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RESEARCH PAPER

Interacting effects of spatial gradients and fishing gears on characterization of fish assemblages in large reservoirs

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Abstract Understanding the variation of fish assemblages in reservoirs is crucial for precise interpretations of ecological processes. However, representative samples in such environments are subjected both to spatial zonation (longitudinal and transversal gradients) and limitations of fishing gears. We used a large zoned reservoir (Itaipu, Brazil) to perform a quasi-experiment that assessed the relative role of spatial gradients and fishing methods on fish diversity and composition. Active (cast nets, electrofishing and seines) and passive (gillnets and longlines) fishing gears were employed in lotic, transitional and lentic habitats of the reservoir and three large tributaries. In total 6281 individuals of 101 species were captured. Sampling methods and spatial gradients had an influence on species composition, with significant interactions between these factors. In addition, results produced by a variation partitioning analysis suggested that 21 % of the species richness was explained by the sampling methods and 7 % by the longitudinal gradient; whereas for species composition, 12 and 3 % corresponded to sampling methods and transversal gradients, respectively. Overall, our results suggest that variations among fishing gears is greater than across strong spatial gradients, emphasizing the importance of using multiple and complementary fishing methods in reservoirs for characterization of fish assemblages. The interactions between spatial gradients and sampling methods were higher with transversal than with longitudinal gradients, suggesting that substantial differences in species richness and composition among sampling gears depend to some extent on habitat. The approach used here would be applicable to any large zoned inland waterscape.

Keywords Dams · Longitudinal gradients · Fishing methods · Quasi-experiment · Transversal gradients

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Introduction

Precise estimations of ichthyofauna attributes in large reservoirs and lakes are affected by the spatial distribution of fish and the selectivity of sampling methods (Jackson and Harvey 1997; Kubečka et al. 2009). Reservoirs commonly share lotic and lentic characteristics (Okada et al. 2005; Irz et al. 2006) and often reveal formation of strong spatial gradients (longitudinal and transversal zonation, Thornton et al.

1990; Agostinho et al. 2007). These zoned waterscapes with both lacustrine (near the dam) and riverine (upstream end) environments produce a high diversity of biotopes (Welcomme 2011), which have critical consequences on fish distribution (Agostinho et al. 2007; Barletta et al. 2010).

Longitudinal gradients form lacustrine zones with gradual upstream transitions to riverine zones. Lacustrine zones are geographically fragmented and consist of lentic environments with low level of organic nutrients and clear waters (Kimmel et al. 1990; Oliveira et al. 2004). Transitional zones share features of both lakes and rivers and have higher primary production, while the upstream riverine zone tends to be lotic with intense flow and higher levels of nutrients (Kimmel et al. 1990; Dai et al. 2013). These physico-chemical and biological features have a strong influence on the structure and dynamics of fish assemblages (Matthews et al. 1989; Vašek et al. 2004; Okada et al. 2005; Agostinho et al. 2007) and can lead to formation of gradients in fish populations, with consequences for fisheries (Okada et al. 2005).

Transversal gradients (downstream-upstream tributaries) affect the tributaries that flow into reservoirs and often form three distinct zones: the proper margins of the reservoir; lentic transitional zones that are influenced by both the lentic lake-like environment and the tributaries; and the riverine zones with lotic waters upstream from the tributaries (Oliveira et al. 2004). This axis of the reservoir is commonly used as a migration route by several species of fish for reproduction (Welcomme 2011) and other purposes (see Ribeiro and Petrere 1990).

In addition to the influence of spatial gradients on fish distribution, different sampling methods are known to produce divergent results. Fishing gears are commonly classified as active or passive. Active gears depend on the movements of the gear upon species (e.g. cast nets, electrofishing and seines) while passive methods depend on the movement of the target species towards the gears (e.g. gillnets, longlines and traps) (Hamley 1975; Rudstam et al. 1984; Kubečka et al. 2012). Due to contrasting behaviors and habitats of different fish species, fishing gears are strongly size- and species-selective (Olin and Malinen 2003; Carol and García-Berthou 2007) and the application of only one or two fishing gears can certainly fail to capture the diversity present in different habitats (Peterson and Paukert 2009). Therefore, combining various passive and active sampling gears (Hinch 1991; Olin et al. 2009) and exploring different spatial gradients is essential for maximizing captures and developing a comprehensive understanding of fish assemblages in zoned waterscapes.

The evaluation of spatial patterns (biological and non-biological) is a useful approach to support ecosystem management in reservoirs (Vanotte et al. 1980; Lindim et al. 2011). Some studies report the effects of longitudinal (Oliveira et al. 2004, 2005; Prchalová et al. 2008) and transversal (Oliveira et al. 2004, 2005) gradients on fish assemblages. However, studies with quasi-experimental designs (Block et al. 2001) that allow evaluation of the interactions between both gradients simultaneously (including biotopes in reservoir and tributaries) and different fishing methods are scarce.

Given the dispersed distribution of fish throughout different biotopes within large reservoirs and the well-known dependence of fish abundance and richness on fishing gears, we suggest that most surveys conducted in large reservoirs (mainly tropical) that used few combinations of sampling gears may have underestimated species richness and composition (Table 1). Here, we aimed at determining the relative role of spatial gradients and fishing methods on assessing fish diversity and composition in large reservoirs based on a quasi-experiment sampling design (for details see Block et al. 2001). We used the Itaipu reservoir (Paraná River basin, Brazil) as a model to simulate other large zoned (longitudinal and transversal gradients) waterscape systems. Lastly, the approach used herein is applicable to any similarly zoned reservoir or lake.

Materials and methods

Study area

The Itaipu reservoir was impounded in October 1982 and is situated on the upper course of the Paraná River along the Brazil-Paraguay border (between 24° 05′ and 25° 27′S/54° 05′ and 54° 48′W). It is 151 km long, with 1350 km^2 of surface area and an average depth of 22 m. Sampling was conducted in three large tributaries of the east margin (Brazilian margin): Arroio Guaçu, São Francisco Verdadeiro and Ocoí (Fig. 1). All of these rivers share common characteristics such

Table 1 A survey of fishing methods used in studies of reservoir fish

Reference	Castnets	Electrofishing	Gillnets	Longlines	Seines	Other
Gido et al. (2000)			+			
Barrela and Petrere (2003)			+			
Matthews et al. (2004)		+	+		+	+
Oliveira et al. (2004)			+			
Irz et al. (2006)		+	+			
Oliveira et al. (2005)			+			
Paller (2005)		+				
Vehanen et al. (2005)		+				+
Carol et al. (2006)		+	+			
Silva et al. (2006)			+		+	
Thapanand et al. (2007)		+	+			
Prchalová et al. (2009)			+			
Chellappa et al. (2009)			+			+
Gido et al. (2009)		+			+	
Říha et al. (2009)					+	
Gao et al. (2010)			+			+
Medeiros et al. (2010)			+		+	+
Oliveira and Tejerina-Garro (2010a, b)			+			+
Quarcoopome et al. (2011)			+			
Terra and Araújo (2011)			+			
Dumitraşcu and Mitrea (2012)		+	+			+
Liu et al. (2012)			+			
Melcher et al. (2012)	+	+	+	+		
Li et al. (2013)		+	+	+	+	+

We searched for publications with the combination of the words "ecolog*", "fish*" and "reservoir*" in the Web of Knowledge database (www.webofknowledge.com) between the years 2000 and 2013. Bold letters indicate reservoirs in tropical areas

as rapids interspersed with backwaters, rocky or sandy bottoms, and margins with native riparian vegetation or crops.

Sampling

Samples were collected in August 2005 and May 2006 at three sites in each tributary river: one in the lotic stretch (~40 km upstream from the reservoir), one in the lentic stretch (~10 km upstream from the reservoir), and one in the body of the reservoir (municipalities of Guaíra, Santa Helena and Foz do Iguaçu). This design aimed to consider both longitudinal and transversal (from inland tributaries to the reservoir) gradients (see Thornton et al. 1990) in Itaipu reservoir. Hereafter, we will refer to longitudinal gradients as LG, transversal gradients as TG and sampling methods as SM.

Fish were caught using active (cast nets, electrofishing and seines) and passive methods (sets of gillnets and longlines). The cast nets (24 mm mesh and 2.5 m in height; 40 mm mesh and 2.5 m in height; 60 mm mesh and 2.88 m in height, with five throws during daylight and five after sunset) were employed in lotic sites. Electrofishing samples consisted of a generator (2.5 KW, 220 V, 1 A DC) coupled to two dip nets, and was conducted from a boat used for surveys in structured areas (macrophytes and trunks), with duration of 10 min twice a day, at 3 and 10 p.m. Seines (5 mm meshes and 20 m long) were employed in coastal areas with no structures twice a day, at 3 and 10 p.m. The sets of gillnets (24, 30, 40, 50, 60, 70, 80,

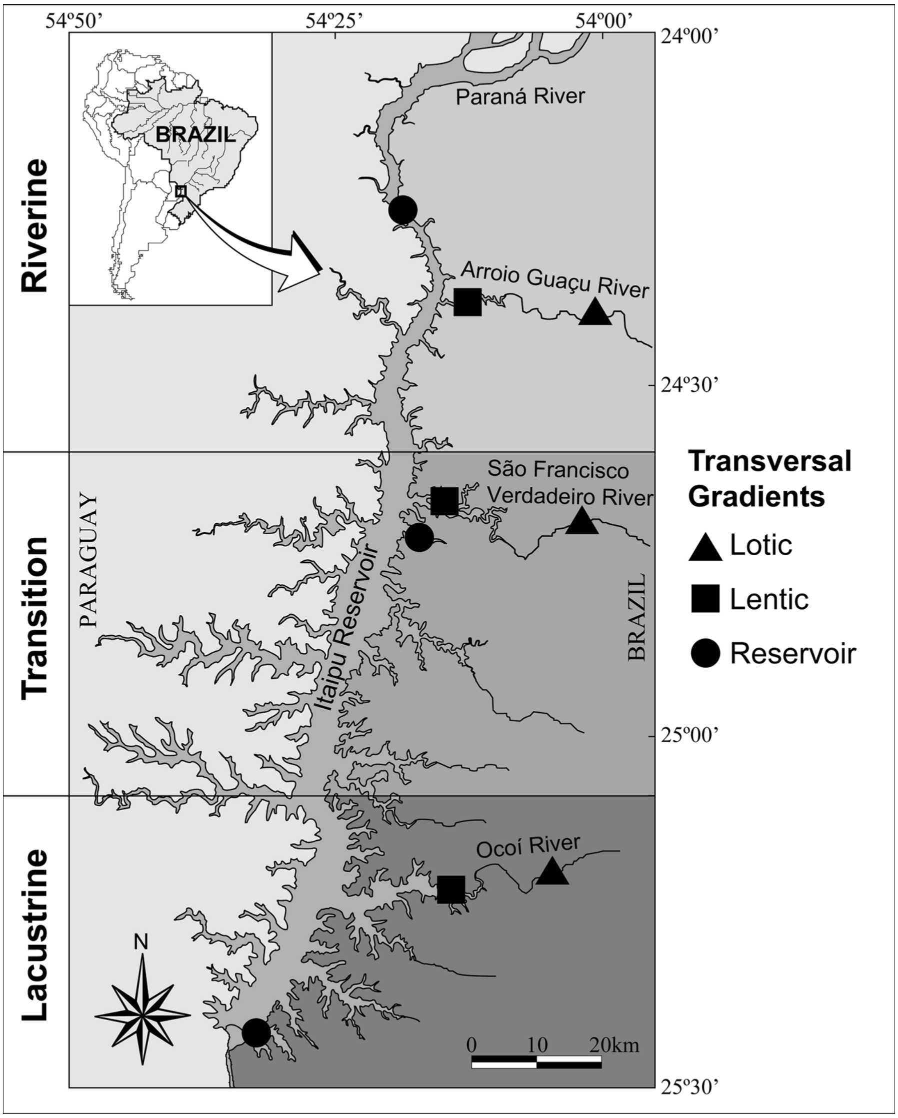

Fig. 1 Map of Itaipu Reservoir showing sampling sites along longitudinal and transversal gradients

90, 100, 120, 140 and 160 mm meshes and 10 m long each) were installed in the shore for 24 h, with catches at 8 a.m., 4 p.m. and 10 p.m. Longlines (10 hooks 28 × 17 mm and 10 hooks 45 × 30 mm) were baited with fish pieces and installed from the shores for 24 h, with catches at 8 a.m., 4 p.m. and 10 p.m., and were employed in the lotic zones of the tributaries (Table 2).

After sampling, fish were anesthetized using benzocaine (up to 40 mg/l), euthanized and preserved in 4 % formalin solution. Each specimen was identified to the species level and deposited in the Museum of Ichthyology at the Nucleus of Research in Limnology, Ichthyology and Aquaculture, State University of Maringá, Brazil.

Data analysis

All analyses were performed using R (R Core Team 2013). In order to assess the representativeness of fish samples, species accumulation curves (rarefaction method) based on sampling sites and species richness were calculated in the “BiodiversityR” package (Kindt and Coe 2005). Diversity was assessed using the Shannon diversity index (*H*) and evenness (*J*). To obtain estimates of the true number of species, we

Table 2 Sampling methods employed in each river and site at Itaipu Reservoir

River	Water flow	Cast nets	Elecrofishing	Gillnets	Longlines	Seines
Arroio Guaçu	Lotic	+	+	+	+	
Arroio Guaçu	Lentic			+	+	+
Arroio Guaçu	Reservoir		+	+	+	+
S.F. Verdadeiro	Lotic	+	+	+	+	
S.F. Verdadeiro	Lentic		+	+	+	
S.F. Verdadeiro	Reservoir			+	+	+
Ocoí	Lotic	+	+	+	+	
Ocoí	Lentic			+	+	+
Ocoí	Reservoir			+	+	+

computed the second-order jackknife richness estimator (Jack2) in "vegan" package (Oksanen et al. 2013). Jack2 is amongst the most recommended nonparametric resampling measures (Palmer 1991; Brose et al. 2003).

To examine how the assemblage sampled differed between different gears, we used nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distances derived from abundance data and plotted sample scores (Legendre and Legendre 1998) by gear type, using "vegan" (Oksanen et al. 2013).

To test if LG, TG and SM differed in species composition, we used permutational multivariate analysis of variance using distance matrices (PERMANOVA, Anderson 2001), as implemented in function "adonis" of "vegan" (Oksanen et al. 2013), with Bray-Curtis distances and 9999 permutations. Because "adonis" can confound location and dispersion effects (Warton et al. 2012), we also tested for the latter using a permutation test of multivariate homogeneity of groups' dispersions (Anderson et al. 2006), as available in the function "permutest.betadisper".

We used variation partitioning (VP) analysis (Borcard et al. 1992, Legendre and Legendre 1998) to evaluate the effects of LG, TG and the SM on species richness (VP1) and composition (VP2). To do so, the total percentage of variance in species richness and composition (transformed with Hellinger distance) was divided into unique (pure effects) and shared (joint effects) contributions of spatial predictors and sampling methods. The variance was explained by redundancy analysis (RDA, with Euclidean distance, Lambert et al. 1988; Legendre and Gallagher 2001) divided into unique and shared contributions, and the significance of pure effects (joint variation is not testable) was tested with ANOVA- like permutations

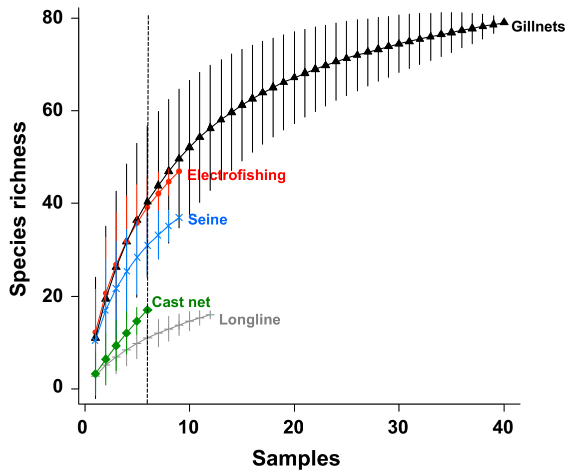

Fig. 2 Accumulation curves of species richness by sampling method in Itaipu Reservoir. Bars represent standard deviation

(9999 permutations). VP is available as function "varpart" of "vegan" (Oksanen et al. 2013).

Results

In total we captured 6281 individuals of 103 species in the Itaipu reservoir and three of its tributaries. The active methods captured 4225 individuals (67.6 %) of 70 species (12 unique, sampled exclusively by these methods) while the passive methods captured 2026 individuals (32.4 %) of 80 species (five unique). Gillnets caught the highest number of species (79) and longline the lowest (16). Cast nets, seine and electrofishing sampled 17, 37 and 47 species, respectively. The accumulation curves did not suggest clear stabilization tendencies (Fig. 2) and the richness estimator

Jack2 pointed to the possible occurrence of a larger number of species (Table 3).

The most abundant species were *Hemigrammus marginatus* Ellis, 1911 (20.0 %), *Hyphessobrycon* sp. (16.2 %), *Bryconamericus stramineus* Eigenmann, 1908 (7.1 %), and *Astyanax altiparanae* Garutti and Britski, 2000 (6.3 %). All other species represented less than 4 % of total. Gillnets produced the highest abundance values for *Satanoperca pappaterra* (Heckel, 1840) and *Steindachnerina brevipinna* (Eigenmann and Eigenmann, 1889), both with 7.4 %. The most abundant species caught by electrofishing was *H. marginatus* (40.2 %), followed by *Hyphessobrycon* sp. (18.9 %). Seines sampled high densities of *Hyphessobrycon* sp. and *B. stramineus* (31.3 and 20.9 %, respectively). Longline produced high numbers of *Pinirampus pirinampu* (Spix and Agassiz, 1829) and *Potamotrygon falkneri* Castex and Maciel, 1963 (21.5 and 16.9 %, respectively). For cast nets the most captured species were *Prochilodus lineatus* (Valenciennes, 1836) and *Hypostomus* cf. *strigaticepis* (Regan, 1908) (26.3 and 21.1 %, respectively, Fig. 3).

NMDS analysis (stress = 0.19) suggested a relationship between sampling methods and species composition. The ordination analysis showed that electrofishing and seine fishing produced similar fish catches, but overall, all sampling methods differed in species composition (Fig. 4).

PERMANOVA suggested that species composition significantly depended on LG, TG and SM and evidenced by significant LG × TG and TG × SM interactions, and non- significant LG × SM and LG × TG × SM interactions (Table 4). The dispersion among groups (factors and combinations) was not significantly different (permutation test, $P = 0.22$).

The relative contribution of spatial and sampling factors was slightly different for species richness (VP1) and species composition (VP2). For VP1, variation partitioning showed pure significant contributions for LG and SM (7 and 21 % respectively, both $P < 0.005$). For VP2, there were significant effects of TG and SM (3 and 12 % respectively, both $P \leq 0.005$) and not significant for LG (1 %, $P = 0.7$). Interacting effects LG × SM (1 %) and TG × SM (3 %) for VP1 and TG × SM (1 %) for VP2 were also present (Fig. 5).

Discussion

Our study (a quasi-experiment) suggests that samples taken over space and time can provide useful data, but fail to accurately describe fish fauna if spatial gradients are not adequately explored through employment of diverse fishing methods. Even for estimates based on repeated surveys along time, fish richness and composition tend to be subsampled in wide and heterogeneous waterscapes.

The results suggest that more samples or additional time spent sampling would increase the species richness estimated (accumulation curves and Jack2). Sampling fish in tropical reservoirs is difficult due to the extent of heterogeneity in the environment, with very distinct biotopes such as forested streams, rivers, ponds and deep lakes. Furthermore, significant economic resources and efforts from a large number of skilled fishers and scientists are required. Considering time, spatial and economic resource limitations, our quasi-experiment design seems a very plausible method for characterizing fish assemblages in large zoned reservoirs or lakes. However, it should be

Table 3 Values of mean species richness observed (mean *S*), total richness (*S* Total), unique species for the gear (Unique *S*), second-order jackknife estimator (Jack2), Shannon index (*H*) and evenness (*J*) for each of the sampling methods in the study

Sampling method	Mean *S*	*S* Total	Unique *S*	Jack2	*H*	*J*
Cast net	3.33	17	1	36.4	0.77	0.34
Electrofishing	12.22	47	8	76.6	1.43	0.62
Gillnet	11.07	79	24	102.4	1.72	0.81
Longline	2.83	16	1	27.7	0.78	0.31
Seine	10.44	37	3	58.2	1.58	0.72
Overall	–	103	37	135.0	1.45	–

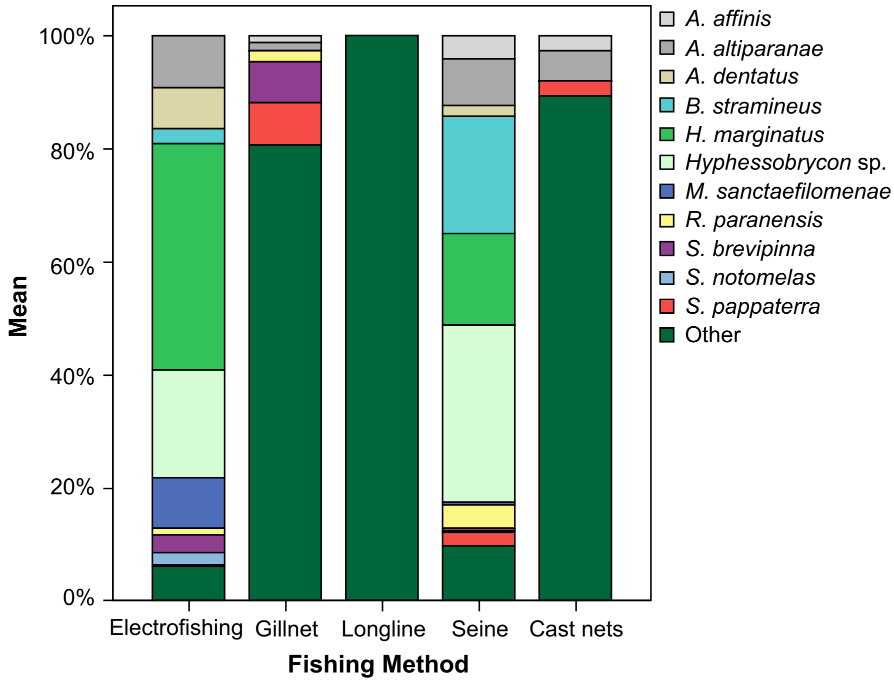

Fig. 3 Proportion of species captured by sampling method in Itaipu Reservoir. "Other" = sum of species with values ≤1 %

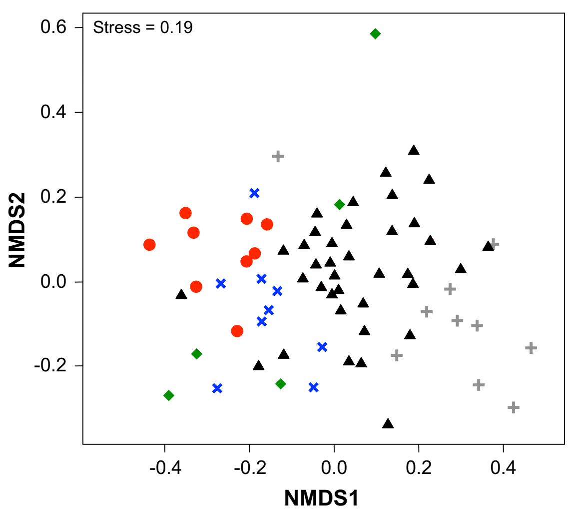

Fig. 4 Nonmetric multidimensional scaling of abundance data from cast nets (*green diamonds*), electrofishing (*blue crosses*), gillnets (*black triangles*), longlines (*grey plus signs*) and seines (*red dots*) ($n = 72$ samples)

Table 4 Permutational multivariate analysis of variance results

Factors	*d.f.*	*F*	*P*
Longitudinal gradient (LG)	2	1.402	**0.022**
Transversal gradient (TG)	2	2.753	**<0.001**
Sampling methods (SM)	4	3.290	**<0.001**
LG × TG	4	1.215	**0.048**
LG × SM	8	0.998	0.486
TG × SM	5	1.287	**0.007**
LG × TG x SM	5	1.104	0.153

Bold letters indicate significant *P* values

d.f. degrees of freedom, *P* significance based on 9999 randomizations

emphasized that we sampled in 2 months along a year. This was done because our objectives were related to show complementarities in fish assemblages as the effect of the gears used. Therefore, we gathered a snapshot of the more common and idiosyncratic fish species found in each visited site that were vulnerable to given sampling methods.

Spatial gradients and sampling methods both explained an important part of the variation in fish richness and composition; and species turnover was observed along the longitudinal gradient. High richness was observed in riverine zones, which constitutes the main habitat for most species (Agostinho et al. 1999), and lower richness was shown for lacustrine zones. This is a common pattern of distribution of fish

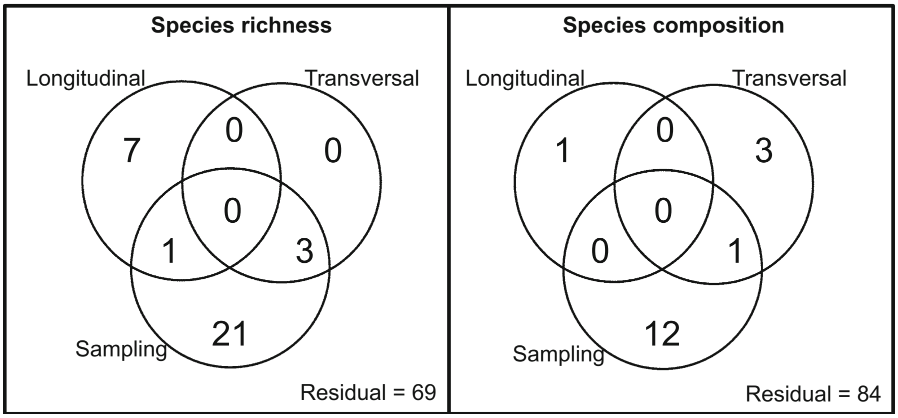

Fig. 5 Relative contribution (% of explained variation) of the spatial gradients, sampling methods and their joint variation in explaining species richness and species composition in Itaipu Reservoir (obtained with the variation partitioning technique). The values of pure fractions are all significant ($P < 0.005$), except for transversal gradients of species richness ($P = 0.2$) and longitudinal gradient of species composition ($P = 0.7$). Joint values are not testable

richness in tropical reservoirs (e.g. Agostinho et al. 1997; Benedito-Cecílio et al. 1997; Carvalho et al. 1998; Welcomme 2001; Oliveira et al. 2005; Okada et al. 2005). The absence of natural lakes in this region and the consequent absence of fish adapted to lentic environments, explains the lack of species pre-adapted to lacustrine waters.

Along the transversal gradient, species composition but not species richness varied significantly. The low variation in species richness in tributaries may be due to the more drastic modification of the regions from lotic to lentic. Although mouths of the tributaries in some reservoirs are known to have low biodiversity (*e.g.* Dai et al. 2013) this is not an expected pattern in Itaipu (and other tropical reservoirs). One of the possible causes promoting low diversity in these regions is that this environment is intensively affected by artificial regulation of the reservoir. The water level and flow in these sites can vary strongly, forcing species to move either into the tributaries or out to the reservoir. Furthermore, the main body of the reservoir is considered a barrier to dispersal of small fish among tributaries (Luttrell et al. 1999).

Although different fishing gears provided biased captures to some degree, sampling methods explained a significant portion of the apparent variation in species richness and composition. Gillnet was the most effective gear for sampling most sites and produced the highest values of species richness and unique species. Due to its versatility and wide range of meshes, gillnets show indisputable advantages over other gears. Despite catches being biased by selecting mainly actively swimmers or by becoming quickly saturated (Minns and Hurley 1988; Olin et al. 2004; Prchalová et al. 2013), selectiveness was lowered by the wide range of mesh sizes and saturation was avoided by regularly removing fish from the nets. Moreover, this gear was set for a whole day, allowing captures of fish with different patterns and times of activity.

Electrofishing captured less species than gillnets but performed better than cast nets and longlines. The results showed that electrofishing and seine samples produced similar richness and composition (accumulation curves and NMDS). Both of these gears are efficient to sample shallow waters, however, while electrofishing is more suited to high complexity areas, e.g. more structured with trunks or macrophytes, seines operate better in un-structured environments, e.g. sandy coasts. The dominant species sampled with both gears are small and common in most of the coastal regions of Itaipu. The high species richness and the high number of unique species captured by these gears reinforce the importance of using two active gears for more accurate ichthyofauna surveys.

Cast nets and longlines produced low species richness and abundance but some exclusive catches (*Leporellus vittatus* to cast nets; *Pinirampus pirinampu*, *Rhaphiodon vulpinus* and *Potamotrygon* cf. *falkneri* to longlines). Cast nets are small (compared with other nets used) and captures may be influenced by environmental characteristics, such as water transparency and deepness. Longlines have a limited number of possible catches due to the pre-determined number of hooks (20 in this case) and are highly selective to large and active piscivorous or omnivorous species. Cast nets and longlines were the least effective methods for assessing species richness but could be useful methods to complement other approaches.

In addition to aiding efficiency of fish surveys in large tropical reservoirs, our findings have important management applications for basins affected by dams and others zoned lacustrine systems. We recommend that fish sampling designs take into account the spatial gradients and use a wide variety of active and passive sampling methods for a more complete characterisation of fish assemblages. The scarcity of reliable information on fish fauna commonly leads to ineffective conservation actions, as the reductionist approaches often focus on a few large or migratory species (Agostinho et al. 2007; Dugan et al. 2010). Besides the need for a comprehensive understanding of fish assemblages to support predictive studies, relevant and robust data are needed to support successful management.

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