 2006). In addition, some cichlid species have great importance in fisheries in

tropical and subtropical regions (KUBITZA, 2007) and in intensive fisheries (CARVALHO et al., 2010). The Tilapiini tribe, which includes the genera *Oreochromis* and *Tilapia*, is an important group of cichlids that is naturally distributed over the African continent (DE SILVA et al., 2004). The fish from this group, constituted of 12 species in the South African region, present a diversified food spectrum, eating mainly plant or sediment (NELSON, 2006). Some species, such as *Oreochromis niloticus* (Linnaeus 1758) (Cichlidae) are widely used in fisheries and fishkeeping worldwide, due to their biological and zootechnical attributes (AGOSTINHO et al., 2007; CARVALHO et al., 2010).

The introduction of tilapiine cichlids in Brazil started in the 1950's, with the Congo Tilapia - *Tilapia rendalli* (Boulenger 1897) (Cichlidae) and, later, the Nile Tilapia - *Oreochromis niloticus*, always with purpose of increasing the fisheries in dammed rivers (SMITH et al., 2005). In the Barra Bonita reservoir, in particular, between 1975 and 1997, around 12 million fingerlings of different fish species were introduced (CESP, 1998). Currently, the Nile Tilapia is the most important fishery resource of this reservoir (DAVID et al., 2006). Additionally, the capture of many other allochthonous species has been registered in the fishery, such as *Tilapia rendalli* (NOVAES; CARVALHO, 2011), another important resource that, together with Nile Tilapia, support the fisheries in this reservoir.

The allochthonous species can unbalance the natural environment, affecting native species in several ways, such as by competing for food resources and space, predation, hybridization and transference of pathogens (BWANIKA et al., 2006;

FERNANDO; HOLCÍK, 1991; MOYLE et al., 2003; PELICICE; AGOSTINHO, 2009; RODRÍGUEZ et al., 2005). The introduction of non-native species can cause a reduction in native stocks, local extinctions and genetic degradation of native species (FORYS; ALLEN, 1999).

The aim of this study was to characterize the feeding habits of juveniles and adults of *Oreochromis niloticus* and *Tilapia rendalli*, considering the hypothesis that these two species present differences in relation to their feeding habits during their ontogenetic development as a strategy to allow coexistence between them.

Material and methods

Study site

The Barra Bonita reservoir is situated in the Middle Tietê river Basin in the central region of São Paulo State, between the coordinates 20° 31'S and 48° 32'W (Figure 1). The dam was constructed in 1963, and the reservoir, formed by Tietê and Piracicaba rivers, is the first of a series of six large reservoirs built in the Tietê river. The reservoir has the following main characteristics: watershed area: $32,330 \text{ km}^2$, inundated area: 324.8 km^2, perimeter: 525 km, total volume: $3,160 \times 10^6 \text{ m}^3$, discharge rate of $402 \text{ m}^3 \text{ s}^{-1}$, retention time of the water: 30 days (summer) and 90 days (winter) and mean depth of 10.2 m (TUNDISI et al., 2008). The reservoir is situated in a region of geographical transition between tropical and subtropical climates, with a rainy season (from October and March) and a dry season (from March to October) (TUNDISI, 1981).
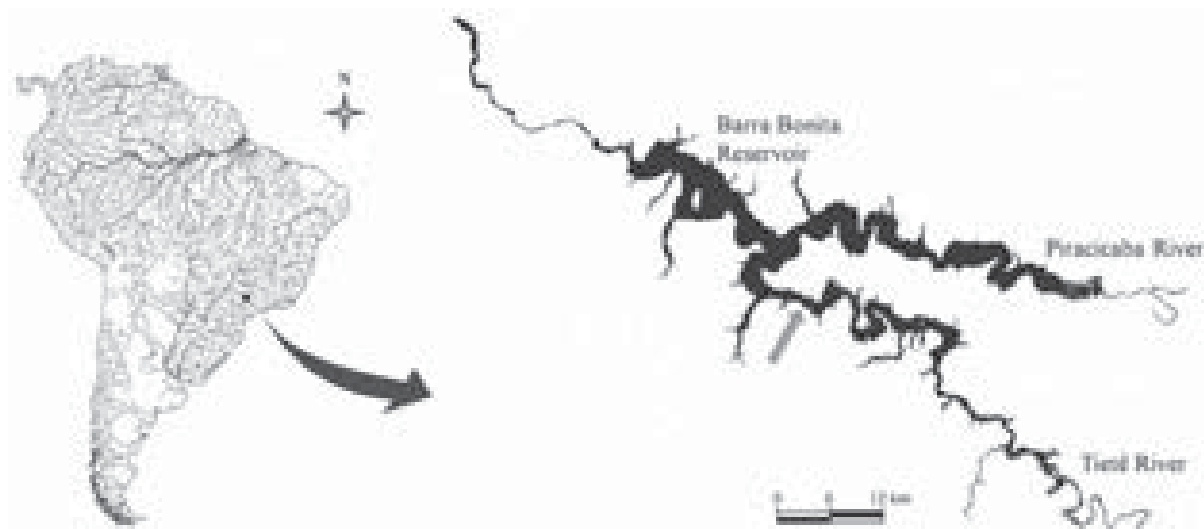

Figure 1. Map of Barra Bonita reservoir, in the grey arrow, the sampling site at Anhembi city.

Situated in one of the most heavily inhabited and urbanized regions of Brazil, this reservoir receives a great amount of sewage from the metropolitan city of São Paulo State and other high density population cities. This ecosystem is a hypertrophic system, due to the heavy input of organic effluents (DAVID et al., 2006). The high nutrient levels permit the development of algae blooms (DELLAMANO-OLIVEIRA et al., 2006).

Field procedures

The fish were obtained from the area of study monthly from March 2007 to February 2008 in the Barra Bonita reservoir, from a fishing community based in the city of Anhembi, São Paulo State. The principal fishing equipments used were gillnets; however, the practice locally known as *batida* (beating) was used actively, where the fishermen put the nets in the water, mainly in the littoral areas, and beat the water surface with a stick to guide the tilapias towards the net (WALTER; PETRERE JÚNIOR, 2007). This fishing technique is widely used in urban reservoirs (PETRERE JÚNIOR et al., 2006).

In addition, experimental samplings were carried out with a castnet, with a mesh size of 3 cm between non -adjacent knots, with the aim of capturing small sized individuals that were not caught using the beating technique. The fish were maintained in ice for no up to two hours until laboratory analyses, and this time did not affect the identification process f the items. Voucher specimens were deposited in the Laboratório de Biologia e Genética de Peixes (LBP), Instituto de Biociências, Unesp - Botucatu.

Laboratory procedures

Only fish specimens with stomach contents were weighed (0.01 g approximation) and measured (standard length, cm). The stomachs were removed and preserved in 10% formalin, and later transferred to 70% alcohol for posterior analysis. The stomach contents were examined under a stereoscopic microscope and optical microscope, when necessary, and contents identified to the smallest possible taxonomic category (food item) based on identification keys and books (BICUDO; MENEZES, 2006; STRIXINO; STRIXINO, 1982). The date of occurrence and volume (mL) of the food items were acquired. The volume of the items was obtained by the compression of the material with a glass over a plate with high known (2.0 mm), and the results converted into ml (1.0 mm^3 = 0.001 mL), according to Hellawel and Abel (1971).

The fish consumed 27 food items, grouped into seven food categories: vegetal matter (leaves, roots, stalk and seeds), algae (Bacillariophyceae, Chlorophyceae, Cyanophyceae, Euglenophyceae, Oedogoniaceae, Zygnemaphyceae), detritus (organic and inorganic matter), fish (remains, scales, eggs and fingerlings), microcrustaceans (Cladocera, Copepoda, Rotifera, Ostracoda), macroinvertebrates (Hirudinea and Oligochaeta) and aquatic insects (Diptera and Coleoptera).

Data analysis

The individuals of each species were grouped in size classes, calculated from the distribution of standard length frequency with the formulae proposed by Sturges (1926): W = K/R, where W is the size class amplitude; K is the number of classes [1 + (3.222 log N)], where N is the number of collected specimens and R is the total amplitude of the data (Ls max - Ls min.).

The results of the diet analysis were expressed as the frequency of occurrence and volumetric method (HYSLOP, 1980), combined in the Alimentary Index (KAWAKAMI; VAZZOLER, 1980):

$$AI = \frac{F_i V_i}{\sqrt{\sum F_i V_i}} \times 100$$

where:

AI = Alimentary Index, i= 1,2...n, food items, F_i = frequency of occurrence of food item i (%), V_i = volume of food item i (%).

To assess the relative specialization level of the species diet, the niche breadth was calculated using the Levins' standardized Index, with volume data:

$$B_i = \left[\left(\sum_j P_{ij}^2 \right) \right]^{-1} (n-1)$$

where:

B_i = Levin's standardized niche breadth; P_{ij} = proportion of the j resource in the diet of specie i; n = number of possible resource state. This index varies from 0 when the specie consumed only one kind of feeding category to 1, when the specie consumed similarly all the feeding categories (HURLBERT, 1978) and was used for all size classes grouped (representing the diet of the species) and for the size classes separated from both species.

To assess the diet overlap between size classes of *O. niloticus* and *T. rendalli*, the Pianka Index (1973) was used according to the formula:

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum (p_{ij}^2) \sum (p_{ik}^2)}}$$

where:

O_{jk} = Pianka's measure of niche overlap index between j and k; p_{ij} = proportion resource i of the total resources used by species j; p_{ik} = proportion resource i of the total resources. The overlap values vary from 0 (absence of overlap) to 1 (total overlap). The results were arbitrarily set as high (> 0.6), intermediate (0.4 - 0.6) and low (< 0.4) (NOVAKOWSKI et al., 2008). A null model was used to evaluate the significance of feeding overlap between size classes of the two species (WINEMILLER; PIANKA, 1990). The matrix with volume (%) of items of each size class was randomized 10,000 times, using the RA3 algorithm randomization option (GOTELLI; ENTSMINGER, 2007; WINEMILLER; PIANKA, 1990). The mean overlap observed was compared with the mean overlap calculated in the null distribution, considering the significance level p < 0.05 (WINEMILLER; PIANKA, 1990). The diet overlap and null model were computed using EcoSim 7.0 (GOTELLI; ENTSMINGER, 2007).

Results

A total of 554 individuals, being 227 of *Oreochromis niloticus* and 327 of *Tilapia rendalli* were analyzed. The individuals of *O. niloticus* presented a variation in standard length from 3.7 to 22.7 cm and weight from 2.6 to 534.3 g. In the *T. rendalli* species, the length varied from 3.7 to 20.2 cm and weight from 2.9 to 390.9 g. The higher number of *T. rendalli* was due to capture of small individuals with castnets, while *O. niloticus* presented more individuals and larger examples when captured by active fishing (Table 1).

Table 1 presents the diet of both species. The most important items in the diet of *O. niloticus*, in terms of frequency of occurrence (FO %) were detritus, Chlorophyceae, vegetal matter and Oligochaeta, while in relative volume (V%) the detritus and Oligochaeta were the most important items, that also represented over 97% of the Alimentary Index. The items that presented higher values of frequency of occurrence and relative volume in the diet of *T. rendalli* were detritus, vegetal matter and Cladocera (*Moina* sp.), where the detritus and vegetal matter had the highest values in the Alimentary Index.

The diet analysis of *O. niloticus* by size classes (Figure 2A) demonstrates that detritus was widely consumed by individuals of all size classes, except classes III and V, which consumed high amounts of microcrustaceans (mainly *Moina* sp.). Vegetal matter had a small participation in the diet of individuals from classes II and III, as had macroinvertebrates in

the diet of fish from classes VII and X. The other food categories were consumed in small proportions, and fish from higher classes fed mainly on detritus.

Table 1. Description of alimentary categories and the items encountered in the diet of *Oreochromis niloticus* and *Tilapia rendalli*.

Food categories	*Oreochromis niloticus*			*Tilapia rendalli*		
	V%	FO%	AI%	V%	FO%	AI%
VEGETAL MATTER (VM)						
Leaves, roots, stalk and seeds	3.4	15.9	0.9	31.6	36.2	33.7
ALGAE (AL)						
Bacillariophyceae	0.06	3.08	0.00	0.05	0.61	0.00
Chlorophyceae	2.74	16.30	0.77	0.01	0.61	0.00
Cyanophyceae	0.22	3.96	0.01	0.22	3.07	0.02
Cylindrospermopsis sp.	-	-	-	0.00	0.31	0.00
Euglenophyceae	0.67	5.73	0.07	0.03	0.31	0.00
Oedogoniaceae	0.00	0.44	0.00	0.10	7.36	0.02
Zygnemaphyceae	0.12	0.88	0.00	0.00	0.31	0.00
Spirogyra sp.	1.09	11.89	0.22	3.19	17.48	1.64
DETRITUS (DE)						
Organic and inorganic matter	56.8	91.6	89.4	23.0	73.0	49.5
FISHES (FI)						
Fingerlings	0.01	0.44	0.00	1.18	0.31	0.01
Scales	-	-	-	0.22	4.91	0.03
Remains	0.00	0.44	0.00	14.62	15.64	6.73
Eggs	0.82	1.76	0.02	0.28	0.31	0.00
MICROCRUSTACEANS (MI)						
Cladocera	2.57	11.45	0.51	0.44	1.84	0.02
Bosmina sp.	0.17	1.76	0.01	-	-	-
Daphnia sp.	0.27	1.32	0.01	0.15	4.60	0.02
Diaphanosoma sp.	0.47	2.64	0.02	0.24	5.52	0.04
Moina sp.	2.02	8.37	0.29	12.97	13.50	5.15
Copepoda	0.02	2.20	0.00	0.00	0.31	0.00
Rotifera	0.02	1.32	0.00	-	-	-
Ostracoda	0.02	3.08	0.00	0.01	0.31	0.00
MACROINVERTEBRATES (MA)						
Hirudinea	0.04	3.96	0.00	0.03	1.53	0.00
Oligochaeta	28.06	15.86	7.65	1.74	6.13	0.31
AQUATIC INSECTS (AI)						
Diptera						
Pupae	-	-	-	3.88	1.53	0.18
Chironomidae (larvae and pupae)	0.37	11.013	0.07	5.97	15.34	2.69
Coleoptera						
Elmidae	0.00	0.441	0.00	-	-	-

*Values in black – high values of Alimentary Index.

Tilapia rendalli (Figure 2B) presents some differences in diet composition when compared to *O. niloticus* and during development.

The detritus was widely consumed by small individuals (classes I to IV) and by individuals of class VIII. The vegetal matter was well used by individuals from class V and was the exclusive item in the diet of individuals of size class X. The microcrustaceans were consumed by individuals from classes II to VI. The fish category was an important food resource in the individuals from classes VI and VII. The aquatic insects were consumed by individuals from classes VIII and IX.

The values of trophic niche overlap (B_i) found for both species were low, although *T. rendalli* presented a high value (B_i = 0.18), when compared with *O. niloticus* (B_i = 0.06). When analyzing the B values for each size class of both species (Figure 3),

O. niloticus was seen to present higher values of niche breadth in the smaller size classes (from I to IV) while for *T. rendalli* the higher values occurred in almost all size classes, especially the larger ones (VI to IX).
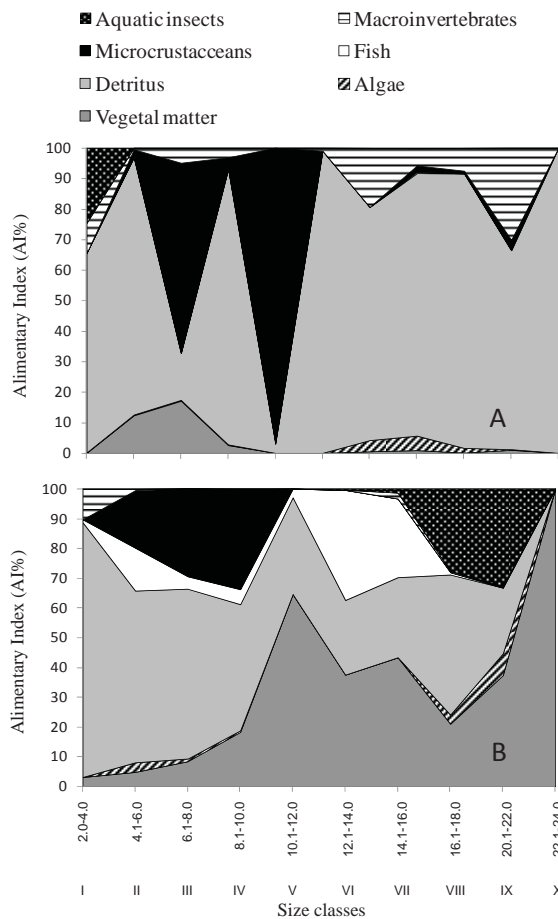

Figure 2. Alimentary Index (AI) of the categories encountered in the diet by size classes of A) *Oreochromis niloticus* and B) *Tilapia rendalli*.
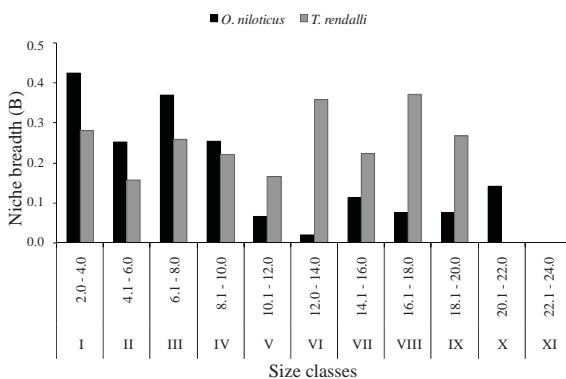

Figure 3. Values of niche breadth (B) for each size class of *O. niloticus* and *T. rendalli*.

The values of diet overlap between size classes of *O. niloticus* and *T. rendalli* were greater than expected by chance (observed mean = 0.53; simulated mean = 0.09; p < 0.00001), which indicates that these values have biological meaning, and do not represent a random pattern. The values of feeding overlap were high between the classes of the same species and also between species, a high frequency of overlap values (> 0.6) was observed between classes of *O. niloticus*, while the high frequency of overlap with intermediate values (among 0.4 and 0.6) was observed between classes of *T. rendalli*. Within the classes of the two species, a high contribution of low values was observed (smaller than 0.4) (Figure 4).
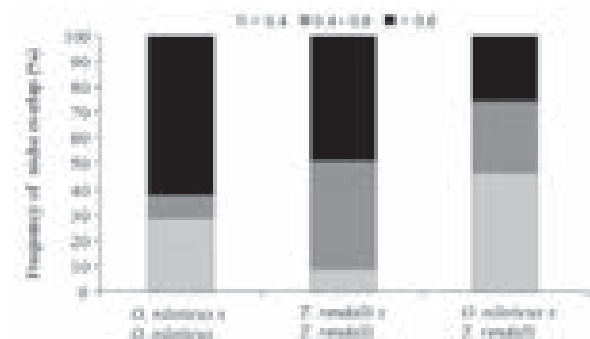

Figure 4. Frequency of niche overlap (%) values between classes of *O. niloticus*, *T. rendalli* and among both species.

When comparing individuals of the same classes of size in both species, in the smaller ones (classes I to IV), *O. niloticus* and *T. rendalli* presented high niche overlap values, but from the class V upward, the values were low (except for class VIII).

Discussion

The cichlids studied are the main fisheries resource in the Barra Bonita reservoir, according to a recent research study, which observed that the tilapias, *O. niloticus*, represent more than 82% of the reservoir's fish population (NOVAES; CARVALHO2011). in some sites of the Barra Bonita reservoir, *T. rendalli* has been found responsible for high proportions of the fish populations, during some periods of the year. This characteristic may explain the high amount of individuals of larger sizes obtained in the samples.

This species was encountered over the entire all year in the local fishery, probably due to success in colonization of the new environment. Such success can be observed in other places, such as the Billings reservoir (MINTE-VERA; PETRERE JÚNIOR, 2000; PETRERE JÚNIOR et al., 2006), and Paranoá Lake (PETRERE JÚNIOR et al., 2006; WALTER; PETRERE JÚNIOR, 2007), and is attributed to a combination of factors, such as high reproductive potential, resistance to low concentration of

dissolved oxygen (KOLDING, 1993) and capacity to use the reservoir phytoplankton as a food resource (FERNANDO; HOLCÍK, 1991).

Oreochromis niloticus is a detritivorous species in the Barra Bonita reservoir, since the detritus was constant in the diet of almost all size classes. This species has also been considered to be detritivorous in reservoirs of Colombia (CALA; BERNAL, 1997), and omnivorous in the Paranoá Lake (Distrito Federal, Brazil) (STARLING et al., 2002).

This species presents some changes in its diet according to the different size classes, as observed in the Sri Lanka reservoirs (WELLIANGE; AMARASINGHE, 2003). Individuals of 10.1 to 12 cm consumed principally microcrustaceans, which can be associated with a bloom of zooplanktonic organisms in August, specifically of the cladocerans group, visible on the water surface. This finding is in agreement with the results of Bwanika et al. (2006), who observed that juveniles of *O. niloticus* exhibit high levels of planktivory compared to large individuals.

The general pattern of the diet of *T. rendalli* may define this species as herbivorous, as observed in the Iraí reservoir, Paraná State (ABILHOA, 2005) and in the Zambezi river, Africa (WINEMILLER; KELSO-WINEMILLER, 2003). However, this species presented a detritivorous feeding in the Tibagi river, Paraná (OLIVEIRA ; BENNEMANN, 2005).

The contribution of food resources to the diet of *T. rendalli* seems to be different from that of *O. niloticus* along the size classes. This species increases the use of vegetal matter during development, consuming great amounts of microcrustaceans, fish and aquatic insects along its growth, as observed by Meschiatti and Arcifa (2002). However, this pattern was not observed in reservoirs of Sri Lanka, where the species' diet do not vary during growth (WELIANGE; AMARASINGHE, 2003). According to Winemiller and Kelso-Winemiller (2003), although many cichlids have the ability to use large numbers of animal and vegetal food resources, ontogenetic changes did not occur in all size classes analyzed in the Zambezi river (Zambia). Abelha et al. (2001) emphasize that modifications in the diet during growth result from differences in the energetic demand and the morphological limitations, implying a different diet during growth.

The feeding ecology data of this species show that individuals can change their feeding habits according to the environment that they are occupying. In Barra Bonita reservoir, the abundances of both species are very high and they use virtually the same kind of food. Many studies have shown that trophic niche overlap is common in freshwater fish. However, this overlap does not necessary imply in food competition. Differences in the spatial occupation and/or in the feeding strategies can avoid such competition (ESTEVES; ARANHA, 1999).

The small individuals of both species occupy the same habitat and share some food items due to their high niche overlap. In the literature, it is common to find a high abundance of small individuals of *O. niloticus* in the littoral areas (KOLDING, 1993), given that the macrophytes and the coastal littoral areas are important habits in the initial stages of many fish, and are used frequently during the search for food and shelter (MESCHIATTI; ARCIFA, 2002; PELICICE; AGOSTINHO, 2006). According to a study accomplished at Monte Alegre Lake, São Paulo State, *T. rendalli* can be abundantly encountered among macrophytes, mainly in the wet season (MESCHIATTI; ARCIFA, 2002).

During growth, food items partition differently presenting segregation in feeding, since the frequency of low niche overlap values (< 0.4) between the two species is higher than the frequency of high values (> 0.6). Fogaça et al. (2003) evaluated the diet and the feeding tactics employed and the manner in which fish from Quebra river (Paraná State, Brazil) occupy their respective microenvironment, and observed that while *Deuterodon langei* feed mainly in the water column, *Characidium pterostictum* search for food at the bottom, guaranteeing resource partitioning through the different feeding strategies. With the decrease in the trophic niche overlap during growth, coexistence may increase between species as both species can maintain a high population abundance, as may be observed in the fish caught from the reservoir.

Conclusion

Morphological differences and differences in feeding allow coexistence of sympatric species, by reducing and avoiding interspecific competition (WOOTTON, 1990). In this study, discrete differences in diet were observed; these species of cichlids were seen to coexist in this environment where they were introduced many years ago and, like many examples of introduction problems in the literature, these two successful species can imbalance the natural environment, affecting native species.

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