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A cascade of dams affects fish spatial distributions and functional groups of local assemblages in a subtropical river

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Dams reduce the longitudinal connectivity of rivers and thereby disrupt fish migration and the spatial distribution of species, impacts that remain poorly studied for some Neotropical rivers from mega-diverse basins. We investigated the spatial distribution of fish species with different trophic and movement/reproductive/size characteristics to assess how functional groups have responded to a cascade of dams on the Uruguai River in southern Brazil. Fish abundance, biomass, and species composition were evaluated at eight locations along the longitudinal gradient. The fish assemblage in the upper stretch was mainly characterized by small and medium-sized species at higher trophic levels, whereas the sites located furthest downstream displayed more medium and large-sized species, including many carnivorous species. Species with high fecundity, seasonal migrants, and catfishes with internal fertilization were common in the river´s middle and lower reaches. Detritivorous species dominated areas distant from the dams. Overall, functional diversity of local fish assemblages was greater in lower reaches. The cascade of dams has impacted the distribution of functional groups of local fish assemblages of Uruguai River. The alteration of functional groups in upper reaches of the river has potential consequences for ecosystem processes and services, such as nutrient cycling and fisheries.

Keywords: Ichthyofauna, Reproductive tactics, Reservoirs, River fragmentation, Trophic groups.

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As barragens reduzem a conectividade longitudinal dos rios e interrompem a migração e a distribuição espacial das espécies, configurando impactos pouco estudados para alguns rios Neotropicais megadiversos. Investigamos a distribuição espacial de espécies de peixes com diferentes características tróficas e reprodutivas para avaliar como grupos funcionais responderam a uma cascata de reservatórios no rio Uruguai, sul do Brasil. Abundância de peixes, biomassa e composição de espécies foram avaliadas em oito locais ao longo do gradiente longitudinal. A assembleia de peixes no trecho superior foi caracterizada principalmente por espécies de pequeno e médio porte em níveis tróficos mais elevados, enquanto que os ambientes localizados mais a jusante apresentaram mais espécies de médio e grande porte, incluindo muitas espécies carnívoras. Espécies com alta fecundidade, migradores sazonais e bagres com fertilização interna foram comuns no curso médio e inferior. Espécies detritívoras dominaram áreas distantes das barragens. A diversidade funcional das assembleias de peixes locais foi maior nas partes inferiores. A cascata de barragens impactou a distribuição dos grupos funcionais das assembleias de peixes locais no rio Uruguai. A alteração da diversidade funcional no curso superior do rio tem consequências potenciais para a dinâmica e serviços do ecossistema, como ciclagem de nutrientes e pesca.

Palavras-chave: Fragmentação de rios, Grupos tróficos, Ictiofauna, Reservatórios, Táticas reprodutivas.

INTRODUCTION

Hydropower dams impact river ecosystems by reducing river longitudinal connectivity (Agostinho *et al*., 2016; Vitule *et al*., 2017; Barbarossa *et al*., 2020), hydrology and sediment dynamics (Araújo *et al*., 2013; Forsberg *et al*., 2017), and water physicochemistry (Zaniboni-Filho, Schulz, 2003). Dams also impact fish populations by altering in-stream and riparian habitats and blocking migration corridors (Mueller *et al*., 2011; Granzotti *et al*., 2018). River fragmentation impacts are both local and regional (Rosenberg *et al*., 1997), with cumulative effects that can affect regions located hundreds of kilometers downstream and upstream of the dam (Grill *et al*., 2015). When dams and their associated reservoirs are built in series, *i.e*., a cascade of dams, impacts to aquatic biota and ecosystem dynamics may be compounded. Hydropower dams constitute one of the main threats to freshwater biodiversity (Vörösmarty *et al*., 2010), and impacts are particularly devastating for the mega-diverse fish faunas in the tropics (Winemiller *et al*., 2016; Vitule *et al*., 2017). Migratory species are especially vulnerable because hydroelectric projects obstruct corridors essential for seasonal movements for reproduction and exploitation of habitats critical for feeding or providing refuge from predation (Carolsfeld *et al*., 2003; Hoeinghaus *et al*., 2009; Pelicice *et al*., 2015). Even for non-migratory fishes, dams cause population fragmentation and reductions in the sizes of local stocks and gene flow among them (Allendorf *et al*., 2012). As a consequence, river fragmentation compromises the adaptive capacity and the long-term persistence of fish stocks (Allendorf *et al*., 2012).

The functional characteristics of fish can be useful for assessing the impacts of dams on river ecology (Hoeinghaus *et al*., 2009; Mouillot *et al*., 2013; Pendleton *et al*., 2014; Santos *et al*., 2017, 2020; Zhang *et al*., 2020). Traits, such as morphology associated with modes of swimming and use of habitat, exploitation of various types of food resources and how food is obtained, defense tactics, reproductive strategies, and other aspects of performance that affect fitness, can be used to group species into functional groups or niches (Violle *et al*., 2007; Winemiller *et al*., 2015). These attributes can be used to assess how fish assemblages respond to human impacts and predicting the fish community's responses to anthropic impacts (Angermeier, Winston, 1998; Arantes *et al*., 2019; Dias *et al*., 2020).

Impacts from dams differentially affect species and locations along the fluvial gradient. Rheophilic species, feeding specialists and species that depended on seasonal access to floodplain habitats generally are excluded from impounded areas (Agostinho *et al*., 2008). Ecological generalists and species adapted for lentic conditions may prosper in modified habitats (Arantes *et al*., 2019). Evaluation of assemblage functional groups facilitates comparative study of natural communities as well as impact assessment for dams and other human disturbances (Hoeinghaus *et al*., 2007; Cella-Ribeiro *et al*., 2017; Pelicice *et al*., 2018). These impacts can be more intense in cascade reservoirs system, in which changes in physical and biological characteristics have a substantial influence on trait compositions of fish communities (Santos *et al*., 2017, 2020; Arantes *et al*., 2019). Here, we assess the distribution of fish functional groups across a dam/reservoir cascade system in the Uruguai River within the subtropical region of South America.

Functional groups of aquatic organisms are expected to be longitudinally distributed in relation to fairly predictable riverscape characteristics, according to the assumptions of the River Continuum Concept (RCC; Vannote *et al*., 1980). For example, greater proportions of insectivorous fishes should occur in the upper river reaches where the riparian vegetation canopy covers the channel and provides allochthonous inputs in the form of terrestrial invertebrates and leaf litter that supports aquatic insects. In lower river reaches, where the channel is broader and sunlight and nutrients fuel autochthonous primary production, omnivorous and detritivorous fishes should comprise greater proportions of fish assemblages. However, this theory applies well to unobstructed rivers. Impoundments disrupt longitudinal connectivity and therefore should alter many predictions of the RCC (Vannote *et al*., 1980). The Serial Discontinuity Concept (SDC; Ward, Stanford, 1995) and Cascading Reservoir Continuum Concept (CRCC; Barbosa *et al*., 1999) predict how reservoir cascades alter physical and biodiversity patterns and processes described by the RCC.

We make several predictions about how the cascade of dams and reservoirs in the Uruguai River should affect the functional composition of local fish assemblages. Areas unaffected by dams with relatively natural flow regimes and habitats with fast-flowing water should retain the full complement of native fishes, including species that are rheophilic, trophic specialists and migratory species (Schork, Zaniboni-Filho, 2018). In areas directly impacted by dams, fish assemblages should be dominated by small and medium-sized fishes with opportunistic life-history strategies (Schork, Zaniboni-Filho, 2017). We further predict that the river's altered longitudinal gradient (with dams blocking fish migration, lentic conditions in reservoirs, modified flow regimes in stretches downstream from dams, and transition zones in between (Thornton *et al*., 1990;

Monaghan *et al*., 2019; Dias *et al*., 2020) has not only affected functional composition of local fish assemblages, but also functional diversity, numerical abundance, and biomass.

MATERIAL AND METHODS

Sampling. The study was conducted along an approximately 600 km reach of the Upper Uruguai River where three hydroelectric dams have been constructed: Barra Grande (Upper stretch – completed in 2005), Machadinho (Middle stretch – completed in 2002), and Itá (Lower stretch – completed in 2000). Barra Grande has an area of 94 km^2 and 90.6 days of the water residence time, while these values are 79 km^2 and 54 days for Machadinho, and 141 km^2 and 55 days for Itá. All of these reservoirs are formed by dams that are more than 100 m height. The spatial distribution of fish functional groups was investigated in eight locations, listed here from upstream to downstream: distant environment upstream from the uppermost dam [Distant Upstream – DU]; Barra Grande Reservoir [R1]; immediately downstream from Barra Grande Dam [Downstream Barra Grande DR1]; Machadinho Reservoir [R2]; immediately downstream from Machadinho Dam [Downstream Machadinho – DR2]; Itá Reservoir [R3]; immediately downstream from Itá Dam [Downstream Itá – DR3]; and distant downstream from the last dam [Distant Downstream - DD] (Fig. 1; Tab. 1). The environments Downstream R1, R2 and R3 were located approximately 250 m downstream from the dams, and the DD is a comparatively long and unimpeded stretch where several free-flowing tributaries join the river.

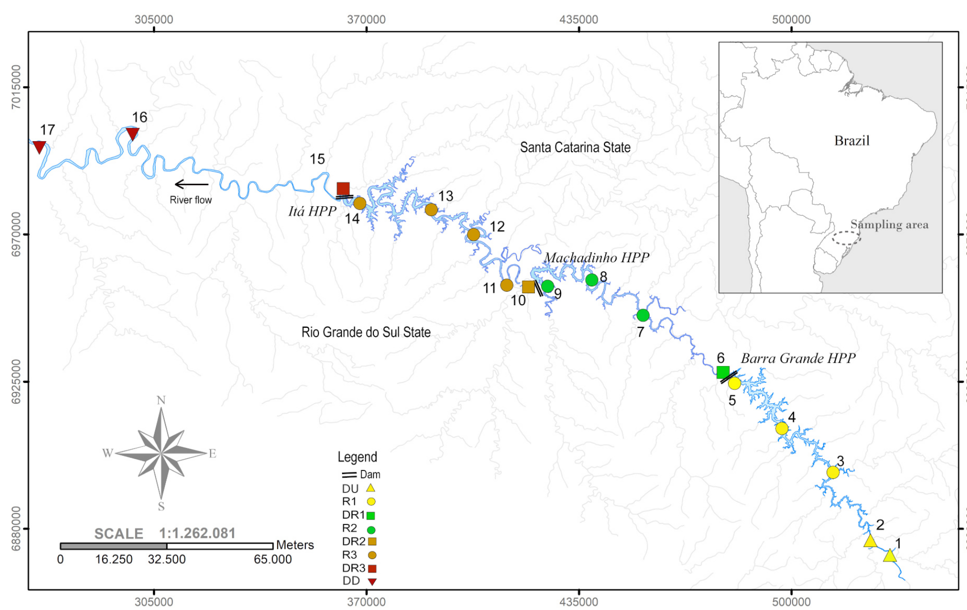

FIGURE 1 | Sampling locations in the Upper Uruguai River, Brazil. The symbols indicate survey sites: circles represent sites within the reservoirs (R1 = site 3 to 5; R2 = site 7 to 9; R3 = site 11 to 14); squares indicate sites located just below dams [Downstream R1 (DR1) = 6, Downstream R2 (DR2) = 10, Downstream R3 (DR3) = 15], and triangles indicate sites that are most distant from dams [Distant Upstream (DU) = 1 and 2; Distant Downstream (DD) = 16 and 17].

TABLE 1 | Characteristics of survey sites within eight locations along the Upper Uruguai River, Brazil. DU (distant location upstream of the most upstream dam), DD (distant and downstream of the most downstream dam), R1 (Barra Grande Reservoir), R2 (Machadinho Reservoir), R3 (Itá Reservoir), DR1 (immediately downstream from Barra Grande Dam), DR2 (immediately downstream from Machadinho Dam), DR3 (immediately downstream from Itá Dam).

Locations	Sample Sites	UTM Coordinate (X)	UTM Coordinate (Y)	Distance downstream from the first sample site (km)	Distance between river banks (km)
DU	1	529400	6873288	0	0.15
DU	2	523534	6880973	11.49	0.22
R1	3	512252	6898513	49.46	0.39
R1	4	496769	6912114	79.06	0.58
R1	5	481753	6926735	105.55	0.74
DR1	6	480779	6927650	106.88	0.11
R2	7	454048	6946672	156.22	0.34
R2	8	438514	6956148	189.55	0.51
R2	9	421924	6955590	224.34	0.96
DR2	10	422047	6954598	225.76	0.33
R3	11	410968	6957484	250.04	0.40
R3	12	402272	6971232	288.40	0.54
R3	13	390945	6978846	311.01	0.67
R3	14	367311	6981165	367.48	0.77
DR3	15	361955	6981341	382.30	0.20
DD	16	299465	7002554	514.81	0.28
DD	17	264480	7001424	583.48	0.56

Fish assemblage data from surveys conducted at 17 sites were grouped into eight study locations (Distant Upstream – DU; Reservoirs – R1, R2, R3; Downstream Reservoirs – DR1, DR2 and DR3; and Distant Downstream – DD). Those sites are grouped considering similarities in geographical location and abiotic characteristics. Field work was done during January–February, April–May, July–August and October–November from 2006 to 2010, totaling 290 survey events successfully concluded. At each site during each survey seven different nets set were used, totaling 2,145 net samples. During each survey, fishes were caught along a stretch of shoreline with a set of four gill nets and three trammel nets with mesh sizes ranging from 1.5 to 5.0 cm between adjacent knots, nets height ranging from 1.6 to 1.8 m and the length ranging from 10 to 40 m. Nets were placed in the evening and removed in the following morning (set for approximately 12 h). All captured fish were counted and identified at the species level, weighed (in grams) and measured (total length in cm). Collecting license was provided by Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis

– IBAMA (52/2007 and 145/2009). The nomenclature of the species list was based on Fricke *et al*. (2021) and in consultation with taxonomic experts. Vouchers of all species were deposited in the fish collection of Museu de Zoologia da Universidade Estadual de Londrina, Paraná, Brazil (MZUEL) (**S1**).

Abundance of each fish species was estimated from of numerical Catch Per Unit Effort (CPUE) (sum of individuals per 100 m^2 net area/12 h – $CPUE_N$) and biomass (sum of grams per 100 m^2 net area/12 h – $CPUE_B$), for each sampling unit (for each sampling site and period). Then, fish species were grouped according to functional groups, and $CPUE_N$ and $CPUE_B$.

Defining functional groups. Functional groups were defined with an emphasis on characteristics predicted to affect responses to damming and reservoir formation: trophic niche, body size, and reproductive strategy (Arantes *et al*., 2019). Information on feeding and reproductive biology of species analyzed in this study were based on the scientific literature (*e.g*., Vazzoler, 1996; Hahn *et al*., 1998; Zaniboni-Filho *et al*., 2004; Reynalte-Tataje, Zaniboni-Filho, 2008; Araújo *et al*., 2009; Gubiani *et al*., 2012), including accounts for congeneric species when no information was available, and body size was recorded as the largest specimen captured from the Upper Uruguai River during regular surveys conducted by our research group from 1995 to 2014.

Fourteen functional groups were classified considering trophic and movement/reproductive/size categories. There were five trophic groups, based on diet: i) detritivore (species which fed on detritus, organic layer, periphytic algae and mud), ii) omnivore (defined as species with a generalist diet without predominance of either plant or animal tissue), iii) invertivore (species which fed on invertebrates), iv) carnivore (*i.e*., invertivore with a tendency for piscivore), and v) piscivore (species which fed mainly on fish). Movement/reproductive/size groups were nine combinations of this three characteristics: movement – considering fish with Sedentary habits or Short Migration (S/SM) or Long Migration (LM); reproductive strategy – with Parental Care (PC), Internal Fertilization (IF) or neither (No Parental Care – NPC); and body size – Small, maximum total length < 20 cm (S); Medium, total length between 20 and 40 cm (M); and Large, total length > 40 cm (L). These characteristics (movement, reproductive strategy and body size) were grouped based on their assumed functional and evolutionary interdependence. Thus, the nine movement/reproductive/size groups were: LNL (LM-NPC-L), SIM (S/SM-IF-M); SIS (S/SM-IF-S), SNL (S/SM-NPC-L), SNM (S/SM-NPC-M), SNS (S/SM-NPC-S), SPL (S/SM-PC-L), SPM (S/SM-PC-M), and SPS (S/SM-PC-S).

Numerical abundance and biomass of each functional group were determined from the sum of $CPUE_N$ and $CPUE_B$ of species for each sampling unit.

Data analysis. The $CPUE_N$ and $CPUE_B$ of the fourteen functional groups were log-transformed (log (x+1)) and n*onmetric multidimensional scaling* (NMDS) using the Bray-Curtis index was applied to evaluate dissimilarity in abundance ($CPUE_N$) and biomass ($CPUE_B$) of the functional groups between the sampled environments. Analysis were performed separately for trophic groups and movement/reproduction/size categories. The differences of functional assemblage structures (based on both trophic and movement/reproductive/size) among the eight locations were tested by Permutational

Multivariate Analysis of Variance (PERMANOVA; Anderson, Walsh, 2013; Anderson, 2014), followed by post hoc tests performed with PERMANOVA pairwise comparisons, and Bonferroni method. The multivariate data were analyzed using the Bray-Curtis index generated from the transformed data with 9.999 permutations.

An analysis of homogeneity of multivariate dispersions (PERMDISP, Anderson *et al*., 2006) using the Bray-Curtis dissimilarity index was applied to evaluate if the eight locations had different degrees of homogeneity of assemblage structures based on different to $CPUE_N$ and $CPUE_B$ of functional groups. All analyzes were performed in software R (Version 3.2.4; http://cran.r-project.org), with Vegan, Mass, Car and RVAideMemoire packages.

RESULTS

Surveys conducted at the eight locations in Upper Uruguai River yielded 77 fish species from 49 genera and 24 families (**S1**), distributed into eight study locations (**S2**). PERMANOVA analyses with adonis function revealed a significant difference between fish assemblage structures in the different habitat categories based on trophic (numerical abundance R = 0.27, P = 0.001; biomass R = 0.23, P = 0.001) and movement/reproductive/size categories (numerical abundance R = 0.32, P = 0.001; biomass R = 0.27, P = 0.001). Results of the PERMANOVA pairwise comparisons for eight environmental presents no differences between DUxR2, DUxDD, DR1xDR2, DUxR3 and DDxR3 for trophic categories (P > 0.05), and DUxR2 for movement/reproductive/size categories (P > 0.05), but with significant differences for the others comparisons.

The results of ordination (NMDS; Fig. 2) indicated that piscivorous fishes were predominant in most upstream reservoir (R1), long-distance migratory and carnivorous fishes were most common immediately downstream from reservoirs (DR), and detritivorous fishes and those with internal fertilization were most common in the location Distant and Downstream from the lowest dam in the cascade (DD).

Approximately half of the total fish abundance and biomass in the assemblage at the location most Distant Downstream (DD) and the assemblage most Distant Upstream (DU) was composed of detritivorous species (Tab. 2).

The assemblage from the uppermost reservoir of the cascade (R1) had the lowest numerical abundance and biomass of detritivores, invertivores and carnivores. R1 had the highest numerical abundance and biomass of piscivores (41% and 65% of total fish abundance and biomass, respectively). Omnivorous fish were abundant in R1, DR1, and DR3 (44%, 68% and 47%, respectively; Tab. 2). The high abundance of omnivores immediately downstream from Barra Grande Dam (DR1) was due to an extraordinary abundance of a single species (*Psalidodon* aff. *fasciatus*).

Fish assemblages at DR1 and Machadinho Reservoir (R2) had highest biomass and numerical abundance, respectively, of invertivorous fishes (Tab. 2). The fish assemblage at Itá, the most downstream reservoir of the cascade (R3), had the greatest numerical abundance and biomass of carnivorous fishes (4%; Tab. 2). Assemblages at the location immediately downstream from R3 (DR3) and the location furthest downstream (DD)

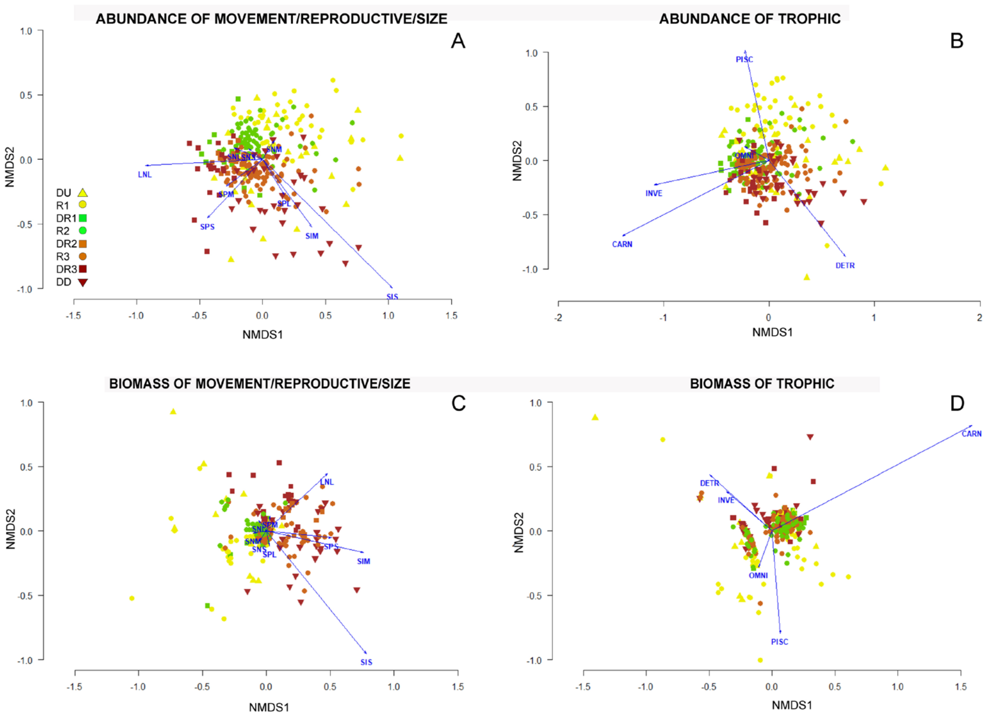

FIGURE 2 | Ordination plots produced by the non-metric multidimensional scaling analysis (NMDS) using the Bray-Curtis index, considering the abundance ($CPUE_N$) of movement/reproductive/size **(A)** and trophic categories **(B)**, and biomass ($CPUE_B$) of movement/reproductive/size categories **(C)** and trophic categories **(D)**, among survey locations. [DU (red triangle), DD (yellow triangle)] = Sampling points away from the dams; [R1 (red circle), R2 (green circle), R3 (orange circle)] = sampling points located in the reservoirs; [DR1 (green square), DR2 (orange square), DR3 (red square)] = locations downstream from dams. Labels are for Detritivores, Invertivores, Carnivores, Omnivores, and Piscivores; S/SM = sedentary/short migration, NPC = no parental care, PC = parental care, IF = internal fertilization, and LM = long migration; and Small, Medium, and Large body sizes.

TABLE 2 | $CPUE_N$ and $CPUE_B$ of five trophic categories within samples of fish assemblages from eight locations along Upper Uruguai River obtained between 2006–2010. DU (distant upstream from the most upstream dam), DD (distant downstream from the most downstream dam), R1 (Barra Grande Reservoir), R2 (Machadinho Reservoir), R3 (Itá Reservoir), DR1 (immediately downstream from Barra Grande Dam), DR2 (immediately downstream from Machadinho Dam), DR3 (immediately downstream from Itá Dam).

	Trophic category	DU	%	R1	%	DR1	%	R2	%	DR2	%	R3	%	DR3	%	DD	%
Abundance	Piscivorous	28	10	85	41	94	8	54	16	104	19	26	10	31	5	11	5
	Carnivorous	2	1	1	0	10	1	4	1	3	1	10	4	20	3	1	0
	Omnivorous	50	18	90	44	801	68	99	29	229	41	108	39	285	47	57	29
	Invertivorous	79	28	22	11	165	14	129	38	91	16	30	11	85	14	31	16
	Detritivorous	121	43	9	4	114	10	54	16	129	23	101	37	183	30	99	50
Biomass	Piscivorous	5817	21	13643	65	17165	22	6997	37	21266	35	3403	25	7473	12	1502	13
	Carnivorous	419	2	203	1	3425	4	486	3	840	1	566	4	1591	3	108	1
	Omnivorous	2847	10	4816	23	19214	25	5353	28	9062	15	3927	29	26011	42	3611	30
	Invertivorous	2735	10	485	2	13311	17	2787	15	6486	11	958	7	2727	4	1660	14
	Detritivorous	15618	57	1741	8	23226	30	3215	17	23817	39	4853	35	24826	40	5023	42

had the lowest numerical abundance and biomass of fish categorized as piscivores.

Sedentary or short migratory species (S/SM) were abundant with large biomass at all eight locations (Tab. 3). Long-distance migratory fishes, including *Prochilodus lineatus* and *Salminus brasiliensis*, were absent in samples from the first reservoir (R1) and location immediately downstream (DR1) (**S2**). However, at Downstream R3 (DR3) and the most distant downstream location (DD) the numerical abundance and biomass of long-distance migrants were relatively high at 10% and 9%, respectively (Tab. 3).

The fish assemblage at the distant downstream location had greater numerical abundance and biomass of species with internal fertilization, but only four species were in this category. No species with internal fertilization were captured from Machadinho Reservoir (R2) or locations upstream. Functional categories with small-bodied species without parental care, stood out immediately downstream of R1, and medium-size species (without parental care – NPC), had greater numerical abundance and biomass at Barra Grande and Machadinho Reservoirs (R1 and R2). The assemblage at the location immediately downstream from Itá Reservoir (DR3) had the highest numerical abundance and biomass of medium-size species with parental care, and the most Distant Downstream location (DD) had the greatest abundance of large-size species with parental care (Tab. 3).

TABLE 3 | $CPUE_N$ and $CPUE_B$ of nine movement/reproductive/size categories within samples of fish assemblages from eight locations along Upper Uruguai River obtained between 2006–2010. Values are presented by annual mean number and percentage, S/SM = Sedentary/Short Migration, LM = Long Migration, PC = Parental Care, NPC = No Parental Care, IF = Internal Fertilization, S = small, M = medium, and L = large. Movement/reproductive/size groups: LNL (LM–NPC–L), SIM (S/SM–IF–M); SIS (S/SM–IF–S), SNL (S/SM–NPC–L), SNM (S/SM–NPC–M), SNS (S/SM–NPC–S), SPL (S/SM–PC–L), SPM (S/SM–PC–M), and SPS (S/SM–PC–S). DU (distant upstream from the most upstream dam), DD (distant downstream from the most downstream dam), R1 (Barra Grande Reservoir), R2 (Machadinho Reservoir), R3 (Itá Reservoir), DR1 (immediately downstream from Barra Grande Dam), DR2 (immediately downstream from Machadinho Dam), DR3 (immediately downstream from Itá Dam).

	Movement/reproductive/size	DU	%	R1	%	DR1	%	R2	%	DR2	%	R3	%	DR3	%	DD	%
Abundance	SNS	46	16	82	40	799	68	105	31	201	36	137	50	195	32	48	24
	SNM	122	43	104	50	232	20	182	54	213	38	54	20	110	18	40	20
	SNL	10	3	11	5	39	3	29	8	43	8	14	5	88	14	7	3
	SPS	0	<1	0	0	0	0	0	0	0	0	1	<1	0	0	0	<1
	SPM	89	32	3	1	46	4	18	5	68	12	26	10	191	32	31	16
	SPL	14	5	7	3	67	6	6	2	28	5	40	15	17	3	66	33
	SIS	0	0	0	0	0	0	0	0	0	0	0	<1	0	0	0	<1
	SIM	0	0	0	0	0	0	0	0	1	0	1	0	0	0	5	3
	LNL	<1	0	0	0	0	0	0	<1	3	<1	0	<1	4	<1	1	<1
Biomass	SNS	1038	4	1944	9	12850	17	2107	11	3027	5	2544	19	2821	5	1218	10
	SNM	9521	35	11476	55	21260	28	8904	47	23936	39	2791	20	4734	8	2311	19
	SNL	2581	9	3078	15	10331	14	4381	23	6726	11	2445	18	23356	37	1854	16
	SPS	2	0	0	0	0	0	0	0	0	0	13	0	0	0	3	0
	SPM	8866	32	443	2	4920	6	1405	7	8499	14	1858	14	21818	35	2034	17
	SPL	5269	19	3946	19	26981	35	2009	11	17036	28	3703	27	3390	5	3170	27
	SIS	0	0	0	0	0	0	0	0	0	0	1	0	0	0	23	0
	SIM	0	0	0	0	0	0	0	0	75	0	46	0	13	0	210	2
	LNL	160	1	0	0	0	0	32	0	2172	4	306	2	6495	10	1082	9

PERMDISP analysis indicated that all locations had different degrees of heterogeneity of assemblage functional groups structure (trophic numerical abundance: $F_{(7,282)} = 9.74$, $P < 0.0001$; trophic biomass: $F_{(7,282)} = 9.06$, $P < 0.0001$; movement/reproductive/size numerical abundance: $F_{(7,282)} = 8.95$, $P < 0.0001$; movement/reproductive/size biomass: $F_{(7,282)} = 6.19$, $P < 0.0001$). Overall, for both functional groups (trophic and reproductive/movement/size) and metrics (numerical abundance and biomass), pairwise differences were consistent, the locations DU and R1 had the highest heterogeneity (larger distance from centroid) compared to the others, and DR2 the lowest heterogeneity. The location DD had a higher movement/reproductive/size heterogeneity compared to locations from the middle stretch of the Uruguai River (Figs. 3A–D; Tabs. 4–5; **S3**).

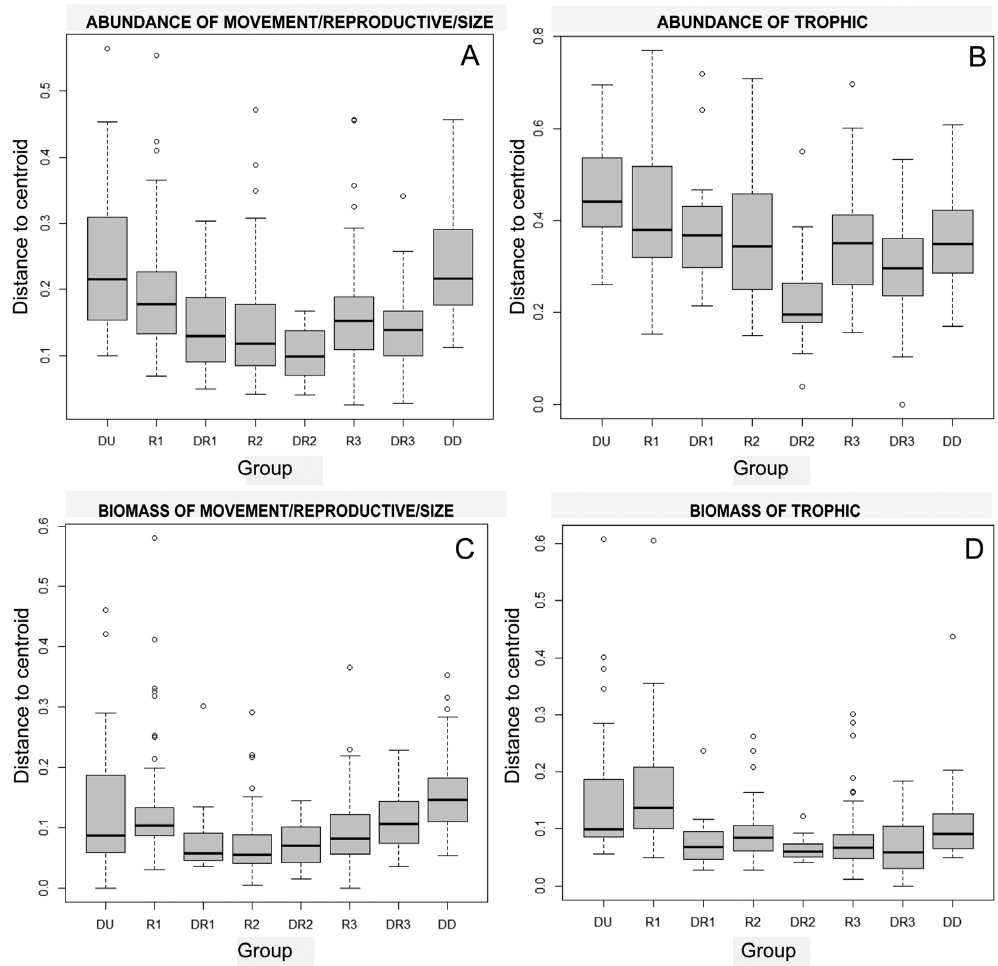

FIGURE 3 | Analysis of multivariate homogeneity of group dispersions (PERMIDISP) by betadisper boxplot, using the Bray-Curtis index, considering the abundance ($CPUE_N$) of movement/reproductive/size **(A)** and trophic categories **(B)**, and biomass ($CPUE_B$) of movement/reproductive/size categories **(C)** and trophic categories **(D)**. The data was based on sampling sites, and presented by environment groups: [DU, DD] = Sampling points away from the dams; [R1, R2, R3] = sampling points located in the reservoirs; [DR1, DR2, DR3] = locations downstream from dams. Greater distance to spatial median indicates larger dispersion and therefore a more diverse/heterogeneous environment. Box lower and upper endpoints represent the 25th and 75th quartiles, respectively. The horizontal bar and plus symbol inside each box represent median, excluding outliers, which are presented by open circles. See Tabs. 4 and 5 for P values from environments comparisons.

TABLE 4 | Summary of PERMDISP permuted P values for comparisons of heterogeneity in movement/reproductive/size structure among locations. Above diagonal p values for numeric abundance and below diagonal for biomass movement/reproductive/size structure. Statistically significant P values (P < 0.05) are highlighted in bold.

Location	DU	R1	DR1	R2	DR2	R3	DR3	DD
DU		0.177	**0.002**	**0.001**	**0.001**	**0.001**	**0.003**	0.989
R1	0.801		**0.023**	**0.003**	**0.001**	**0.028**	**0.043**	0.128
DR1	0.088	**0.043**		0.868	**0.039**	0.280	0.758	**0.001**
R2	**0.001**	**0.001**	0.785		**0.046**	0.187	0.878	**0.001**
DR2	**0.019**	**0.007**	0.652	0.778		**0.002**	**0.022**	**0.001**
R3	**0.018**	**0.004**	0.392	0.070	0.104		0.442	**0.001**
DR3	0.453	0.310	0.136	**0.013**	**0.010**	0.247		**0.001**
DD	0.293	0.415	**0.001**	**0.001**	**0.001**	**0.001**	**0.019**	

TABLE 5 | Summary of PERMDISP permuted P values for comparisons of heterogeneity in trophic assemblage structure among locations. Above diagonal p values for numeric abundance and below diagonal for biomass trophic structure. Statistically significant P values (P < 0.05) are highlighted in bold.

Location	DU	R1	DR1	R2	DR2	R3	DR3	DD
DU		0.572	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.023**
R1	0.710		**0.004**	**0.003**	**0.001**	**0.001**	**0.001**	0.076
DR1	**0.019**	**0.003**		0.260	**0.001**	0.134	0.824	**0.035**
R2	**0.001**	**0.001**	0.366		**0.001**	0.828	0.170	0.286
DR2	**0.002**	**0.001**	0.341	0.026		**0.001**	**0.003**	**0.001**
R3	**0.001**	**0.001**	0.796	0.358	0.200		0.065	0.284
DR3	**0.005**	**0.001**	0.802	0.200	0.666	0.529		**0.020**
DD	0.089	**0.012**	0.111	0.126	**0.007**	**0.023**	0.060	

DISCUSSION

The fish assemblage in the lowest reach (R3, DR3 and DD) and the upper portion (DU), within the dam and reservoir cascade of the Upper Uruguai River, had greater functional group diversity, and this might indicate that environmental impacts were lower compared to upstream locations in the reservoirs cascade. Although this pattern also could reflect a legacy of a natural longitudinal gradient of fish diversity during the period preceding construction of the hydroelectric dams (Lowe-McConnell, 1975; Araújo *et al*., 2009), the high diversity and presence of piscivorous in the upstream portion may corroborate with the reservoir cascade environmental impact. Piscivorous fishes were relatively abundant in the uppermost reach and the location downstream from the Machadinho Reservoir. Overall, fish assemblages at all locations surveyed in the Upper Uruguai River were dominated by small and medium-sized species that lack parental care. Medium-sized and large carnivorous species dominated assemblages in lower reaches between Itá Reservoir and the most Distant Downstream location, and these assemblages included diverse life history attributes, such as internal fertilization, parental care, and long-distance migratory behavior. The presence of medium-sized and large-sized fish and species with a diversity of life history attributes was associated with habitats less affected by human impacts resulting from dams, but another influence could have been the natural tendency for fish species richness to increase in the downstream direction along longitudinal river gradients (Araújo *et al*., 2009).

Migratory fishes were largely restricted to middle-lower reaches of the cascade system where several free-flowing tributaries, including the Ligeiro and Peixe rivers (located between DR2 and R3), join the Uruguai River (Reynalte-Tataje *et al*., 2012). The connectivity provided by these rivers is crucial for migratory fishes that undergo seasonal long-distance migrations (Agostinho *et al*., 2002; Cote *et al*., 2009; Silva *et al*., 2017). Dams in a cascade system create insurmountable barriers to migratory fish species, both in terms of upstream and downstream movement (Vörösmarty *et al*., 2010; Pelicice *et al*., 2018). The absence of large migratory fishes, such as *Salminus brasiliensis* from the upper stretches (DU, R1 and DR1) have the potential to alter top-down trophic dynamics structuring local fish assemblages (Taylor *et al*., 2015).

Habitats within reservoirs and immediately downstream from them often have hydrological regimes that vary more as a function of dam releases than seasonal precipitation and runoff (Graf, 2006; Räsänen *et al*., 2012). Consequently, the magnitude and timing of changes in hydrology and water quality tend to be lower and less variable and predictable compared to the natural flow regime (Vannote *et al*., 1980; Link *et al*., 2008). These conditions likely are not conducive to fish species that are seasonal spawners with recruitment dependent upon access to flooded riparian areas or other habitats formed in special hydrological conditions that serve as nurseries (Winemiller, 1989; Winemiller *et al*., 2008). Daily water-level fluctuations in nearshore areas of reservoirs and in tailraces are disruptive to fishes that deposit eggs in nests and guard them (Agostinho *et al*., 2008). It is unclear why auchenipterid catfishes with internal fertilization were absent in upper reaches of the dam/reservoir cascade. These fishes have a relatively equilibrium-type life history strategy of relatively large egg size and low fecundity (*sensu* Winemiller, Rose, 1992). Like cichlids and other brood-guarding fishes that also would be considered equilibrium strategists, these catfishes should be adapted for relatively stable environments (Tedesco *et al*., 2008).

High percentages of small and medium-sized sedentary and short-migration fishes throughout the Upper Uruguai River suggests that these species are ecological generalist in terms of feeding and habitat requirements. Neotropical fishes in these categories have been shown previously to dominate fish assemblages within reservoirs (Agostinho *et al*., 2007; Pelicice *et al*., 2018). Many of the fishes in these categories are omnivorous with broad diets that vary in response to food availability (Agostinho *et al*., 2007). It is notable that distributions for these fishes contrast with those of detritivorous (Agostinho *et al*., 2016; Dias *et al*., 2020) and long-distance migratory fishes (Agostinho *et al*., 2002; Cote *et al*., 2009; Silva *et al*., 2017) that were uncommon at locations most strongly impacted by dams and reservoirs.

Following dam construction, the reservoir filling phase generally produces a marked increase in aquatic primary production (trophic upsurge, Baranov, 1961) and availability of food resources for fishes, especially for small omnivorous and invertivorous fishes, which in turn often leads to an eventual increase in the abundance of piscivores that exploit them as prey (Agostinho *et al*., 2007). The trophic upsurge and abundant prey may explain the high abundance of piscivorous fishes in the most recently created reservoir (R1). In contrast, the relatively low abundance of large piscivores within reservoirs in the lower stretch of the cascade system might account for the greater abundance of smaller carnivorous species, owing to lower predation mortality as well as competition for some of the same food resources (Petry, Schulz, 2006; Araújo *et al*., 2009). Detritivorous fish can play an important role in nutrient cycling in both rivers (Taylor *et al*., 2015) and reservoirs (Vanni *et al*., 2005), and therefore could influence food web structure and other trophic guilds along river longitudinal gradients. However, this trophic guild is known to be negatively impacted by creation of reservoirs (Santos *et al*., 2020), and was not abundant in the deep reservoirs of the Upper Uruguai River. Fish in reservoirs avoid deep areas where thermal stratification reduces dissolved oxygen concentrations, which can result in a loss of nutritional quality of detritus (Santos *et al*., 2020) and places much of the phytoplankton-derived detritus out of reach for detritivores (Baumgartner *et al*., 2020). Detritivorous fishes were most common at the Distant-Upstream and Distant-Downstream locations, the two areas with flow regimes that were least affected by dams. They also were common in river reaches downstream from dams, where they likely exploit phytoplankton-derived detritus in water released from dams (Hoeinghaus *et al*., 2007).

The spatial distribution of fish functional groups in the dam/reservoir cascade of the Upper Uruguai River suggests that the downstream area (R3, DR3 and DD) have retained more the natural environmental characteristics that support riverine fish diversity. The DD location lies within an extensive unimpeded reach where several free-flowing tributaries enter the river and contribute to fluvial connectivity and a more natural flow regime compared to river reaches directly downstream from reservoirs. Consequently, this location has greater fluvial connectivity and a more natural flow regime compared to upstream locations that are more impacted by dams. Dams cause profound changes in not only the taxonomic structure of river fish assemblages (Freedman *et al*., 2014), but also the functional groups of aquatic communities with likely effects on food-web dynamics. Our findings contribute to understanding the effects of reservoir cascades on the distribution and abundance of fish with diverse ecological characteristics. Tributaries appear to have fundamental importance for maintaining a high diversity of fish reproductive groups, and reservoir cascades create large-scale environmental heterogeneity that apparently determines the distribution of fish trophic guilds and food web structure. Future management actions should prioritize the maintenance of fluvial habitat connectivity and environment conditions to facilitate fish migration, reproduction and life cycle completion by species spanning diverse life history strategies, and food web dynamics that allow persistence of the full complement of native species.

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Josiane Ribolli: Conceptualization, Supervision, Writing-review and editing.
Cristhiana Röpke: Formal analysis, Supervision, Writing-review and editing.
Kirk O. Winemiller: Conceptualization, Supervision, Writing-review and editing.
Evoy Zaniboni-Filho: Conceptualization, Funding acquisition, Project administration, Supervision, Writing-review and editing.

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