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Differences in ichthyofauna feeding habits among lateral lagoons and the river channel in a large reservoir

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(With 5 figures)

Abstract

In this study, we investigated differences in feeding habits of small-sized ichthyofauna among lateral lagoons and the river channel in a large reservoir. The study was performed in four lagoons and in one sampling site of the main channel in Rosana Reservoir, Paranapanema River, Brazil. The samples were taken in September and November of 2004 and in January, March, May, and August of 2005. Fish were sampled with a 7.5 m^2 hand net. Five manual throws were made toward aquatic macrophytes stands. The sampling design favored the collection of small-sized fish fauna (juveniles/small-sized species). The stomach contents of 42 species were analyzed. A total of 183 different items were consumed by fish. These items were grouped in 11 food categories, which were used to classify fish into seven trophic guilds. Aquatic insects were consumed by 32 species and were the predominant feeding item. In the river, the most consumed items were aquatic insects, cladocerans, and phytoplankton, whereas in the lagoons aquatic insects, copepods, and cladocerans were the main items. By comparing each trophic guild, the number of insectivores, algivores, and zooplanktivores species was higher in the lagoons than in the river, and the opposite was found only for omnivore fish. Low niche width in all sites indicates high trophic specialization and low niche overlap between pairs of species. Fish assemblage in the lateral lagoons presents feeding habits distinct from those of the river species, indicating that the coexistence and high abundance of small-sized fish in the sampling sites are explained by their high feeding adaptability, which includes a tendency toward dietary specialization, low feeding overlap, and resource partitioning, along with different temporal resource uses.

Keywords: Paranapanema River, small fish, trophic guilds, diet, feeding pattern.

As diferenças nos hábitos alimentares da ictiofauna entre lagoas laterais e o canal do rio em um grande reservatório

Resumo

O objetivo deste estudo foi avaliar a diferença no hábito alimentar da ictiofauna entre lagoas laterais e o canal do rio num reservatório de grande porte. O estudo foi realizado em quatro lagoas e um ponto no reservatório de Rosana, rio Paranapanema, Brasil. As amostras foram coletadas em setembro e novembro de 2004 e janeiro, março, maio e agosto de 2005. Foram realizados cinco arrastos manuais com uma rede de 7,5m^2, junto aos bancos de macrófitas aquáticas. O desenho amostral favoreceu a coleta de peixes juvenis e espécies de pequeno porte. Os conteúdos estomacais de 42 espécies foram analisados. Um total de 183 diferentes itens foi consumido, que foram agrupados em 11 categorias alimentares. Sete guildas tróficas foram estabelecidas. Insetos aquáticos foram consumidos por 32 espécies de peixes, sendo o item alimentar predominante. O padrão alimentar da ictiofauna no rio foi diferente quando comparado as lagoas, como demonstrado na Análise de Correspondência Destendenciada. No rio, os principais itens alimentares foram insetos aquáticos, cladóceros e fitoplâncton, enquanto que nas lagoas os principais itens foram insetos aquáticos, copépodes e cladóceros. Comparando-se cada guilda trófica, o número de espécies de insetívoros, algívoros e zooplanctívoros foi maior nas lagoas do que no rio e o oposto foi encontrado somente para os onívoros. Foram registrados baixos valores de amplitude de nicho, indicando que as espécies apresentam alta especialização trófica, e baixa sobreposição de nicho trófico entre os pares de espécies. Finalmente, este estudo mostra que a coexistência e alta abundância das espécies de peixe de pequeno porte encontrada nas lagoas laterais são explicadas pela adaptabilidade alimentar, o uso temporal dos recursos pelos peixes e pela ampla disponibilidade de alimento existente nas lagoas.

Palavras-chave: Rio Paranapanema, peixes de pequeno porte, guildas tróficas, dieta, padrão alimentar.

1. Introduction

The dam construction for hydropower production is a major form of human interference in river systems and has been increasing for decades in several countries. The interruption of rivers by dams is responsible for several alterations in limnological features in the river and in adjacent habitats (Tundisi and Matsumara-Tundisi, 2008) and in food resource availability for fish fauna (Hahn and Fugi, 2007). Thus, reservoirs can endanger local ichthyofauna once they transform a lotic and diversified system in a more simplified lentic environment (Agostinho et al., 2008). The effects of reservoirs can extend to lateral lagoons and other floodplain habitats that are of major importance for the ichthyofauna life cycle , especially for small-sized species (Ferrareze and Nogueira, 2011a).

Studies on reservoir ichthyofauna feeding habits are extremely important to understand how fish communities adjust to such drastic environmental transformation, as variation in the ecosystems physical attributes often leads to changes in food resources. Such studies can also provide fruitful insights into community structuring and the interactions among species and their habitat. Moreover, the feeding spectrum reflects the role of each fish species in the ecosystem (Hahn et al., 2000). Within this context, the available food resources and their use can be a relevant factor for the success of species that persist through the new environment's formation process (Rodríguez-Ruiz, 1998).

Knowledge about trophic interactions can provide a better understanding of the interactions among ichthyofauna components and with other aquatic communities or even with semi-terrestrial and terrestrial organisms (Hahn et al., 1997a; Uieda and Motta, 2007). Fish feeding data can also provide information about habitat integrity, food availability, behavioral features and the ecological role of each species (Hahn et al., 1997a).

Studies on resource partitioning among fish are also important for elucidating the mechanisms that permit a high number of organisms to coexist in the same assemblage (Schoener, 1974; Gerking, 1994). Resource partitioning can be defined as any difference in resource use by coexistent species (Ross, 1986). Some factors, such as competition, can influence the spatial and temporal segregation among species (Ross, 1986). A common approach employed to study resource partitioning in ichthyofauna assemblages is diet overlap or niche overlap analysis (Winemiller and Pianka, 1990; Uieda et al., 1997; Esteves et al., 2008). Most studies on Neotropical freshwater ichthyofauna have highlighted the predominance of insectivores and the tendency of feeding overlap reduction associated with spatial and seasonal variability and trophic level differences (Uieda and Motta, 2007), though few investigations consider changes in feeding habits in relation to food availability (Deus and Petrere-Junior, 2003).

The present study was developed under the hypothesis that the small-sized ichthyofauna of lateral lagoons has distinct feeding habits from those of river ichthyofauna because of the different availability of resources between these environments. To investigate this hypothesis, we conducted a diet analysis of fish sampled in four lateral lagoons and in the main river channel of the Rosana Reservoir in the Paranapanema River, Southeastern Brazil.

2. Material and Methods

2.1. Study area

The study area corresponds to the upstream (tail) zone of the Rosana Reservoir, approximately 80 km above the dam (Figure 1), which is located at 22° 36' S and 52° 52' W. The reservoir is the last of a series of eleven reservoirs along the Paranapanema River (border of the States of São Paulo and Paraná, Brazil). The Rosana Reservoir has a surface area of 276 km^2 with a watershed of 11,000 km^2, a water retention time of 21 days (annual mean values), low depth (maximum of 26 m close to the dam), and oligo-mesotrophic features (Nogueira et al., 2006).

The climate is subtropical humid (average temperature of 21°C). During the study period, the rainy season ranged from September 2004 to January 2005 (month average of 157 mm), while the dry period ranged from February to August 2005 (month average of 70.7 mm). The annual accumulated precipitation in the study period was 1,207 mm. The rain precipitation data were provided by the meteorological station of "Morro do Diabo" State Park, Teodoro Sampaio municipality (São Paulo State).

2.2. Sampling and laboratory analyses

The study was performed in four lagoons and one sampling site in the Paranapanema River/Rosana Reservoir channel, close to the river bank. All lagoons are permanently connected with the reservoir (Figure 1, Table 1), and their depth changed by approximately 0.3 m along the study period. Among the selected lagoons, one originated from inundation of a mine digging (Mine Digging Lagoon - MDL), two are natural (Natural Lagoon 1 - NL1, Natural Lagoon 2 - NL2) located inside a preservation area (Morro do Diabo State Park), and one is located in an agricultural and cattle breeding area (Agriculture/Cattle Lagoon - ACL). The dominant macrophytes of each lagoon, in terms of stand area, were identified (Table 1). The samplings were performed in September and November of 2004 and January, March, May, and August of 2005. The position of the sampling sites, the area of each lagoon (integration of geometric distances), and their connectivity (transversal section of the lagoon mouth) with the river-reservoir main channel were determined using Garmin E-trex GPS.

Fish were sampled with a 7.5 m^2 hand net (1.5 × 5 m, 0.3 cm mesh size). For each point/period, five manual throws were made toward aquatic macrophytes stands. This sampling system was chosen for its effectiveness for capturing small fishes. The organisms were immediately fixed in 10% formalin.

In the laboratory, the organisms were transferred to 70% ethanol for permanent storage. Voucher specimens are deposited in the Freshwater Fish Collection of the Department of Zoology (FFCZ 2005-21), São Paulo

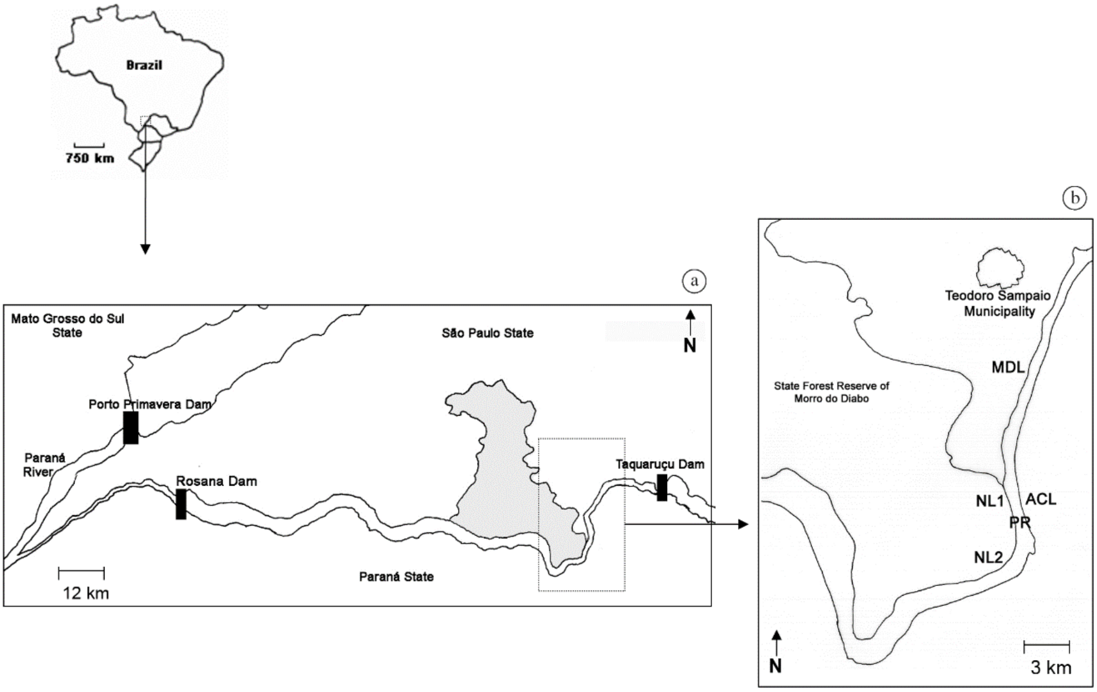

Figure 1. (a) Study area, in the region of Paraná and Paranapanema Rivers confluence, in the States of São Paulo (SP), Paraná (PR), and Mato Grosso do Sul (MS), showing the positioning of Rosana, Taquaruçu, and Porto Primavera dams and the State Park of “Morro do Diabo” (gray area). (b) Location of the sampling sites and Teodoro Sampaio municipality (PR = Paranapanema River; MDL = lagoon originated by the flood of mining digging; NT1and NT2 = natural lagoons located inside a preservation area; ACL = lagoon under influence of agriculture and cattle breeding).

Table 1. Sampling sites names, geographical positioning, lagoons surface area, main aquatic macrophytes, and estimated area of lagoon connectivity (MDL, mining digging lagoon; NL, natural lagoons; ACL, lagoon influenced by agriculture and cattle breeding) with the river main channel (PR).

Sampling sites	Geographical coordinates	Area (km^2)	Dominant macrophytes	Connectivity (m^2)
MDL	22°34’03.3”S 52°09’11.4”W	0.110	*Typha*, *Eichhornia*, *Brachiaria*, *Pontederia*, *Salvinia*	50
NL1	22°36’56.5”S 52°09’47.3”W	0.024	*Eichhornia*, *Brachiaria*, *Pontederia*, *Salvinia*, *Pistia*, *Egeria*, *Nymphaea*	6.5
NL2	22°38’22.0”S 52º09’29.0”W	0.063	*Eichhornia*, *Brachiaria*, *Pontederia*, *Salvinia*, *Pistia*, *Nymphaea*	60.2
ACL	22°37’28,9”S 52°09’21.1”W	0.721	*Eichhornia*, *Brachiaria*, *Pontederia*, *Salvinia*,*Egeria*	525
PR	22°37’51.6”S 52°09’30.5”W	-	*Typha*, *Eichhornia*, *Brachiaria*, *Pontederia*, *Salvinia*, *Pistia*	-

State University, Botucatu campus. The biometry of all collected organisms was obtained through measurements of weight (0.01 g accuracy) and length (0.1 mm accuracy) (total length for species of the orders Gymnotiformes and Synbranchiformes and standard length for other species). Specialized literature was used for taxonomical identification of the fish species, and specialists from São Paulo State University (UNESP - DZSJRP) and the University of São Paulo (USP - MZUSP) were consulted to confirm the identifications.

2.3. Diet analysis

Fish diet was determined through stomach content analysis. Food item identification was made under a stereomicroscope and a microscope to reach the most detailed taxonomic level. Frequency of occurrence (F) and biovolume (B) methods were used. Frequency of occurrence (Hyslop, 1980) was calculated by considering the number of fish having eaten a given item in relation to the total number of the item’s occurrence. Biovolume (adapted from Esteves and Galetti Junior, 1995) was calculated by considering the area occupied by a given item in relation to the total area occupied by all items. The occupied area was determined using a graded dish (mm^2) where the stomach contents were disposed. The feeding habit was determined by the feeding index IAi, using the formula $IAi = (F \text{ x } B) / \Sigma (F \text{ x } B)$ (Kawakami and Vazzoler, 1980).

The food items were grouped into 11 categories. Aquatic insects were represented by insect debris, Coleoptera, Plecoptera, Diptera (Chironomidae, Tanypodinae, Ceratopogonidae, Tipulidae, Culixidae, and Chaoboridae), Ephemeroptera (Caenidae and Polymitarcyidae), Trichoptera (Polycentropodidae and Leptoceridae), Belostomatidae, Notonectidae, and Odonata (Libelullidae, Gomphidae, and Coenagrionidae). Terrestrial insects were represented by insect debris, Diptera, Hymenoptera, Coleoptera, Hemiptera, Trichoptera, Lepidoptera, Orthoptera, Thysanoptera, Homoptera, and Blattodea. Crustaceans were represented by *Macrobrachium amazonicus*, *M. acanthurus*, and Branchiura (Argulidae). Fish were represented by entire scales, muscles, and bones. Macroinvertebrates were represented by Mollusca, Araneae, Pseudoscorpian, Acarina, Hirudinea, Plathyhelminthes, Nematoda, and invertebrate eggs. Microcrustaceans were represented by Cladocera, Copepoda, Rotifera, Ostracoda, and Conchostraca. Algae were represented by different classes of phytoplankton. Vegetal matter was represented by stalks, leaves, roots, and seeds in different digestion stages. Detritus/sediment was represented by all kinds of bottom material, organic film, mud, and sand. Scales were represented solely by fish scales, without fish debris. Finally, birds were represented by feathers.

The trophic group of each species was determined by the identification of the most representative feeding categories and was determined by cluster analysis using the Bray-Curtis coefficient and the UPGMA method in the Primer software, version 6.0 (Clarke and Gorley, 2006). For this analysis, the IAi values for each grouped food item were square-root transformed.

To identify spatial patterns interfering with food consumption, a detrended correspondence analysis (DCA, Hill and Gauch Junior (1980)) was performed with the data of the biovolume of each feeding item, considering all the species examined from each site (PCOrd software; MacCune and Mefford (1997)). To ordinate samples according to the biomass of each trophic guild and to describe the most important feeding items, nonmetric multidimensional scaling analysis was conducted using the Primer 6 software (Clarke and Gorley, 2006).

The niche breadth was calculated by the Levin's index (Hurlbert, 1978): $B_i = [(\Sigma P_{ij}^2)^{-1} - 1] (n - 1)^{-1}$, where B_i is the niche standardized index, P_{ij} is the proportion of food item $_j$ in the diet of the species $_i$, and n is the number of food items. The B_i value ranges from 0 (species consumed mainly one food resource) to 1 (species consumed all food resources in similar proportions). Niche breadth was considered high if $B > 0.6$, intermediate if $B = 0.4 - 0.6$, or low if $B < 0.4$ (Novakowski et al., 2008).

The diet overlap between species was calculated with the relative weight of food items using the Pianka Index (Pianka, 1973): $\theta_{jk} = \Sigma P_{ij} . P_{ik} / [\Sigma (P_{ij}^2). \Sigma (P_{ik}^2)]^{-2}$, where θ_{jk} = Pianka's measure of diet overlap index between j and k species, P_{ij} = proportion of resource $_i$ of the total resources used by species $_j$, P_{ik} = proportion of resource $_i$ of the total resources used by species $_k$, and n = total number of resource states. This index varies from 0 (no overlap) to 1 (total overlap). Diet overlap was considered high if $\theta > 0.6$, intermediate if $\theta = 0.4$-0.6, or low if $\theta < 0.4$ (Novakowski et al., 2008).

A null model was used to evaluate the significance of food overlap between species (Gotelli and Entsminger, 2007). The matrix was randomized 10,000 times using the following options: niche amplitude retained and zeroes reshuffled (RA3, Winemiller and Pianka (1990)). The mean observed overlap was compared with the mean overlap calculated in the null distribution ($p < 0.05$). The feeding overlap and null model analysis were computed using EcoSim 7.0 (Gotelli and Entsminger, 2007).

A one-way ANOVA test was performed to verify whether differences in ecological descriptors were significant among sampling sites, after checking normality and homoscedasticity presuppositions (Statistic software; Statsoft (2001)). When differences were detected, the Tukey test was applied to determine the level of significance (Underwood, 1997). Differences between the periods were tested by the t-student test, using variable mean values for each season (dry and rainy). Significantly different values were considered when $p < 0.05$ (Underwood, 1997). These analyses were performed using Statistica version 6.0 software (Statsoft, 2001).

3. Results

From the 3,156 stomach content samples of the 42 species (Appendix 1) analyzed, a total of 183 consumed items were registered. Aquatic insects (mainly Chironomidae, Trichoptera, and Ephemeroptera) were consumed by 32 fish species (74% of all species), followed by phytoplankton (30 species), microcrustaceans (28 species), macroinvertebrates (24 species), and vegetal matter (21 species).

The diet composition of the community (all species grouped together) indicated that the most frequent, and dominant food category was aquatic insects (IAi = 38.4%), followed by microcrustaceans (IAi = 25.8%), phytoplankton (IAi = 11.6%), and detritus/sediment (IAi = 8.8%). The other food resources represented less than 15.4% of the diet.

The fish from the river exhibited a different feeding pattern from the ones of the lagoon. The main items consumed by the river fish were aquatic insects, cladocerans, and phytoplankton, whereas the main items consumed by the lagoon fish were aquatic insects, copepods, and cladocerans. Higher proportions of aquatic insects and fish were registered in the stomachs of the river fish. The fish from the lagoons exhibited a higher consumption of microcrustaceans, and macroinvertebrates, compared with those from the river. Seasonally, no differences among the proportion of consumed items by the fish were registered (*P* = 0.981).

Fish species were assigned to seven trophic guilds, as identified by cluster (Figure 2) and DCA analyses (Figure 3). The insectivore guild was represented by the highest number of species and, despite the high consume of aquatic insects, individuals belonging to this guild complemented their diet with fish, other macroinvertebrates, microcrustaceans, algae, and detritus. Zooplanktivores was the second most important guild in terms of number of species. This group fed mainly on microcrustaceans, and some species complemented their diet with aquatic insects, algae, and vegetal matter. Detritivores were the third group. This group fed on detritus, and some species complemented their diet with algae and vegetal matter. Another discriminated guild was the algivores, which preferentially fed on algae, and some species complemented their diet with detritus and vegetal matter. The omnivores fed mainly on vegetal fragments and complemented their diet with aquatic insects, microcrustaceans, and detritus

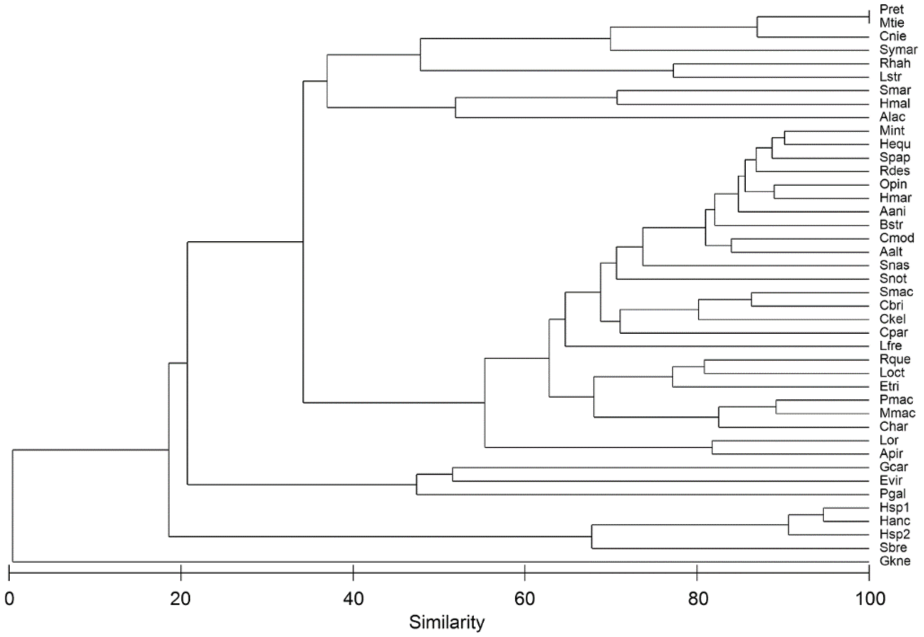

Figure 2. Cluster analysis based on diet similarity among species from the different sampling sites. See Appendix 1 for abbreviations.

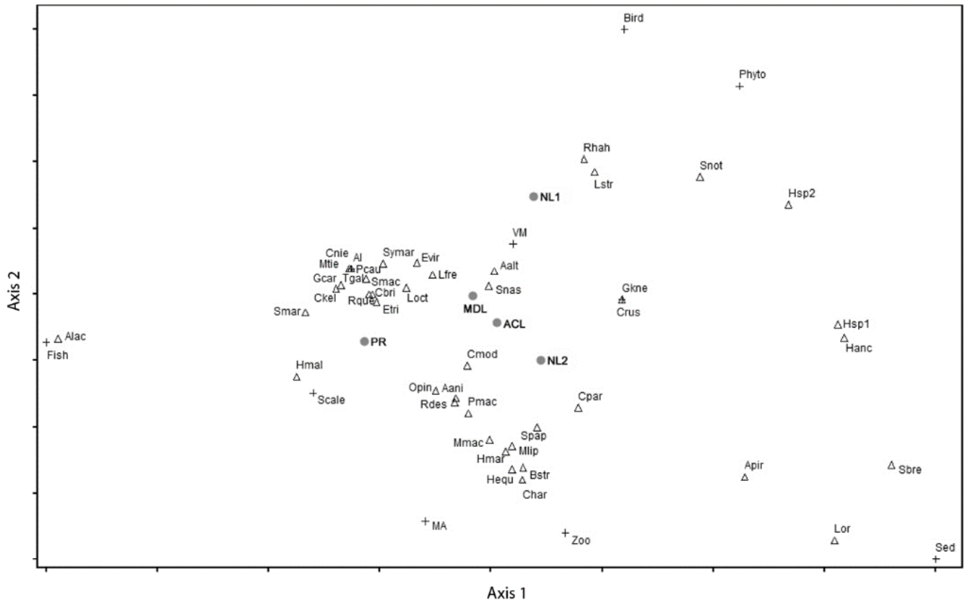

Figure 3. Detrended correspondence analysis showing fish species distribution in relation to the feeding items.

in similar proportions. Rarer guilds were the piscivores, which preferentially fed on fish, and the carcinophagous species, which fed on shrimps.

The insectivores, zooplanktivores, omnivores, algivores, and detritivores occurred in all sampling sites. Five trophic guilds were registered in the river and seven (all categories) in the lagoons. Seasonally, no carcinophagous species was registered during the dry period, due to the absence of *Galeocharax knerii* (Steindachner, 1875) (the only species with this habit). In general, the number of species belonging to each trophic guild varied among sampling sites (*P* = 0.039). When compared each trophic guild, the number of insectivore, algivore, and zooplanktivore species was higher in the lagoons than in the river (*P* = 0.0489), and only omnivores had more species in the river than in the lagoons (*P* = 0.044).

According to resource consumption, the ordination of species along the first two axes of the DCA (*P* = 0.002) (Figure 3) showed a segregation among carcinophagous species (r = –0.69), detritivores (r = –0.77), algivores (r = –0.59), insectivores (r = 0.66), and piscivores (r = 0.81) in axis 1 (r = 0.6). In the axis 2 (r = 0.33), a segregation occurred between zooplanktivores (r = –0.7) and algivores (r = 0.5). This analysis also evidenced a segregation among sampling sites; the river was associated with the positive side of axis 1 (r = 0.49), and the MDL (r = –0.43), NL1 (r = –0.41), ACL (r = –0.42), and NL2 (r = –0.41) lagoons were associated with the negative side of the same axis.

According to the NMDS biplot, while aquatic insects were the most consumed item by the majority of species, the zooplanktivores guild was the most important for fish biomass. Zooplanktivores showed high biomass in all sampling sites, except in the NL1 lagoon, where the insectivores exhibited higher weight. This analysis also showed that algivore biomass increases as insectivore biomass decreases (Figure 4).

Only six species showed high values of niche breadth (> 0.6): *Rhamphichthys hahni* (Meinken, 1937), *Crenicichla haroldoi* Luengo and Britski, 1974, *Pimelodus maculatus* Lacepède, 1803, *Phalloceros caudimaculatus* Lucinda, 2008, *C. niederleinii* (Holmberg, 1891), and *Metynnis lippincottianus* (Cope, 1870); in contrast, eleven species had moderate values, and 25 had low values (Table 1). The high number of species with low niche breadth values indicates a specialized diet, with preference for a restricted number of food items.

The trophic niche breadth values were higher in the lagoons, especially at the lagoon located inside the preservation area, compared those of the Paranapanema River (*P* = 0.002). An exception was found in ACL, where lower niche breadth values were observed (*P* = 0.01). The niche breadth was lower in the dry season (*P* = 0.03), indicating that species were more generalist in the rainy period.

The feeding overlap values were higher than expected through the model calculation (p < 0.00001), indicating that the values obtained were not found at random. However, the obtained values of diet overlap were low (mean = 0.22) for 68% of the species pairs (Figure 5). The species with intermediate or high diet overlap

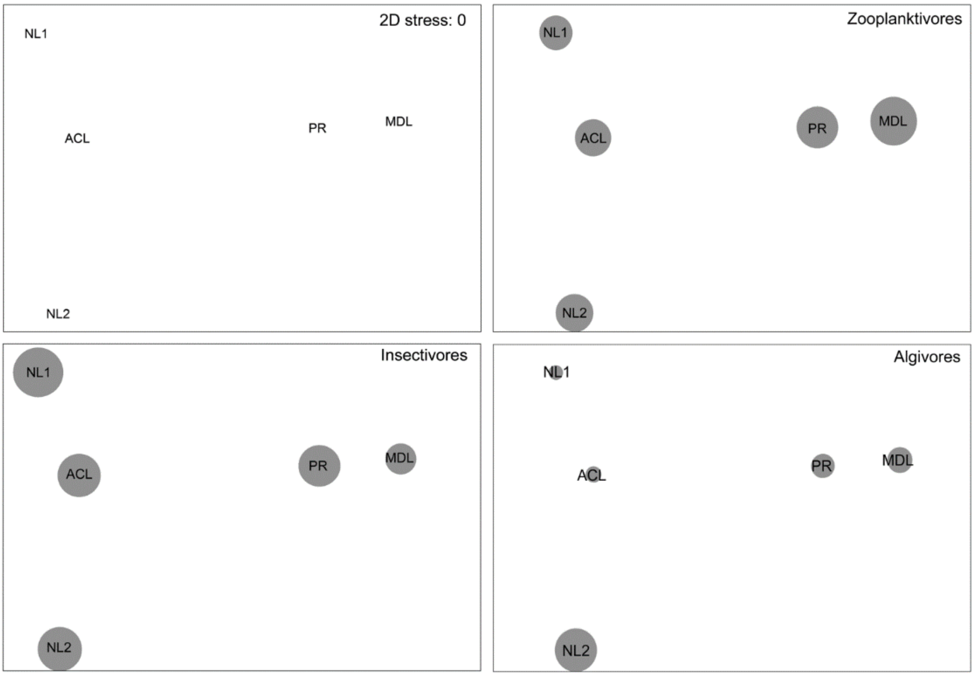

Figure 4. Ordination diagram representing the two first axis of a Non Metric Multidimensional Scaling (NMDS) analysis for different trophic guilds. NMDS stress indicates excellent representation with no prospect of misinterpretation (Clarke and Warwick (2001)).

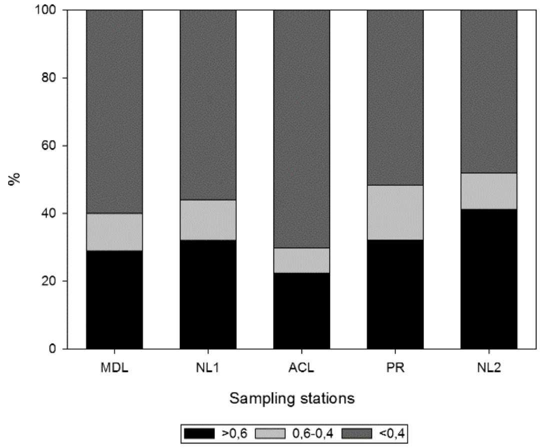

Figure 5. Relative frequency (%) of diet overlap between all the species pairs from the different sampling stations.

were mainly those grouped into the same trophic guild. Among the insectivores, intermediate/high values of diet overlap occurred in 42% of the species pairs. Among the zooplanktivores, intermediate values were observed in 55% of the species pairs. For all species pairs of algivores, detritivores, and piscivores, intermediate or high values of overlap were verified. Eleven other values of intermediate or high overlap occurred among fish from different guilds because they shared resources such as detritus, vegetal matter, and macroinvertebrates.

No significant seasonal and spatial differences in feeding overlap were registered ($P = 0.637$ and $P = 0.07$, respectively). Nevertheless, it is noteworthy that a high frequency of low feeding overlap ($P = 0.04$) and a high frequency of high feeding overlap ($P = 0.042$) were registered in ACL and NL2, respectively.

4. Discussion

The results corroborate our hypothesis that the ichthyofauna of lateral lagoons and rivers demonstrates distinct feeding habits. They exhibit a clear segregation among river and lagoons segments. In lagoons, a higher number of trophic guilds are represented as well as higher values of niche amplitude and lower values of niche overlap, despite the greater abundance of fish living in these environments (Ferrareze and Nogueira, 2011a). This result confirms the importance of lateral river lagoons and other kinds of floodplain habitats for fish ecology, including feeding processes (Hahn et al., 1997b; Meschiatti and Arcifa, 2002; Crippa et al., 2009).

The trophic guilds, in general, are composed of few species, indicating a quite uniform distribution of food resource exploitation among fishes. This finding could suggest avoidance from trophic competition (Angel and Ojeda, 2001), whereas it is most probable that the fish fauna of lateral lagoons optimized the use of the food resources available, as reported by Jaksic (1981) and Hahn and Fugi (2007).

Phytoplankton and zooplankton are widely consumed by the fish. The biomass of planktivores fish was higher than the other guilds. Nevertheless, aquatic insects are the most consumed item by fish. The high predation on microcrustaceans and insects by fish suggests that these arthropods support the high density of small-sized fish, mainly in the lateral lagoons where the biomass of fish was higher (Ferrareze and Nogueira, 2011a). These results corroborate the pattern found in ponds of the same main basin (Hahn and Fugi, 2007; Crippa et al., 2009). In contrast with other studies (mostly based on large-sized fish) on the diet of Neotropical fish (Meschiatti and Arcifa, 2002; Piana et al., 2005), our results indicate that plankton significantly contributed to the energy and matter transfer. This process is fundamental for the biomass formation and maintenance of small-sized fish, a result that mirrors patterns from temperate regions (Carpenter and Kitchell, 1993). Moreover, the high consumption of plankton in this study presumably reflects the environment. Lateral lagoons are important habitats for plankton development (Straškraba and Tundisi, 2000), and they have adequate limnological conditions for plankton capture by fish, such as high water transparency, low turbidity, and low water flow (Ferrareze and Nogueira, 2011b). Nevertheless, the river also exhibits good conditions for plankton ingestion due to the influence of the Taquaruçu Reservoir, located just upstream, which exports a high amount of plankton organisms to the lotic stretch of the Rosana Reservoir (Nogueira et al., 2008, 2010).

The present study refers to fish assemblages sampled in the littoral zones, which can explain the high consumption of aquatic insects by several species. The littoral zones exhibit high spatial heterogeneity due to the presence of macrophytes and woody debris that allow the colonization of a diversified fauna of crustaceans and aquatic insects, commonly associated with periphyton (Oliveira et al., 2005); these are abundant food resources for species from many trophic guilds (Hahn et al., 1997b) and, therefore, can sustain high fish diversity (Gido et al., 2002).

Despite the great number of food items explored by fish species, most of them show preferential consumption, as evidenced by low values of niche breadth in all sampling stations. The high dominance of relatively few kinds of resources suggests a correlation with resource abundance in the environment (Novakowski et al., 2008) rather than morphological limitations for the consumption of particular items (Gerking, 1994; Resende, 2000; Crippa et al., 2009). Fish are more generalist in the rainy period, in agreement with other studies in the neotropics that have reported a more generalist diet in this season, when most resources are more abundant (Deus and Petrere Junior, 2003).

In the lagoons, fish assemblage shows higher values of niche breadth and higher representativeness of trophic guilds when compared with fish from river, reflecting this fauna's feeding plasticity by the use of different food resources, according to their availability (Hahn et al., 2004). First, high diversity and abundance of resources can lead to their opportunistic use, resulting in a more generalist feed spectrum. In this case, however, specialization can be interpreted as a result of the choice of feeding on items that are energetically more important among the many available resources (Ceneviva-Bastos and Casatti, 2007). Indeed, when comparing the lagoons with the river, fish at the lagoons were more generalist because they have greater food availability in these environments (Ferrarereze and Nogueira, 2011b, 2013). It is important to mention, however, that these fish still exhibits a narrow niche breadth, which can be explained by preferential predation (personal observation) upon items which, among such wide variety, are probably easier to catch (reducing the niche breadth).

Low diet overlap indicates differences in diet composition, and, in combination with low niche breadth, these results suggest a high degree of food partitioning, in agreement with other studies on neotropical fish communities (Ross, 1986; Uieda et al., 1997; Esteves et al., 2008; Novakowski et al., 2008). However, when overlap was analyzed independently within each trophic guild, some different patterns emerge. The insectivore, algivore, and zooplanktivore guilds show high trophic niche overlap. Within this context, species coexistence may be associated with different explanations, such as habitat spatial heterogeneity and complexity combined with temporal, populational or behavioral variability (May, 1986; Schoener, 1974). Differential feeding or foraging strategies can explain species segregation along the feeding dimension, as observed in streams (Uieda et al., 1997) and macrophyte stands (Casatti et al., 2003; Pelicice and Agostinho, 2006). Similarly, in Rosana reservoir fish assemblages, species from different trophic guilds can explore varied microhabitats, such as macrophyte stands (insectivores and algivores), bottom sediments (invertivores and detritivores), and the water column (piscivores, zooplanktivores, and algivores), resulting in low values of niche overlap (Gerking, 1994; Matthews, 1998).

This similar pattern of low values of niche overlap can also be observed in other ichthyofauna assemblages with low seasonal diet variation (Gomes and Verani, 2003; Novakowski et al., 2008) and under the influence of environmental gradients (Esteves et al., 2008). Despite the overall low niche overlap, the foraging patterns within the fish assemblage evidences significant resource partitioning, because all observed values of niche overlap are significantly higher than those expected by chance, indicating that the observed patterns are not created randomly and therefore reflect biological processes. The variance data are also higher than the simulated data because the pairs of species that belong to the same guild showed overlap values higher than the species pairs that belong to different guilds, generating high variances (Inger and Colwell, 1977; Winemiller and Pianka, 1990).

In conclusion, the ichthyofauna of the lateral lagoons has feeding habits distinct from those of the river ichthyofauna. The results also show that the coexistence and high abundance of small-sized fish in the studied environments are explained by their high feeding adaptability, which includes a tendency toward dietary specialization, low feeding overlap, and resource partitioning, along with different temporal resource uses.

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Appendix 1. Collected species, acronyms (ACR), number of examined stomachs and niche breadth (in parentheses) calculated for fish diet from lagoons (MDL, NL1, NL2, ACL) and river (PR) sampling sites.

Species	ACR	MDL	NL1	NL2	ACL	PR
Characiformes						
Astyanax altiparanae Garutti and Britski, 2000	Aalt	3 (0.53)	6 (0.31)	7 (0.29)	27 (0.21)	7 (0.27)
Acestrorhynchus lacustris (Lütken, 1875)	Alac	-	-	-	-	3 (0.55)
Apareiodon piracicabae (Eigenmann, 1907)	Apir	-	-	-	6 (0.05)	4 (0.30)
Aphyocharax anisitsi Eigenmann and Kennedy, 1903	Aani	25 (0.26)	7 (0.20)	96 (0.18)	12 (0.30)	29 (0.22)
Bryconamericus stramineus Eigenmann, 1908	Bstr	30 (0.32)	57 (0.23)	98 (0.32)	50 (0.46)	95 (0.42)
Cyphocharax modestus (Fernández-Yépez, 1948)	Cmod	3 (0.45)	4 (0.50)	9 (0.23)	8 (0.37)	11 (0.35)
Galeocharax knerii (Steindachner, 1875)	Gkne	-	1 (0)	-	-	-
Hemigrammus marginatus Ellis, 1911	Hmar	200 (0.14)	198 (0.23)	100 (0.27)	300 (0.35)	140 (0.37)
Hoplias malabaricus (Bloch, 1794)	Hmal	-	2 (0.22)	3 (0.11)	1 (0)	-
Hyphessobrycon eques (Steindachner, 1882)	Hequ	80 (0.29)	108 (0.26)	54 (0.28)	104 (0.27)	50 (0.50)
Leporinus friderici (Bloch, 1794)	Lfre	-	7 (0.49)	13 (0.36)	-	-
Leporinus octofasciatus Steindachner, 1915	Loct	-	6 (0.33)	4 (0.24)	-	-
Leporinus striatus Kner, 1858	Lstr	-	-	11 (0.31)	-	-
Metynnis lippincottianus (Cope, 1870)	Mlip	11 (0.51)	-	-	10 (0.72)	-
Moenkhausia intermedia Eigenmann, 1908	Mint	29 (0.23)	23 (0.34)	-	40 (0.41)	22 (0.42)
Myleus tiete (Eigenmann and Norris, 1900)	Mtie	-	3 (0.69)	-	-	2 (0.22)
Oligosarcus pintoi Amaral Campos, 1945	Opin	-	29 (0.61)	12 (0.23)	9 (0.79)	4 (0.41)
Roeboides descalvadensis Fowler, 1932	Rdes	13 (0.65)	22 (0.38)	16 (0.43)	22 (0.46)	16 (0.36)
Schizodon nasutus Kner, 1858	Snas	12 (0.22)	3 (0.97)	-	21 (0.45)	-
Serrapinnus notomelas (Eigenmann, 1915)	Snot	68 (0.08)	55 (0.11)	22 (0.11)	58 (0.07)	31 (0.12)
Serrasalmus maculatus Kner, 1858	Smac	23 (0.24)	20 (0.06)	15 (0.22)	35 (0.19)	11 (0.15)
Serrasalmus marginatus Valenciennes, 1836	Smar	4 (0.69)	1 (0)	-	7 (0.54)	-
Steindachnerina brevipinna (Eigenmann and Eigenmann, 1889)	Sbre	12 (0.08)	26 (0.11)	16 (0.02)	35 (0.02)	-
Gymnotiformes						
Eigenmannia trilineata López and Castello, 1966	Etri	1 (0)	9 (0.18)	8 (0.43)	16 (0.23)	-
Eigenmannia virescens (Valenciennes, 1842)	Evir	-	5 (0.41)	-	-	-
Gymnotus sylvius (Albert and Fernandes-Matioli, 1999)	Gsyl	-	16 (0.32)	-	14 (0.32)	5 (0.45)
Rhamphichthys hahni (Meinken, 1937)	Rhah	4 (0.95)	-	-	-	-
Siluriformes						-
Hypostomus ancistroides (Ihering, 1911)	Hanc	16 (0.11)	-	15 (0.44)	-	20 (0.11)
Hypostomus sp.1	Hsp1	14 (0.23)	7 (0.53)	21 (0.32)	-	14 (0.07)
Hypostomus sp.2	Hsp2	-	14 (0.59)	-	-	-
Loricariichthys platymetopon Isbrücker and Nijssen, 1979	Lor	-	6 (0.29)	-	6 (0.07)	-
Trachelyopterus galeatus (Linnaeus, 1766)	Tgal	-	-	1 (0)	-	-
Pimelodus maculatus Lacepède, 1803	Pmac	-	-	-	8 (0.67)	-
Rhamdia quelen (Quoy and Gaimard, 1824)	Rque	-	-	-	-	4 (0.08)
Perciformes						
Cichla kelberi Spix and Agassiz, 1831	Ckel	8 (0.22)	3 (0.80)	2 (0)	6 (0.74)	-
Cichlasoma paranaense Kullander, 1983	Cpar	13 (0.18)	13 (0.24)	-	14 (0.37)	-
Crenicichla britskii Kullander, 1982	Cbri	12 (0.19)	16 (0.13)	16 (0.11)	11 (0.56)	14 (0.16)
Crenicichla haroldoi Luengo and Britski, 1974	Char	-	-	8 (0.72)	-	-
Crenicichla niederleinii (Holmberg, 1891)	Cnie	-	-	6 (0.27)	3 (0.97)	-
Satanoperca pappaterra (Heckel, 1840)	Spap	-	-	28 (0.13)	15 (0.39)	15 (0.65)
Synbranchiformes						
Synbranchus marmoratus Bloch, 1795	Smar	-	-	-	2 (0.47)	-
Cyprinodontiformes						
Phalloceros harpagos Lucinda, 2008	Phar	-	3 (0.67)	-	-	-