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Can dams affect the trophic structure of ichthyofauna? A long-term effects in the Neotropical region

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ABSTRACT. Dams are considered an important source of modification upon the structure of aquatic communities and their reflexes are diverse on the fish fauna. Although there are several hydroelectric power plants in Brazil, the long-term effects on feeding activity of ichthyofauna are unknown. Thus, this study aimed to investigate the long-term effects of an old reservoir (fifty years) on the trophic dynamics of fish fauna. The diet of 20 fish species was analyzed, identifying 37 food items belonging to six trophic categories, which enable to create six trophic groups. The results found here suggests that throughout the creation of a reservoir, the trophic structure of the fish assemblages tend to reach trophic homeostasis, in which the fish community will be capable of exploring the most available food resources being maintained primarily by the items placed in the categories organic matter and fragments of fish and vegetal.

KEYWORDS. Feeding ecology; old dam; trophic stabilization; resource availability; fishes.

RESUMO. Podem barragens afetar a estrutura trófica da ictiofauna? Efeitos de longo prazo na Região Neotropical. As barragens são consideradas uma importante fonte de modificação na estrutura das comunidades aquáticas e seus reflexos são diversos na fauna de peixes. Embora existam várias usinas hidrelétricas no Brasil, os efeitos a longo prazo sobre a atividade de alimentação da ictiofauna são desconhecidos. Assim, este estudo teve como objetivo investigar os efeitos a longo prazo de um antigo reservatório (50 anos) sobre a dinâmica trófica da ictiofauna. A dieta de 20 espécies de peixes foi analisada, identificando 37 itens alimentares pertencentes a seis categorias tróficas, que possibilitaram a criação de seis grupos tróficos. Os resultados aqui encontrados sugerem que, ao longo da formação de um reservatório, a estrutura trófica das assembleias de peixes tende a atingir a homeostase trófica, na qual a comunidade de peixes será capaz de explorar os recursos alimentares mais disponíveis sendo mantidos principalmente pelos itens colocados nas categorias matéria orgânica e fragmentos de peixes e vegetais.

PALAVRAS-CHAVE. Ecologia alimentar; reservatório antigo; estabilização trófica; disponibilidade de recursos; peixes.

The action of dams upon the structure of aquatic communities is an important source of modification throughout the longitudinal and transversal gradients of these systems, bringing about distinct influences in the restructure of remaining communities (Agostinho *et al.*, 2007, 2015).

Hydrological disturbances arising from damming are determinants of reorganization of fish assemblages in the new environment. In this way, the availability of food supplies, the plasticity of feeding strategies and pre-adaptive characteristic of trophic guilds to lacustrine conditions are considered key elements for the establishment and accommodation of the ichthyofauna in reservoirs (Piet, 1998; Rodrigues-Ruiz, 1998).

In the initial phases of reservoirs formation, it is observed an intense heterotrophic activity (from items of allochthones origin) due to the flooding of the vegetation and soil that incorporate a series of resources into the environment, mainly vegetation and terrestrial invertebrates (Baxter, 1977; Agostinho *et al.*, 1999; Crippa & Hahn, 2006). Thus, it is possible to establish that the impacts involved in the early stages of impoundments are directly related to changes in primary productivity caused by the release of nutrients from the decomposition of submerged organic matter (Balon, 1973; Petrere-Junior, 1996). This phase was designated by Kimmel & Groeger (1986) as a trophic outbreak period in which it is observed that the fish assemblage shows an increase in the consumption of either terrestrial invertebrates (Albrecht & Caramaschi, 2003; Balassa *et al.*, 2004) and terrestrial vegetation (Cassemiro, 2005). On the other hand, Monteiro *et al.* (2009) observed that in a small reservoir there were not significant alterations in the fish feeding dynamics, with only some subtle changes related to an increase of aquatic insects and algae consumption.

After a few years, the reservoirs have a second moment, when it is possible to detect a process of trophic accommodation (Cunha-Santino *et al.*, 2013). This second stage is known as a period of trophic depression, when it is observed a sharp decrease in the nutrient availability, due to the sedimentation processes and water exportation through the turbines and spillways by the hydroelectric power-plant (HPP), causing the reservoir to achieve a new productivity level (Agostinho *et al.*, 1999, 2015; Williams *et al.*, 1998). During the development of a reservoir, the fish assemblages begin to have intense random use of aquatic insects, terrestrial vegetation, organic matter, fishes, and crustaceans in their diet (Mérona *et al.*, 2001; Luz-Agostinho *et al.*, 2006; Vidotto-Magnoni & Carvalho, 2009).

Agostinho *et al.* (2007) propose that changes in dammed environments tend to achieve trophic stabilization obeying a temporal perspective. This trophic accommodation is part of a third moment that refers to the status found in older reservoirs, defined in this paper as a period of ecological homeostasis. On this occasion, the biological processes resulting from drowning in marginal areas no longer have great influence on the trophic structure of fish assemblages. This approach is still little known scientifically as, in most Neotropical reservoirs, the operating time is less than twenty-five years and so is not possible yet the establishment and definition of the processes occurring at this stage Lowe-Mcconnell (1999).

As Brazilian reservoirs age, it becomes feasible to develop studies involving the ichthyofauna and its feeding strategies in environments that have long been dammed, and such information may permit the consolidation of the knowledge pertaining to the third phase that is equivalent to the trophic balance in reservoirs. Thus, the hypothesis of this work is that Jurumirim reservoir, which has been operating for more than five decades, has already passed by the trophic stabilization process, being their community stable in terms trophic guilds.

MATERIAL AND METHODS

The Jurumirim reservoir was formed with the construction of the hydroelectric power plant (HPP) "Armando Laydner", which started at the end of the 1950's and began to operate in 1962. This dam is considered as large size (Henry & Nogueira, 1999), and divided into three zones: lotic, transition and lentic (Nogueira *et al.*, 1999; Tundisi, 1993) (Fig. 1; Tab. I).

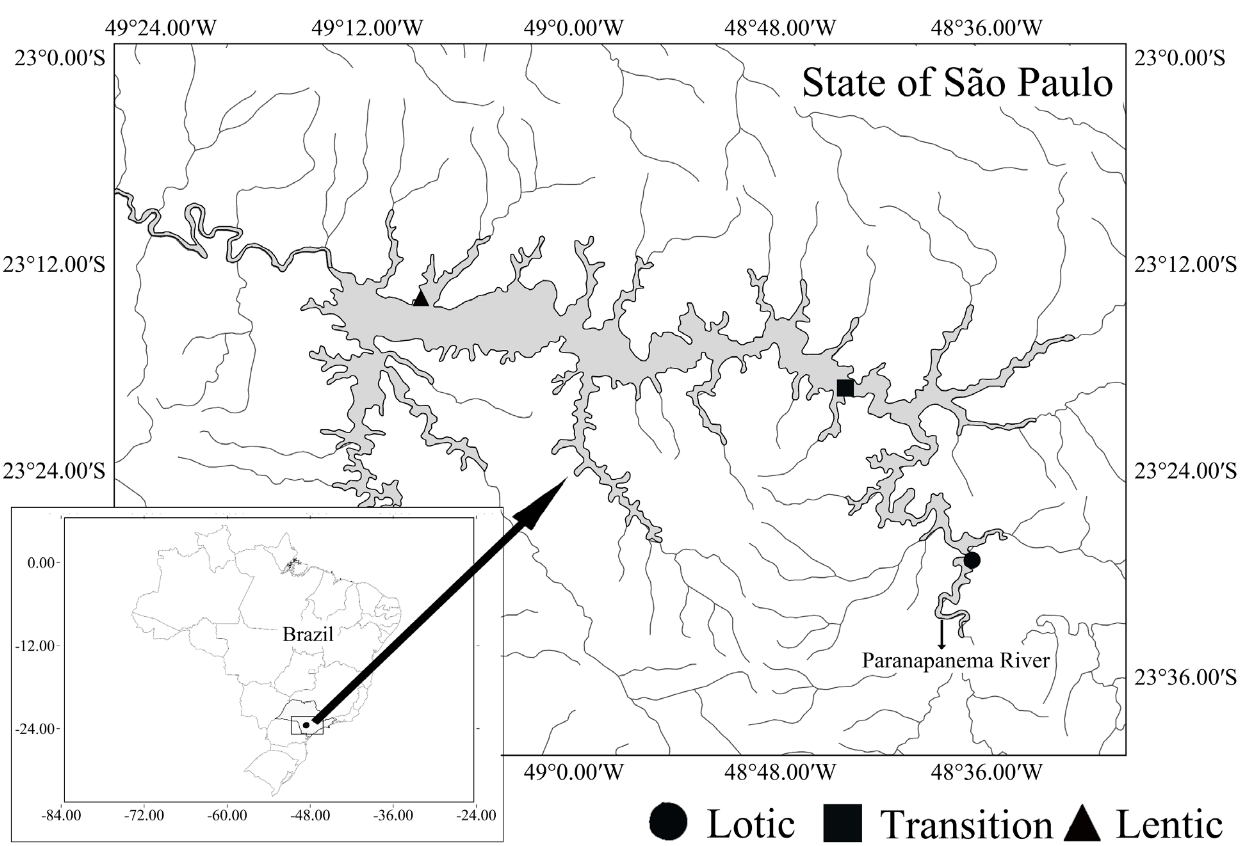


Fig. 1. Map of Jurumirim Reservoir (Upper Paranapanema River, state of São Paulo, Brazil) indicating the three samplings zones.

Tab. I. Environmental characteristics of the sampling zones in Jurumirim Reservoir, Upper Paranapanema river, state of São Paulo, Brazil.

Stretch	Locality	Environmental characteristics
Lotic	Angatuba municipality/ Paranapanema River channel.	Important ecotone between fluvial and lacustrine environments (HENRY, 2003) subject to the effects of the flooding pulse (NEIFF, 1999) very attenuated by the water mass of the reservoir body that works as a buffering agent (HENRY *et al.*, 2006).
Transition	Paranapanema municipality/ Close to the mouth of three tributaries (Jacu, Santo Inácio and Veados rivers), in the old bank of Paranapanema River (SAMPAIO, 1944).	Semilentic's water with a few aquatic macrophytes and high number of decaying trees. Presents oscillation of the water level imposed by the impoundment and the carrying of allochthonous matter and sediment from Paranapanema river and some tributaries.
Lentic	Arandu municipality/ Close to the impoundment zone in the main channel of the Jurumirim Reservoir HPP	Lentic environment and deep water up to 30 m (HENRY, 1992). Sediment composed by sand and gravel, a few aquatic macrophytes in the shore area, and some remaining forest.

Six fish samplings were carried out (ICMBio license nº 15549-1) bimonthly from April/2010 to February/2011, in three sampling sites, representing the three zones of reservoir: lotic (1), transition (2) and lentic (3). Fish were passively caught with gillnets, with mesh varying from 3 to 14 cm between opposite knots, that were installed at dusk and set aside at dawn, performing 14 hours of exposition. Voucher specimens were deposited in the Fish Collection of the Laboratory of Fish Biology and Genetics (LBP) of the Department of Morphology, Institute of Biosciences of UNESP - Botucatu and in the Museu de Zoologia da Universidade Estadual de Londrina (MZUEL).

For stomach content analyses were selected species that showed at least four individuals with some food content. The stomach contents were analyzed in the lab with the aid of a stereomicroscope and eventually under an optic microscope. The food items were weighted using analytical scale and afterward analyzed by the Alimentary Index (%Ai) that was proposed by KAWAKAMI & VAZZOLER (1980).

The food items identified were grouped in categories and the fish species were classified into trophic groups following the Alimentary Index values (≥ 50% of the index in a determined trophic category). The data on the fish species feeding were ordered with the different trophic categories and submitted to a Detrended Correspondence Analysis (DCA) (HILL & GAUCH, 1980). To do so, the values of the total weight of the food items transformed were used (constant summed one and logarithmic) and the analysis were done in the software PC-ORD – 5 (MCCUNE & MEFFORD, 2006). The importance (in numeric abundance and biomass) of the trophic guilds was also estimated using the percentage of the total capture of specimens since in all stretch the capture efforts were always standardized.

The assessment of resources availability used was made with the weight of all items present in the stomach contents of all species in each studied stretch. WINEMILLER & KELSO-WINEMILLER (1996) premise that the species clusters analyzed explore every eatable resource found in the environment. Considering that not all the stomachs had their content analyzed and the number of the ones analyzed for each species was not proportional to the participation in the sample, the weight was corrected according the equation proposed by GASPAR DA LUZ *et al.* (2001).

Finally, the trophic interaction networks have been set up with the ichthyofauna and diet data of the species (Tab. III) using the Pajek software, version 4.01a (BATAGELJ & MRVAR, 1998). The parameters calculated for the nets were: number of trophic species (fish species), number of resources consumed (food items), resource density (number of resources per species), number of trophic links (lines in nets indicating interactions between resource-consumer), density of trophic links (number of connections per species).

RESULTS

It was analyzed 20 fish species distributed in three orders and nine families, with a record of the nonnative species *Cichla monoculus* Spix & Agassiz, 1831 (Tab. II).

The diet analysis was carried out with the identification of the food items of 999 stomachs. It was recorded 37 food items in which 29 were considered autochthonous and eight allochthonous, distributed in six trophic categories (*Vegetal matter*: *Spirogyra* sp., *Desmidium aptagonum*, Cyanophyceae, Zygnemaphyceae, Chlorophyceae, Plant fragment, Seeds; *Detritus*: Amorphous organic matter; *Fishes*: Unidentified fish, Characiformes, *Gymnotus* sp., scales; *Insects: Aquatic*: unidentified exoskeleton fragments, Chironomidae (Larvae and pupae), Odonata – Gomphidae - and other families, Hemiptera, Trichoptera, Ephemeroptera, Ceratopogonidae, Chaoboridae; and *Terrestrial*: unidentified exoskeleton fragments, Diptera adults, Coleoptera adults, Hymenoptera, Orthopteran; *Crustaceans*: *Macrobrachium* sp. (larvae and adults), Copepoda, Ostracoda; *Other*: Bivalvia, Gastropoda, Araneae, Tecameba, Acari). Thus, six trophic groups were identified in values of the Alimentary Index (%AIi) (Tab. III).

According to the Detrended Correspondence Analysis (DCA), the axis one and two explained 49.29% of the relation among fish species and the trophic categories. The total variance ("Inertia") found for this analysis was 2.41 and the auto-values of the axis one and two were 0.82 and 0.36 respectively. The DCA demonstrated that

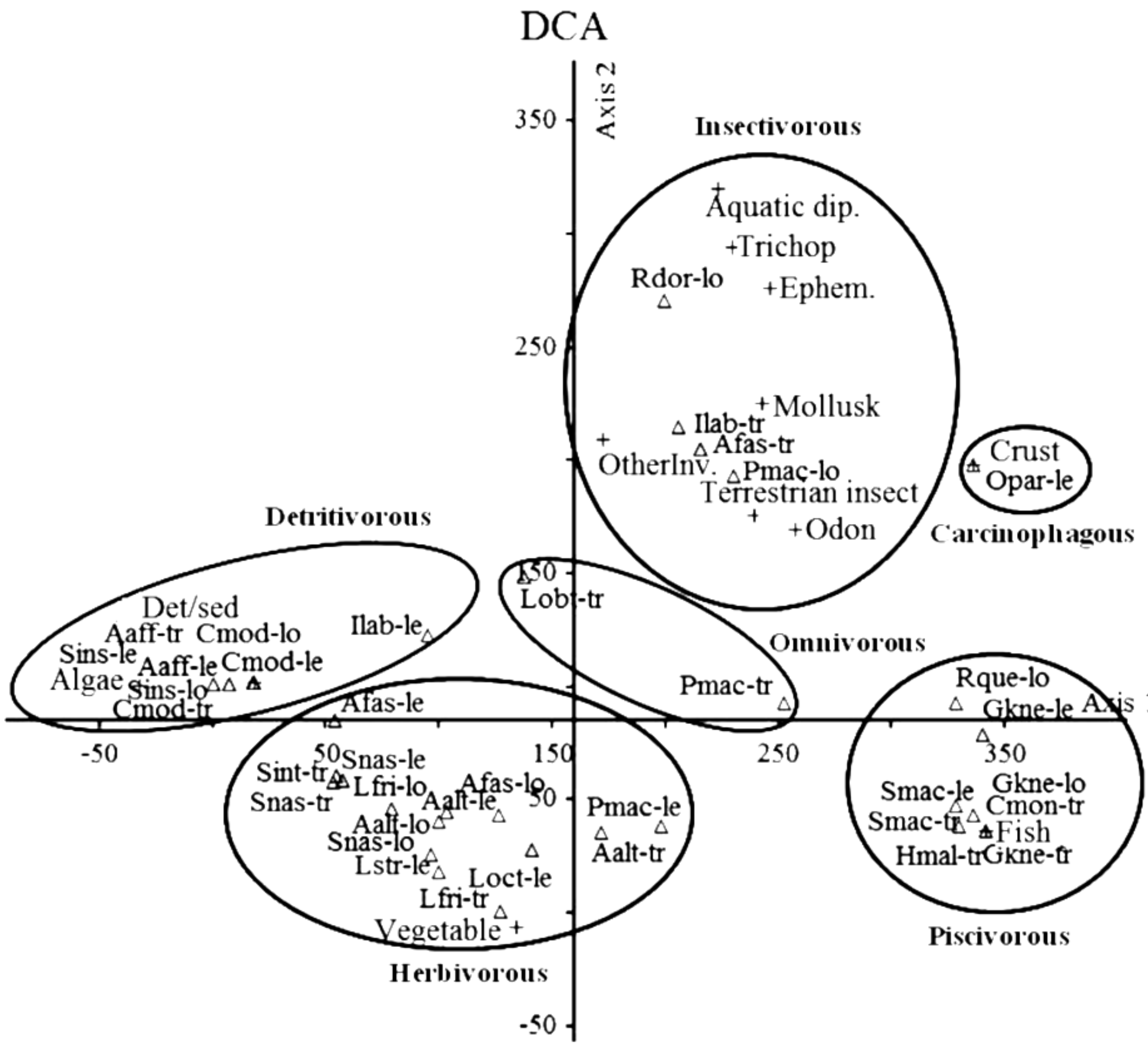


Fig. 2. Detrended Correspondence Analysis (DCA) (biplot) considering the fish species of each stretch and the different trophic categories in Jurumirim Reservoir, Upper Paranapanema River, state of São Paulo, Brazil. Acronym of the species in the Table III.

the fish species were related with the trophic categories respecting the evaluation performed based on the values of the alimentary index, evidencing six trophic guilds in the DCA graphic analysis (Fig. 2). The acronyms of the main resources and trophic categories used in de Figure 2 are presented below: (1) Insect categories – Chironomidae: Aquatic dip.; Trichoptera: Trichop.; Ephemeroptera: Ephem.; Odonata: Odon.; (2) Detritus category – Det/Sed.; (3) Vegetal matter category – Vegetable and Algae; (4) Crustaceans category – Crust; (5) Other category – OtherInv; (6) Fishes category – Fish pie.

In terms of abundance and biomass, it was observed relevant contribution of species with feeding habit considered specialist, as detritivorous, herbivorous, and piscivorous. In the zones lotic and lentic, both in number and biomass, there were a dominance of the herbivorous guild while in the stretch transition, the detritivorous guild showed greater contribution considering these parameters (Fig. 3). Together, the three guilds considered as trophic specialists, correspond with more than 70% of the numeric abundance and biomass in the three zones.

The availability of resources among zones was similar, however the proportion among them, inferred from the weight of the sets of the gastric contents analyzed, showed that the availability varied according to the type of resource (Fig. 4). Thus, in the lotic stretch, the most available resources were vegetal matter (41.87%) followed by organic matter (36.38%), and fish (16.37%). For the stretch transition, organic matter was the most used resource (47.57%) followed by fish (27.78%) and vegetal matter (19.71%). In the lentic stretch, vegetal matter was the most representative item (35.36%) followed by fish (32.18%) and organic matter (25.56%).

Among the three zones sampled, although lotic zone had fewer items consumed, it was the point with higher density of resources. However, lentic zone presents greater density of connections between them (Tab. IV).

Tab. II. List of the fish species and number of stomachs analyzed in the three zones (lotic, transition and lentic) of Jurumirim Reservoir, located in the Upper Paranapanema river, state of São Paulo, Brazil (Non-native*).

ORDER / Family / *Species*	Voucher	Number of analyzed stomachs		
		Lotic	Transition	Lentic
CHARACIFORMES				
Characidae				
Astyanax lacustris (Lütken 1875)	MZUEL 5676	5	30	35
Astyanax fasciatus (Cuvier, 1819)	MZUEL 5669	10	20	42
Galeocharax knerii (Steindachner, 1879)	LBP 13302	7	7	10
Oligosarcus paranensis Menezes & Géry, 1983	MZUEL 5677	-	-	5
Serrasalmus maculatus Kner, 1858	MZUEL 5665	-	34	69
Curimatidae				
Cyphocharax modestus (Fernández-Yépez, 1948)	LBP 13297	21	77	17
Steindachnerina insculpta (Fernández-Yépez, 1948)	LBP 13313	39	4	26
Erythrinidae				
Hoplias malabaricus (Bloch, 1794)	MZUEL 5662	-	-	4
Parodontidae				
Apareiodon affinis (Steindachner, 1879)	LBP 13316	-	38	85
Anostomidae				
Leporinus friderici (Bloch, 1794)	LBP 13304	9	5	-
Megaleporinus obtusidens (Valenciennes, 1837)	LBP 13318	-	6	-
Leporinus octofasciatus Steindachner, 1915	LBP 13294	-	-	6
Leporinus striatus Kner, 1858	LBP 13300	-	-	5
Schizodon intermedius Garavello & Britski, 1990	LPB 13311	-	58	-
Schizodon nasutus Kner, 1858	MZUEL 5678	15	79	57
SILURIFORMES				
Pimelodidae				
Iheringichthys labrosus (Lütken, 1874)	LBP 13306	-	11	21
Pimelodus maculatus LaCépède, 1803	LBP 13317	6	18	64
Heptapteridae				
Rhamdia quelen (Quoy & Gaimard, 1824)	LBP 13310	5	-	-
Doradidae				
Rhinodoras dorbigny (Kner, 1855)	LBP 7446	30	-	-
PERCIFORMES				
Cichlidae				
Cichla monoculus Spix & Agassiz, 1831	MZUEL 5671	-	19	-

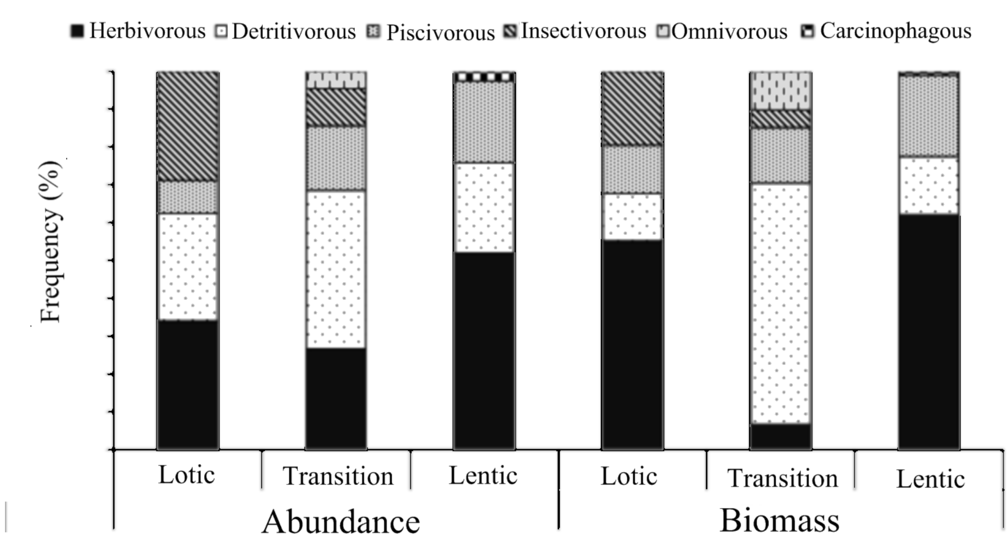


Fig. 3. Importance of trophic guilds (in numeric abundance and biomass) by stretch (lotic, transition, and lentic) of Jurumirim Reservoir, Upper Paranapanema River, state of São Paulo, Brazil.

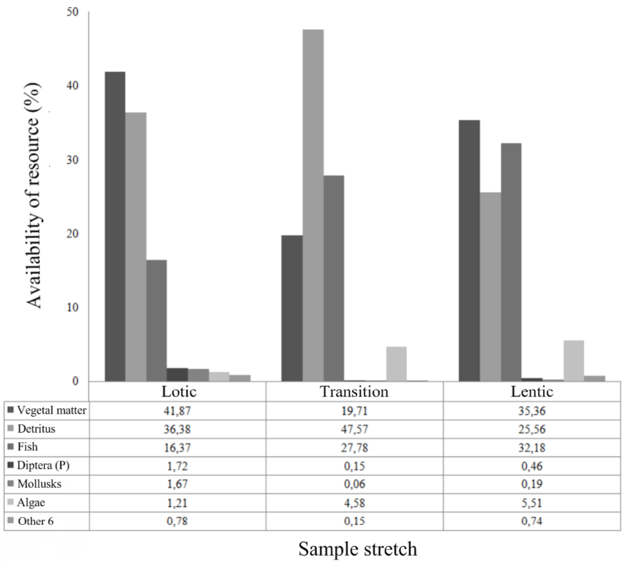
Tab. III. Trophic group determined by the main food categories, highlighted in bold, consumed by the fish species in three zones (1, 2, and 3) of Jurumirim Reservoir, Paranapanema river, Upper Paranapanema River, state of São Paulo, Brazil.

Species	Acronym	Stretch	Trophic Group	Trophic Category					
				Vegetal	Insects	Fishes	Organic Matter	Crustaceans decapods	Other invertebrates
Astyanax lacustris	Alac	Lotic	Herbivorous	**95.87**	4.13	-	-	-	-
		Transition	Herbivorous	**71.54**	20.26	8.20	-	-	-
		Lentic	Herbivorous	**86.19**	8.39	0.29	4.77	0.36	-
Astyanax fasciatus	Afas	Lotic	Herbivorous	**87.90**	5.67	-	6.43	-	-
		Transition	Insectivorous	47.34	**50.51**	-	2.15	-	-
		Lentic	Herbivorous	**87.77**	5.68	-	5.90	-	0.66
Apareiodon affinis	Aaf	Transition	Detritivorous	11.60	-	-	**88.40**	-	-
		Lentic	Detritivorous	19	-	-	**81**	-	-
Cyphocharax modestus	Cmod	Lotic	Detritivorous	0.10	-	-	**99.90**	-	-
		Transition	Detritivorous	0.21	-	-	**99.79**	-	-
		Lentic	Detritivorous	-	-	-	**99.75**	-	0.25
Cichla kelberi	Ckel	Transition	Piscivorous	-	0.01	**99.99**	-	-	-
Galeocharax knerii	Gkne	Lotic	Piscivorous	-	-	**100**	-	-	-
		Transition	Piscivorous	-	-	**100**	-	-	-
		Lentic	Piscivorous	-	-	**57.20**	-	42.80	-
Hoplias malabaricus	Hmal	Transition	Piscivorous	-	0.07	**99.93**	-	-	-
Iheringichthys labrosus	Ilab	Transition	Insectivorous	27.77	**58.61**	-	8.17	3.24	2.20
		Lentic	Detritivorous	2.66	28.32	0.23	**59.61**	0.55	8.63
Leporinus friderici	Lfri	Lotic	Herbivorous	**69.25**	-	0.15	30.60	-	-
		Transition	Herbivorous	**97.73**	-	-	2.27	-	-
Megaleporinus obtusidens	Mobt	Transition	Omnivorous	34.87	17.15	-	46.47	-	1.51
Leporinus octofasciatus	Loct	Lentic	Herbivorous	**83.98**	12.18	-	0.88	-	2.95
Leporinus striatus	Lstr	Lentic	Herbivorous	**94.89**	-	-	5.11	-	-
Oligosarcus paranensis	Opar	Lentic	Carcinophagous	-	2.26	-	-	**97.74**	-
Pimelodus maculatus	Pmac	Lotic	Insectivorous	10.25	**58.30**	-	-	-	31.45
		Transition	Omnivorous	22.60	9.60	28.20	25.03	4.95	9.62
		Lentic	Herbivorous	**55.61**	15.21	18.57	7.04	0.89	2.69
Rhinodoras dorbignyi	Rdor	Lotic	Insectivorous	1.59	**91.58**	-	3.06	-	3.78
Rhamdia quelen	Rque	Lotic	Piscivorous	5.48	1.04	**62.93**	0.49	30.06	-
Serrasalmus maculatus	Smac	Transition	Piscivorous	-	0.19	**99.81**	-	-	-
		Lentic	Piscivorous	0.25	-	**99.75**	-	-	-
Steindachnerina insculpta	Sinc	Lotic	Detritivorous	0.12	-	-	**99.88**	-	-
		Lentic	Detritivorous	1.06	-	-	**98.94**	-	-
Schizodon intermedius	Sint	Transition	Detritivorous	49.45	-	-	**50.55**	-	-
Schizodon nasutus	Snas	Lotic	Herbivorous	**87.18**	-	-	12.82	-	-
		Transition	Detritivorous	35.81	-	-	**64.19**	-	-
		Lentic	Herbivorous	**63.76**	-	-	36.24	-	-

Tab. IV. Trophic interaction networks parameters based on assemblages and the resources consumed by fish in Jurumirim Reservoir, Upper Paranapanema River, state of São Paulo, Brazil.

	Stretch 1	Stretch 2	Stretch 3
Trophic species	10.0	**14.0**	13.0
Resource	31.0	**38.0**	34.0
Density resources	**3.1**	2.7	2.6
Trophic linkages	78.0	**140.0**	136.0
League density trophic	7.8	10.0	**10.5**

In the lotic zone, the resources most used by the assemblage were vegetal matter and detritus, used by seven species, and terrestrial insect and seed, both being consumed by five species. The species that concentrated the largest number of items (14) was *Astyanax fasciatus* (Cuvier, 1819). *Rhinodoras dorbigny* (Kner, 1855), *Rhamdia quelen* (Quoy & Gaimard, 1824) and *Pimelodus maculatus* LaCépède, 1803 consumed respectively 13, 11 and 10 items in this environment (Fig. 5). In transition zone, it was observed that the items with the highest number of links are vegetal matter, Chironomidae larvae, detritus and aquatic insect with respectively 10, 10, 9 and 8 links in the chain. The species that used a greater number of means were *P. maculatus*, *A. fasciatus*, *Schizodon intermedius* Garavello & Britski, 1990 and *A. fasciatus*, which 19, 16, 16 and 13 items consumed respectively (Fig. 6). Finally, in lentic zone of the items with the highest number of interactions were detritus (10), vegetal matter and aquatic insect, both with 8 links. Regarding the fish species, those called to the largest number of items were *P. maculatus* (24), *Astyanax altiparanae* Garutti & Britiski, 2000 (15) and *Iheringichthys labrosus* (Lukten, 1874) (14) (Fig. 7).



	Lotic	Transition	Lentic
Vegetal matter	41,87	19,71	35,36
Detritus	36,38	47,57	25,56
Fish	16,37	27,78	32,18
Diptera (P)	1,72	0,15	0,46
Mollusks	1,67	0,06	0,19
Algae	1,21	4,58	5,51
Other 6	0,78	0,15	0,74

Fig. 4. Proportion of the resources used by the species in the three studied zones in Jurumirim Reservoir, Upper Paranapanema River, state of São Paulo, Brazil: 1, Lotic; 2, Transition; 3, Lentic.

DISCUSSION

The time required by fish community structure to achieve certain degree of stability after reservoir closure may vary widely, and there is no consensus about it (PETRERE-JUNIOR, 1996). There are evidences of stabilization of the fish abundance and species richness between 15 and 40 years after a reservoir is formed (MOL *et al.*, 2007; ORSI & BRITTON, 2014) but, little is said about the trophic structuring.

The trophic structure of a reservoir is the reflection of the interaction between the quality/quantity of food available in the environment and the degree of morphological/behavioral constraints showed by the species, though this last is liable to ontogenetic variations (GASPAR DA LUZ *et al.*, 2001).

The short-term effects of impoundments upon fish feeding dynamic have already been widely studied (HAHN *et al.*, 1997, 1998; ALBRECHT & CARAMASCHI, 2003; LUZ-AGOSTINHO *et al.*, 2006; NOVAES *et al.*, 2004; SCHNEIDER *et al.*, 2011), being their reflections discussed in the review made by HAHN & FUGI (2007). This review gives us a pattern of changes that occur in the food chain of fish pre and post damming remedying the absence of previous information about the damming of the HPP Jurumirim before and immediately after your formation.

As seen, the literature about questions involving trophic reservoirs is wide. However, when the diet of fish is associated with the formation time, the literature draws only perspectives about the effects of dams on the feed composition of fish communities. In this context, authors like AGOSTINHO *et al.*(2007) and ARAUJO-LIMA *et al.*(1995) emphasize that the fish community should, as time goes by, be maintained by autochthonous items, as observed in the networks of trophic interactions formed by the species evaluated in the Jurumirim reservoir, thus enhancing the effects of trophic accommodation on the local ichthyofauna.

Among the few studies that approach the long-term effects of reservoir upon trophic dynamics of fish assemblages, it was observed that in old reservoirs, although of small size, fish still take advantage of allochthones items in their diet (DIAS *et al.*, 2005). On the other hand, in old medium and large reservoirs, mainly autochthonous items and vegetal debris maintain the food chain of fish species (ABELHA *et al.*, 2005; BENNEMANN *et al.*, 2011; RIBEIRO *et al.*, 2014; SOUTO *et al.*, 2017).

Such items are always found in available and constant in the vast majority of hydroelectric systems (SOUTO *et al.*, 2016). These factors (availability and consistency) can be considered as the basic elements that explain the processes of trophic accommodation of fish assemblages in these systems.

Possibly, the use of this resource might be a reflection of the ichthyofaunistic adjustment to the hydrological regime that most of the reservoirs are submitted (SOUTO *et al.*, 2016). These data corroborate with other systems analyzed, as well as with the perspectives drawn for old reservoirs (ARAUJO-LIMA *et al.*, 1995; ABELHA *et al.*, 2005; DIAS *et al.*, 2005; AGOSTINHO *et al.*, 2007; BENNEMANN *et al.*, 2011).

The trophic specialization was observed here presenting dominance of the guild of herbivores, both in abundance and biomass in lotic and lentic zones. GOULDING (1980) reports that herbivory is largely influenced by spatial and temporal variations, mainly in flooded areas or under the influence of dams.

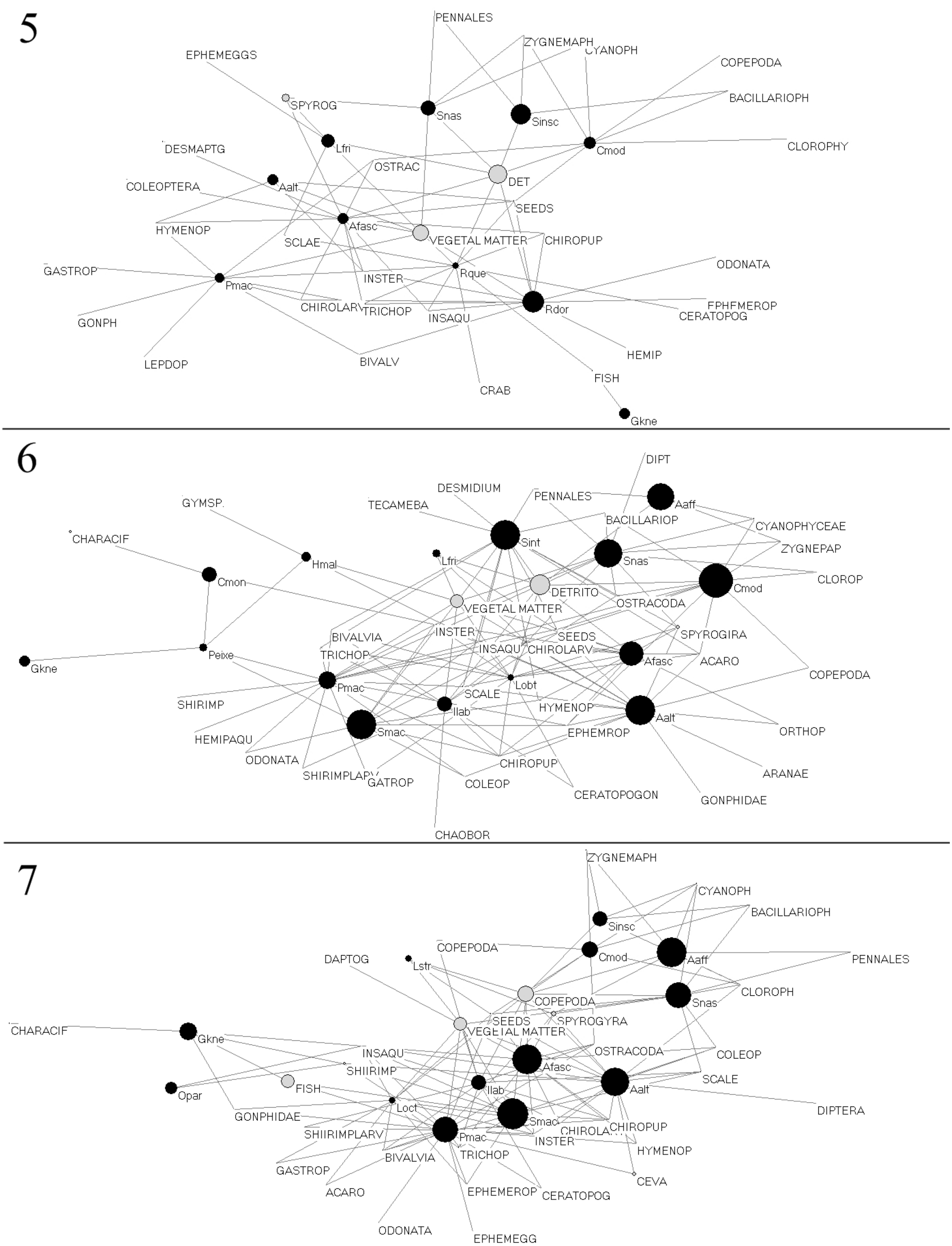
XIMENES *et al.* (2011) corroborate our findings, reporting in the Ibicuí River that the composition and distribution of species that compose the trophic guilds are dependent on several complex and interactive factors. Among these factors, these authors emphasized the habitat structure, food availability, fish assemblage richness, environmental factors such as physical and morphological characteristics, and the time that the reservoir is formed.

Spanned the timeframe evaluated in this study, it is considered that the trophic structure of fish assemblages in old reservoirs is reflective of various components mentioned above and especially the relationship between the remaining fish species in the process of colonization and the time of formation of this reservoir.

AGOSTINHO *et al.* (2015) reports that species with pre-adaptive characteristics favorable to the consumption of a big resources variety are considered favored in the colonization phase of reservoirs. Thus, in new reservoir, normally the most abundant trophic guild is omnivorous, composed by opportunist and trophic generalist species.

In Jurumirim Reservoir, which is old, the majority species presented specialized feeding habit. This feeding structure is considered a reflection of trophic accommodation of species in the environment throughout the time that the reservoir was formed. MÉRONA *et al.* (2003) corroborates this tendency in the fish assemblages.

The results presented in this study are considered as a general overview of trophic accommodation of fish assemblages in old reservoirs, in which the ichthycenosis are



Figs 5-7. Trophic interactions networks built with fish species (black) and resources consumed (gray): Fig. 5, Stretch 1 (lotic); Fig. 6, Stretch 2 (transition) and Fig. 7, Stretch 3 (lentic) in Jurumirim Reservoir, Upper Paranapanema River, state of São Paulo, Brazil.

able to exploit the most available food resources throughout the formation of the reservoirs, finding a way to avoid overlapping food and competition for resources. Thus, the length of time of formation of the reservoirs reflects in the ichthyofauna, making the remaining fish assemblages show a tendency to express specificity in their diet, with the common groups defined as trophic specialist mainly piscivorous, detritivorous, and herbivorous.

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