

Article

Diets and Trophic Structure of Fish Assemblages in a Large and Unexplored Subtropical River: The Uruguay River

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Abstract: The Neotropics represent a hotspot for freshwater biodiversity with vast number of fish species of scarce ecological knowledge. This holds true for the Uruguay River, where fish assemblages and their diets remain unexplored. Fish assemblages were surveyed in 14 sites along the river main course, from headwaters to mouth (approximately 1800 km), with the aim to identify the trophic roles of fishes and to describe trophic structure of these assemblages, following standardized sampling campaigns and laboratory procedures. One hundred species (2309 gut contents) were analysed and classified into four trophic groups subdivided into eight lower-level groups: Piscivore, piscivore-invertivore, detritivore, omnivore-detritivore, omnivore-invertivore, omnivore-planktivore and omnivore-herbivore. The trophic structure of the assemblages varied along the river, with the relative species richness of fish consuming terrestrial invertebrates increasing towards the middle river section, probably driven by the large floodplains in that areas, supporting global theories such as the flood pulse concept. This study describes the feeding habits of fish along the Uruguay River, being the first dietary description for 29 species. This knowledge is essential for management and conservation, serving as baseline in the context of future environmental changes while generating novel evidence on the functioning of ecosystems in this scarcely studied climatic region.

Keywords: trophic groups; Uruguay River fish; feeding habits; trophic guilds; fish feeding ecology

1. Introduction

The knowledge about trophic structure of communities is essential to understand some of the main relationships among species in ecosystems [1–3]. Information of the feeding habits of species permits a holistic understanding of ecosystem functioning [4]. In aquatic ecosystems, fish are used to describe

food webs since they occupy a great diversity of trophic niches and circulate matter and energy from basal resources to the highest levels of the web [5,6]. They are also capable to move between different habitats within the water body and even connect different ecosystems through feeding interactions, for example by feeding on allochthonous material from the riverbanks and riparian zones [5–7] or by migrating between rivers and the sea. The analysis of fish diets is also important to better understand the behaviour of the species [8,9]. Large-scale trophic groups' classification is the basis to understand the trophic structure of assemblages and their natural spatial or temporal variability (e.g., [10,11]). In fluvial ecosystems, longitudinal gradients in fish assemblage trophic structure are often found, where the relative importance of different trophic groups shifts from headwaters to mouth, possibly following changes in energy availability and habitat structure (e.g., [12–17]). Some evidence suggests that the trophic structure of the fish assemblages changes from dominance of small compressed-bodied benthivorous fishes in headwaters towards higher importance of omnivores-herbivores, planktivorous and piscivorous strategists in the lower sections [12–15]. However, most of this evidence comes from streams and low order river ecosystems (e.g., river orders 1–5), but longitudinal patterns in fish trophic structure in large river ecosystems remain largely unexplored.

Moreover, most of the theories that aim to explain river functioning have been generated in temperate regions of the northern hemisphere. Despite that the Neotropical region represents one of the largest hotspots for freshwater fish biodiversity [18,19], the functioning of its riverine ecosystems and the biology of the vast majority of the species remains understudied [20,21]. Besides, while most Neotropical fish assemblage studies focus on tropical and subtropical rivers, with marked flow seasonality (e.g., Amazonas River, Parana River, Orinoco River [22–25]), less research effort has been made in large irregular flow rivers of southern subtropical areas (see [26–28]). Particularly within the La Plata River basin, most studies describing aspects of fish biology focused on the large Parana River (e.g., [29–31]) while its smaller tributary—a 1800 km long and 6000 m³/s river bearing at least 10 species of long-distance migratory fish of commercial importance—the irregular-flow subtropical Uruguay River remains largely unstudied in its total extension [32]. Research on this region is highly necessary given that, as most freshwaters in South America, it faces a growing biodiversity loss rate [19,29,33].

The knowledge about South America's fish assemblages is based almost exclusively on taxonomical records and species distribution analyses [19,34]. The scarce information available for the Uruguay River is not the exception, consisting mostly on scientific notes reporting length-weight relationships [10,35], or new records of a few rare species [36,37]. Moreover, most fish ecology research made in the Uruguay River has been focused on few commercially important migratory species such as sabalo (*Prochilodus lineatus*), boga (*Megaleporinus obtusidens*) and dorado (*Salminus brasiliensis*) (e.g., [26,38]). Most of these migratory species migrate between Paraná, Río de la Plata and Uruguay Rivers to use different feeding and reproduction grounds along the fluvial gradient; but several local species exist along the river as well [26]. Regarding fish trophic ecology, and to the extent of our knowledge, only few studies describing the diet of limited key species exist (e.g., [39–42]).

The objective of this study was to report the fish species present in the Uruguay River, describing their diets with the aim of reaching a standardized and objective classification in trophic groups. Furthermore, this study was also aimed to describe the spatial variation in the trophic structure of assemblages from upper to lower river sections, facilitating the comprehension of the structure and functioning of the unstudied fish assemblages in this large subtropical river serving as baseline information for management purposes.

2. Materials and Methods

2.1. Study Area and Fish Sampling

This research was conducted in the Uruguay River, the second largest tributary of the La Plata River drainage basin. This river rises at the confluence of the Pelotas River and the Canoas River in Brazil, and extends for 1800 km to its mouth in the La Plata estuary shared between Uruguay and

Argentina [43]. The drainage basin covers three countries: Brazil, Argentina and Uruguay, with the largest area in the states of Santa Catarina and Rio Grande do Sul, Brazil [44]. According to geological characteristics, the Uruguay River could be divided into three main regions; upper, middle and lower sections. The Yucuma Falls in Brazil represent the division between the upper and middle section, while the Salto Grande Dam (Uruguay) divides the middle from the lower section of the river [45]. The hydrology of the Uruguay River is determined by the precipitation patterns in the upper two-thirds of the catchment (upper and middle sections) and, as opposite to the Parana River, does not show a seasonal pattern in flow, being highly irregular [46]. The hydrological conditions differ between the three sections, with a steeper slope and faster current velocities in the upper than in the middle section. On the other hand, the river flow in the lower section is constrained by the hydroelectric dam of Salto Grande [26]. The dominant substrates in the upper and middle region of the river are typically hard rocks, whereas in the lower section, sandstone substrate prevails [43]. In all the extension of the Uruguay River four hydroelectric dams were built (three in the upper section, and one in the lower section). The middle section remains largely hydrologically undisturbed.

Fish samplings were performed during austral autumn of 2017 (May–early June) in 14 sites of the main course of Uruguay River, from its headwaters (States of Santa Catarina and Rio Grande do Sul, Brazil) to the mouth (Colonia, Uruguay). Three locations were sampled in the upper river section, five in the middle section, and six in the lower section (Figure 1, Tables S1 and S2). Sampling locations were chosen considering available monitoring programs along the river easing logistics for this study. At all sites, littoral habitats of depths from 1–4 m were sampled to cover for a similar range of environmental variability in each area. In large river ecosystems, littoral areas usually host the highest biodiversity. Furthermore, the autumn season was chosen to sample because during that season, a higher diversity of fish size ranges might be expected as the spawning of most species of the region usually occur in spring-summer and then, both juvenile and adults of most species could be collected during autumn.

In the middle and lower sections of the river, fish collections were carried out using multi-mesh Nordic gillnets. In each site, four sets of benthic gillnets were placed in the littoral zone (1.5–2.0 m deep areas at 50–100 m away from the shore) and four in a deeper zone (2–5.0 m deep) about 500 m away from the shoreline. Each Nordic gillnet was 30 m long by 1.5 m high and were composed of 12 mesh sizes (5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0, and 55 mm knot to knot). Gillnets were set from sunset to sunrise (c.a. 12 h). The same sampling effort was performed in each site. Fish sampling and handling procedures were approved by the Honorary Commission of Animal Experimentation (CHEA) in Uruguay (Permit ID 309).

In the upper river section, due to a different standardization of the ongoing monitoring programs subsidizing this study, a set of gill and trammel nets were used, with mesh sizes ranging from 15.0 to 80.0 mm knot to knot, instead of Nordic gillnets. However, time of net set was comparable as net were also set overnight. Gillnets ranged from 20 to 120 m in length and from 1.6 to 8.0 m in height; while trammel nets varied between 30 to 40 m in length with 1.8 m height. Both set of nets were placed in the littoral zone in the evening and removed in the following morning, being set for approximately 12 h. At each site, additional sampling was performed with seine nets and cast nets (both with mesh size of 8.0 mm) in the littoral zone.

In addition to our own sampling campaigns, some commercially important large fish specimens were also obtained from local fishermen in the middle and lower sections of the river, as to complete the sampling wherever these species (known to be present along all the river) were not captured. Furthermore, to complement the diet description of some rare species (i.e., with less than five individuals collected during sampling) gut content data from two previous sampling campaigns arrayed in spring 2014 and autumn 2016 in the lower section of Uruguay River was used (Table S1).

In the field, fishes were identified to the lowest taxonomic level possible (i.e., species level in most cases), measured (total and standard length in cm) and weighed (total fresh biomass in g). For the gut content analysis, the stomach and intestines of 15 individuals per species and site, considering a wide size range (or all individuals obtained, when <15 were caught) were removed and preserved in 10%

formalin for posterior laboratory analysis. A previous study in Uruguayan streams using prey species accumulation curves has established that 15 individuals usually suffice to represent well the richness of diet items [47]. Individuals were selected to cover all length classes obtained at each site (Table S1).

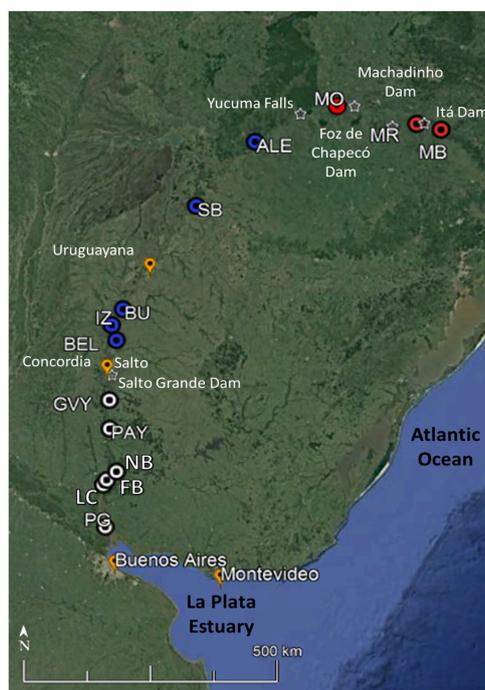


Figure 1. Location of the 14 sampling sites of the Uruguay River. The Uruguay River sampling sites are coloured according to the different sections; red: Upper; blue: Middle, and white: Lower. MB: Barracão, at the confluence of Canoas River and Pelotas River; MR: Marcelino Ramos; MO: Mondai; Ale: Alecrim; SB: São Borja; BU: Bella Unión; IZ: Isla del Zapallo island; Bel: Belén; GVV: Guaviyú; Pays: Paysandú; NB: Nuevo Berlín; FB: Fray Bentos; LC: Las Cañas, and PG: Punta Gorda, at the mouth of the Uruguay River. Major towns (orange) and waterfalls and dams (white star) are represented in the figure.

Gut content analysis (GCA) was performed in the laboratory. The occurring food items were classified broadly into eight item types as follows: Detritus, plankton (zooplankton and phytoplankton), periphyton (diatoms and filamentous algae), aquatic macroinvertebrates (insects, molluscs, and macrocrustaceans), terrestrial macroinvertebrates (terrestrial insects and arachnids), fish remains (entire fish, scales, fins and fish remains) aquatic macrophytes, and terrestrial vegetal matter (seeds, fruits and vegetal tissues). Zooplankton and phytoplankton were pooled because phytoplankton was only present in few individuals along with large amounts of zooplankton. The absolute volume of each food item was measured using standardized Hyslop's indirect volumetric method. With this information, the relative contribution of each food item type to the diet of individuals was calculated [48].

The frequency of occurrence was calculated as the number of occurrences of a food item in the guts of a given species divided by the total number of individuals analysed. Then, the Index of Relative Importance (IRI) of each item for each species was calculated, considering the unit volume of food items weighted by its frequency of occurrence and expressed as percentage [49]:

$$IRI = (V_i \times F_i) / \left(\sum V_i \times F_i \right) \times 100$$

where: V_i = volume of the food item i and F_i = frequency of occurrence of the food item i . Data from empty guts and those that only had indeterminate prey items were excluded from the analysis.

For the trophic classification of species, data from each individual belonging to a species from the different river sections was pooled. This procedure was applied in order to obtain a broader view of diet plasticity and to minimize the potential effect of the short time scale and the strong habitat

specificity typically considered by GCA [50]. This procedure was followed to use variability in space along the whole river as a proxy of the potential variability across time and different habitat scenarios for a given species. For the classification purpose, the term “omnivores” was used to define species feeding at contrasting trophic levels, such as primary producers and consumers of any kind. This is a pragmatic use of the definition that allows a rather conservative but unequivocal visualization of this feeding strategy [11], but acknowledging that omnivores are strictly those feeding on more than one trophic level [51,52].

2.2. Data Analysis

Fish species were grouped and diets were compared using a cluster analysis, following the Bray–Curtis ordination method and Euclidian distance as an index of dissimilitude. This kind of group analysis is commonly used in studies of trophic ecology (e.g., [53]). To complement the cluster analysis, the data was visualized in a principal component analysis (PCA). To test for significant differences in the diet composition between the groups that emerged from the cluster analysis, a non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA; Bray Curtis index; with 999 random permutations) was performed [54]. PCA analysis and the PERMANOVA test without data from detritivore and piscivore fish groups were also run to better visualize and classify the omnivore fish groups. A special focus on this group was made because of the known high relative richness of omnivore species in subtropical and tropical systems [11]. All the statistical analyses were conducted using the free statistical software PAST and the “vegan” package in R (R Development Core Team [55]).

Afterwards, the relative biomass, abundance and species richness of each trophic group was estimated for each sampled site within each river section. In this way, an aim to describe potential changes in trophic structure of assemblages between the upper, middle and lower river sections was made. The relative abundance, biomass and species richness data was used instead of total numbers, to avoid a potential bias given by the slightly different sampling methodologies (different distribution of net mesh sizes) displayed in the upper river section. To analyze potential changes in trophic structure between these sections we performed PERMANOVA tests ($\alpha = 0.05$; Bonferroni-corrected P-values), using metrics for each trophic groups as response variables (i.e., relative biomass, relative abundance, and relative species richness), and the sampling sites within a river section as a replicates. Furthermore, changes in the relative biomass, abundance and species richness of each particular trophic group among river section were tested using Analysis of Variance (One way ANOVA) or Kruskal Wallis, depending on the accomplishments of data homoscedasticity and normality.

To compare the generality of the results, a bibliographic review of dietary descriptions for the same species in other locations was performed using the Google Scholar search engine. For the dietary review of each species, the terms “species name” + “feeding” + “diet” were used as keywords, and we considered the first ten results obtained. This information can help identify the diet plasticity of many species and also the gaps of information for certain species (Table 1).

3. Results

One hundred species were recorded in the main course of Uruguay River belonging to nine orders, with the Characiformes and Siluriformes being the most represented (42% and 41% of all the species, respectively) (Table S1). Most were native species, with the record of only one exotic species (*Oreochromis niloticus*, Nile tilapia) collected in the upper river section (Table 1).

From a total of 2309 stomachs analysed, 1890 (82%) were used in the feeding groups classification. The remaining stomachs were empty or with indeterminate dietary content.

Table 1. Diet and trophic classification of fish species sampled along a longitudinal gradient in Uruguay River. The values for each dietary item type in each species represent the index of relative importance, which combines the frequency of occurrence and the relative volume of each dietary item to describe the diet of a species. For n and size ranges analysed see Table S2. Previous trophic classification of species for other systems surveyed from literature is shown in the last column and in References Table 1. NA = No data available. The species with * have not been grouped due to unique dietary characteristics.

Trophic Group	Fish Species	Entire Fish & Fish Remains	Aquatic Invertebrates	Terrestrial Arthropods	Detritus	Aquatic Macrophytes	Terrestrial Plant Remains	Periphyton	Plankton	Trophic Groups in Literature	
Piscivore	<i>Ageiosius militaris</i>	0.842	0.04	0.106	0.01	<0.001	<0.001	<0.001	0	Piscivore [42]	
	<i>Acestrorhynchus pantaneiro</i>	0.999	<0.001	<0.001	0	0	<0.001	0	0	Carnivore [42]/Piscivore [41,56,57]	
	<i>Cynopotamus argenteus</i>	0.995	<0.001	0.001	0	<0.001	0.003	0	<0.001	Piscivore [42]	
	<i>Catathyridium jenynsi</i>	1	0	0	0	0	0	0	0	NA	
	<i>Cynopotamus kincaidi</i>	0.999	0.001	0	0	0	0	0	0	Piscivore [58]	
	<i>Crenicichla scotti</i>	1	0	0	0	0	0	0	0	Benthi-piscivore [47]	
	<i>Crenicichla vittata</i>	0.999	0	0.002	0	0	<0.001	0	0	Piscivore [59]	
	<i>Galeocharax humeralis</i>	0.987	0.002	0.001	0	0.003	0.006	0	0	Piscivore [60]	
	<i>Hoplias lacerdae</i>	1	0	0	0	0	0	0	0	NA	
	<i>Hoplias malabaricus</i>	1	0	0	0	0	0	0	0	Carnivore-piscivore [61,62]/Piscivore [63–65]/Carcinophagous [66]	
	<i>Lycengraulis grossidens</i>	0.854	0.013	0.01	0.004	0	0.094	0	0.025	Piscivore [67]/Carnivore-Piscivore [68]	
	<i>Luciopimelodus pati</i>	0.923	0.008	0.06	0	0	0.005	0	0.005	NA	
	<i>Oligosarcus jenynsii</i>	0.788	0	0.209	0	0	0.003	0	<0.001	Carnivore-Piscivore [69–72]/Piscivore [73]	
	Piscivore	<i>Oligosarcus oligolepis</i>	0.98	0	0.02	0	0	0	0	0	Omnivore-Benthivore [74]
		<i>Pellona flavipinnis</i>	0.936	0.064	0	0	0	0	0	0	Piscivore [60]/Carnivore-Piscivore [75]/Carnivore [76]
<i>Pseudopimelodus mangurus</i>		1	0	0	0	0	0	0	0	NA	
<i>Pygocentrus nattereri</i>		0.831	0	0	0	0	0.169	0	0	Piscivore [60,77,78]	
<i>Parastegophilus sp.</i>		1	0	0	0	0	0	0	0	NA	
<i>Roeboides affinis</i>		0.922	0.06	0.016	0	0	0.003	0	0	Lepidophagous-invertivore [60]/Lepidophagous [79]	
<i>Roeboides microlepis</i>		0.786	0.002	0.02	0.023	0	0.17	0	0	Piscivore [60,80]	
<i>Raphiodon vulpinus</i>		0.987	0.005	0.007	0	0	0	0	0	Opportunistic piscivore [42]/Piscivore [64,81]	
<i>Salminus brasiliensis</i>		0.912	0.005	0	0	0	0.075	0.007	0	Piscivore [60,81]/Carnivore-piscivore [82]	
<i>Serrasalmus maculatus</i>		0.984	0.002	0	<0.001	0	0.013	0	0	Omni-piscivore [77]	

Table 1. Cont.

Trophic Group	Fish Species	Entire Fish & Fish Remains	Aquatic Invertebrates	Terrestrial Arthropods	Detritus	Aquatic Macrophytes	Terrestrial Plant Remains	Periphyton	Plankton	Trophic Groups in Literature
Piscivore-invertivore	<i>Ageneiosus inermis</i>	0.59	0.401	0	0	0.009	0	0	0	Carnivore-insectivore [83]
	<i>Gymnotus sp.</i>	0.417	0.167	0.417	0	0	0	0	0	Insectivore [84]
	<i>Megalonema platanum</i>	0.562	0.009	0.397	0.032	0	0	0	0	NA
	<i>Potamotrygon brachyura</i>	0.6	0.4	0	0	0	0	0	0	NA
	<i>Pimelodella gracilis</i>	0.144	0.196	0.148	0.295	<0.001	0.203	0.011	0.003	Omni-piscivore [81]/Carnivore [85]/Omnivore [86]/Insectivore (Aq) [87]
Piscivore-invertivore	<i>Pimelodus maculatus</i>	0.293	0.352	0.076	0.065	0.011	0.203	0	<0.001	Piscivore [60]/Omni-piscivore [88,89]/Omnivore [90]
	<i>Pseudobuonocephalus sp.</i>	0.572	0.249	0	0	0	0.179	0	<0.001	NA
	<i>Rhamdia quelen</i>	0.294	0.323	0.007	0.304	0	0.072	0	0	Carnivore [66]/Carnivore-piscivore [91]
	<i>Sorubim lima</i>	0.405	0.595	0	0	0	0	0	0	Piscivore [92]
Detritivore	<i>Cyphocharax platanus</i>	0	<0.001	0	0.999	0.001	<0.001	0	<0.001	NA
	<i>Cyphocharax saladensis</i>	0	0	0	1	0	0	0	0	Detritivore [93]/Iliophagus [94]
	<i>Cyphocharax spilotus</i>	0	0.012	0	0.987	0	0.001	0	0	Detritivore [95]
	<i>Cyphocharax voga</i>	0	0	0	1	0	0	0	0	Detritivore-Algivore [62]/Detritivore [93,96]/Iliophagus [97]
	<i>Hypostomus aspilogaster</i>	0	0	0	1	0	0	0	0	NA
	<i>Hypostomus commersoni</i>	0	0.001	0	0.995	0	0.004	0	0	Detritivore-algivore [62]/Iliophagous [98]/Periphyton-feeder-detritivore [99]
	<i>Hypostomus isbrueckeri</i>	0	0	0	1	0	0	0	0	NA
	<i>Hypostomus laplatae</i>	0	0	0	1	0	0	0	0	NA
	<i>Hypostomus luteomaculatus</i>	0	0	0	1	0	0	0	0	Detritivore [84]/Detritivore-algivore [100,101]
	<i>Hypostomus roseopunctatus</i>	0	0	0	0.999	0	<0.001	0	0	NA
	<i>Hypostomus uruguayensis</i>	0	0	0	0.977	0	0	0.016	0.007	NA
	<i>Loricariichthys melanochelius</i>	0	0.028	<0.001	0.923	0	0.042	<0.001	0.008	Omnivore [102]

Table 1. Cont.

Trophic Group	Fish Species	Entire Fish & Fish Remains	Aquatic Invertebrates	Terrestrial Arthropods	Detritus	Aquatic Macrophytes	Terrestrial Plant Remains	Periphyton	Plankton	Trophic Groups in Literature
Detritivore	<i>Loricariichthys platymetopon</i>	0	0	0	1	0	0	0	0	Detritivore [103,104]
	<i>Oreochromis niloticus</i>	0.013	0	0.014	0.908	0	0.064	<0.001	0	Omnivore [105]
	<i>Prochilodus lineatus</i>	<0.001	<0.001	<0.001	0.971	0	0.028	0	<0.001	Detritivore [60]/Iliophagous [103,104]
	<i>Potamorhina squamoralevis</i>	0	0	0	0.998	0	0	0	0.002	Detritivore [60,106]
	<i>Rineloricaria parva</i>	0	0.003	0	0.997	0	0	0	0	Detritivore [107]
	<i>Steindachnerina brevipinna</i>	0	<0.001	0	0.999	0	<0.001	0	0	Detritivore [108,109]
	<i>Steindachnerina insculpta</i>	0	0	0	1	0	0	0	0	Iliophagous [103]
Omnivore-detritivore	<i>Apareiodon affinis</i>	<0.001	0.013	<0.001	0.78	<0.001	0.057	0.149	<0.001	Omnivore-detritivore [81]/Algivore [110,111]
	<i>Characidium tenue</i>	0	0.023	0.276	0.69	0	0.011	0	0	NA
	<i>Iheringichthys labrosus</i>	0.004	0.266	0.006	0.650	0.006	0.053	0.001	0.014	Benthivore [40,103,112,113] /Necto-benthonic-insectivore [114]/Invertivore [115]
	<i>Loricariichthys anus</i>	0	0.201	0	0.779	0	0.019	0.001	0	Detritivore [95]
	<i>Pimelodella australis</i>	0.05	0.112	0.025	0.705	0	0.107	0	0	Benthi-herbivore [74]
<i>Rhinodoras dorbygni</i>	0.005	0.201	0.012	0.632	0.004	0.145	<0.001	<0.001	NA	
Omnivore-Invertivore (Aq)	<i>Brochyloricaria chauliodon</i>	0	1	0	0	0	0	0	0	Carnivore (mollusk consumer) [116]
	<i>Bryconamericus iheringii</i>	0.004	0.568	0	0.011	0	0.417	0	0	Omnivore-herbivore [47]/Omnivore [62]/Benthophagus-omnivore [73]/Benthivore [117]

Table 1. Cont.

Trophic Group	Fish Species	Entire Fish & Fish Remains	Aquatic Invertebrates	Terrestrial Arthropods	Detritus	Aquatic Macrophytes	Terrestrial Plant Remains	Periphyton	Plankton	Trophic Groups in Literature
Omnivore-Invertivore (Aq)	<i>Crenicichla jurubi</i>	0.005	0.988	0	0.007	0	0	0	0	NA
	<i>Crenicichla missioneira</i>	0	0.965	0.035	0	0	0	0	0	NA
	<i>Corydoras paleatus</i>	0	0.608	0	0.203	0	0	0.152	0.038	Detritivore-Invertivore [95,118]
	<i>Characidium rachovii</i>	0	0.583	0.417	0	0	0	0	0	Omnivore [62]/Opportunistic invertivore [119]
	<i>Charax stenopterus</i>	0	1	0	0	0	0	0	0	Invertivore [120]
	<i>Characidium zebra</i>	0	0.750	0	0	0	0	0	0.250	Detritivore [60]
	<i>Eigenmania sp.</i>	0.012	0.849	0.068	0.017	0.015	0.037	<0.001	0.001	Invertivore [60,121]/Invertivore (Aq) [122]/Carnivore [123]
	<i>Gymnogeophagus aff. gymnogenis</i>	0	0.505	0.0	0.303	0.0	0.192	0.0	0	Omnivore [124,125]
	<i>Leporinus amae</i>	0.005	0.953	0.005	0.003	0	0.024	0.011	0	NA
	<i>Leporinus striatus</i>	0	0.714	0.004	0.140	0.003	0.138	0	0	Herbivore [126]
	<i>Megaleporinus obtusidens</i>	0.033	0.561	<0.001	0.006	0	0.399	<0.001	<0.001	Omnivore [82]/Herbivore [95]
	<i>Odonthestes argentinensis</i>	0	0.764	0.140	0	0.096	0	0	0	NA
	<i>Odonthestes humensis</i>	0.005	0.879	0.108	0	0	0.007	<0.001	0	Benthonic carnivore [127]
	<i>Pimelodus absconditus</i>	0.028	0.774	0.014	0.023	0	0.161	0.001	<0.001	Omnivore [109]
	<i>Pachyurus bonariensis</i>	<0.001	0.522	0.007	0.449	0.007	0.013	0.001	<0.001	Insectivore [128–130]
	Omnivore-Invertivore (Terr)	<i>Paraloricaria vetula</i>	0	0.985	0	0.011	0	0.004	<0.001	<0.001
<i>Ricola macrops</i>		0	0.535	0	0.420	0	0.045	<0.001	<0.001	NA
<i>Rineloricaria sp.</i>		0	0.677	0	0.081	0	0.242	0	0	NA
<i>Auchenipterus nuchalis</i>		0.005	0.106	0.835	<0.001	<0.001	0.050	0	0.003	Invertivore [130]
<i>Auchenipterus osteomystax</i>		0	0.031	0.957	<0.001	0	0.001	<0.001	0.010	Insectivore [9,81,84]/Insectivore-carnivore [131–133]
<i>Bryconamericus stramineus</i>		<0.001	0.203	0.779	0	<0.001	0.005	<0.001	0.012	Invertivore [110,118,134]/Insectivore [135]
<i>Cyanocharax alburnus</i>		0	0.068	0.803	0	0	0.129	0	0	Benthivore [93]/Omnivore-benthivore [136]/Invertivore (Terr) [137]/Omnivore-carnivore [138]
<i>Odonthestes perugiae</i>		0	0.061	0.939	0	0	0.000	0	0	Omnivore-carnivore [139]
<i>Pseudocorynopoma doriae</i>		0	0	1	0	0	0	0	0	Insectivore [62,140]/Generalist insectivore [141]
<i>Trachylepterus galeatus</i>		0.027	0.079	0.768	0	0	0.127	0	0	Carnivore-insectivore [142]/Insectivore [143]

Table 1. Cont.

Trophic Group	Fish Species	Entire Fish & Fish Remains	Aquatic Invertebrates	Terrestrial Arthropods	Detritus	Aquatic Macrophytes	Terrestrial Plant Remains	Periphyton	Plankton	Trophic Groups in Literature
Omnivore-planktivore	<i>Hoplosternum littorale</i>	0	0.436	0.007	0	0	0.028	0	0.529	Omnivore-planktivore [144]/Scavengers [145]
	<i>Loricariichthys edentatus</i>	0	0.214	<0.001	0.024	0	0.008	0	0.754	NA
	<i>Odontostilbe pequirá</i>	0	0.009	0.009	0	0	0.074	0	0.907	Omnivore [146,147]/Benthivore [148]/Herbivore [149]
Omnivore-Herbivore (Terr)	<i>Platanichthys platana</i>	0	0	0	0	0	0.024	0	0.976	Microphagus-carnivore [150]/Omnivore [151]
	<i>Parapimelodus valenciennis</i>	<0.001	0.027	0.049	0.219	0.007	0.057	<0.001	0.640	NA
	<i>Astyanax lacustris</i>	0.002	0.013	0.148	0.001	0.001	0.836	<0.001	<0.001	Omnivore (terrestrial vegetation) [73]/Omnivore-herbivore [95]/Omnivore [152]
	<i>Astyanax obscurus</i>	0.017	0.197	0.393	0	0	0.393	0	0	Invertivore (Terr.) [73] Omnivore-herbivore [95]/Omnivore [155]
	<i>Astyanax spp. aff. fasciatus</i>	0.002	0.078	0.337	0.005	0.072	0.501	0.006	<0.001	[138,153,154]/Zooplanktivore [155]/Omnivore-zooplanktivore [156]
	<i>Brycon orbignyanus</i>	0.001	<0.001	0.095	0	0	0.903	0	0	NA
	<i>Geophagus brasiliensis</i>	0	0	0	0.225	0	0.775	0	0	Insectivore [66]/Omnivore [95,157–159]/Invertivore [95]
	<i>Pimelodus albicans</i>	0.117	0.016	0.397	0.002	0	0.468	0	0	NA
	<i>Pterodoras granulosus</i>	0.002	0.003	0	0.190	0.176	0.628	0	0	Herbivore [60]/Omnivore-Invertivore [160]/Omnivore [39,161]
	<i>Schizodon nasutus</i>	0	0.001	0	<0.001	0.024	0.975	0	0	Herbivore [68,114,162,163]
<i>Trachyloperus teaguei</i>	0.050	0.005	0.258	0.003	0	0.685	0	0	NA	
* <i>Schizodon platae</i>	0	0	0	0	1	0	0	0	Herbivore [164]	
* <i>Otocinclus arnoldi</i>	0	0	0	0.222	0	0	0.778	0	NA	

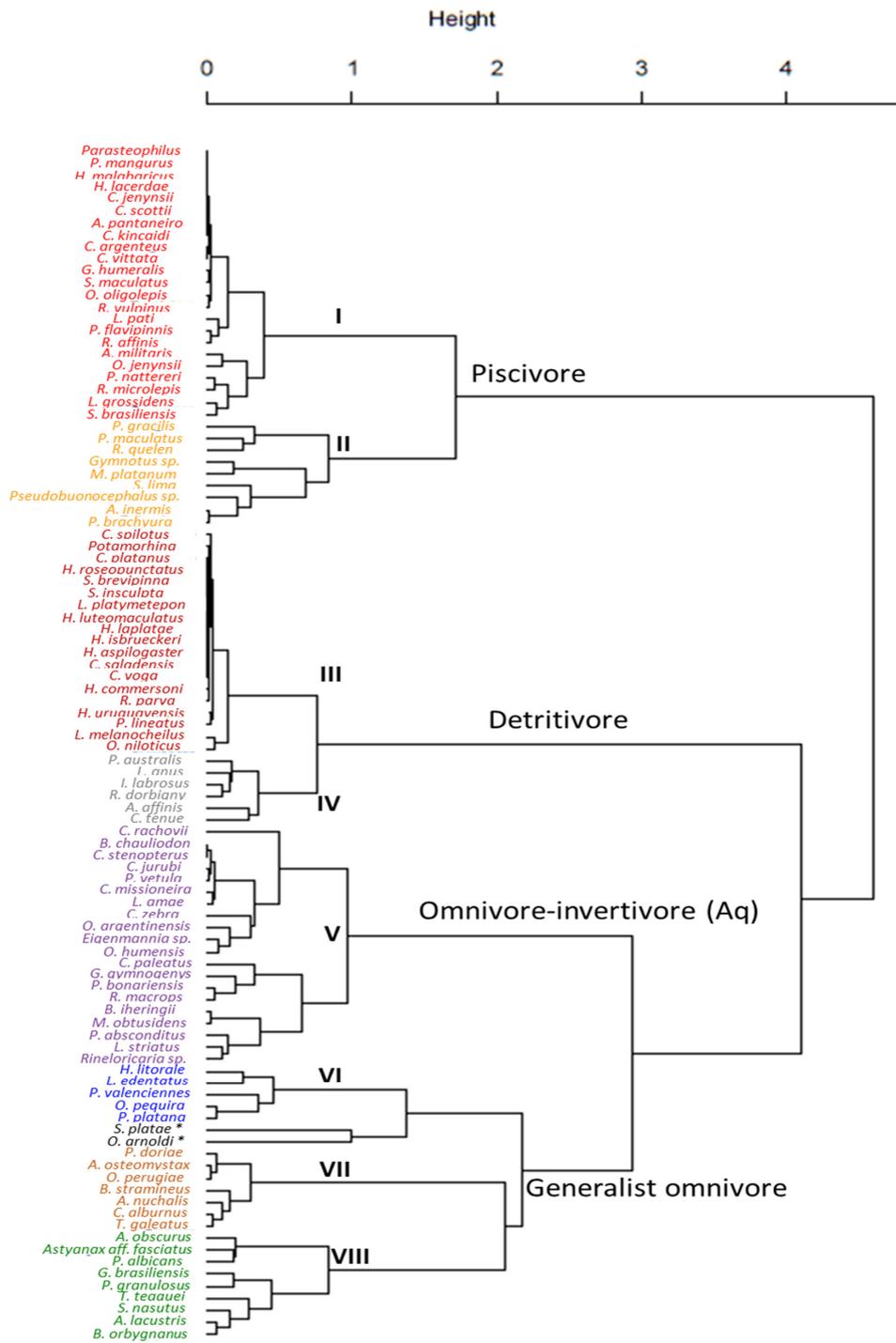


Figure 2. Cluster analysis showing trophic classification of 100 fish species along the Uruguay River. The text in the main tree branches corresponds to the broad scale trophic classification into four large trophic groups. Within each group, a statistically significant separation into more detailed sub-groups is made and marked with numbers and different text font colours. The final eight trophic groups are: I: Piscivore; II: Piscivore-invertivore; III: Detritivore; IV: Omnivore-detritivore; V: Omnivore-invertivore—(Aq.); VI: Omnivore-planktivore; VII: Omnivore-invertivore—(Terr.); and VIII: Omnivore-herbivore—(Terr.). The two species with * were excluded from groups due to their unique diet composition. Species abbreviations are shown, for full species names and detailed dietary characterization see Table 1.

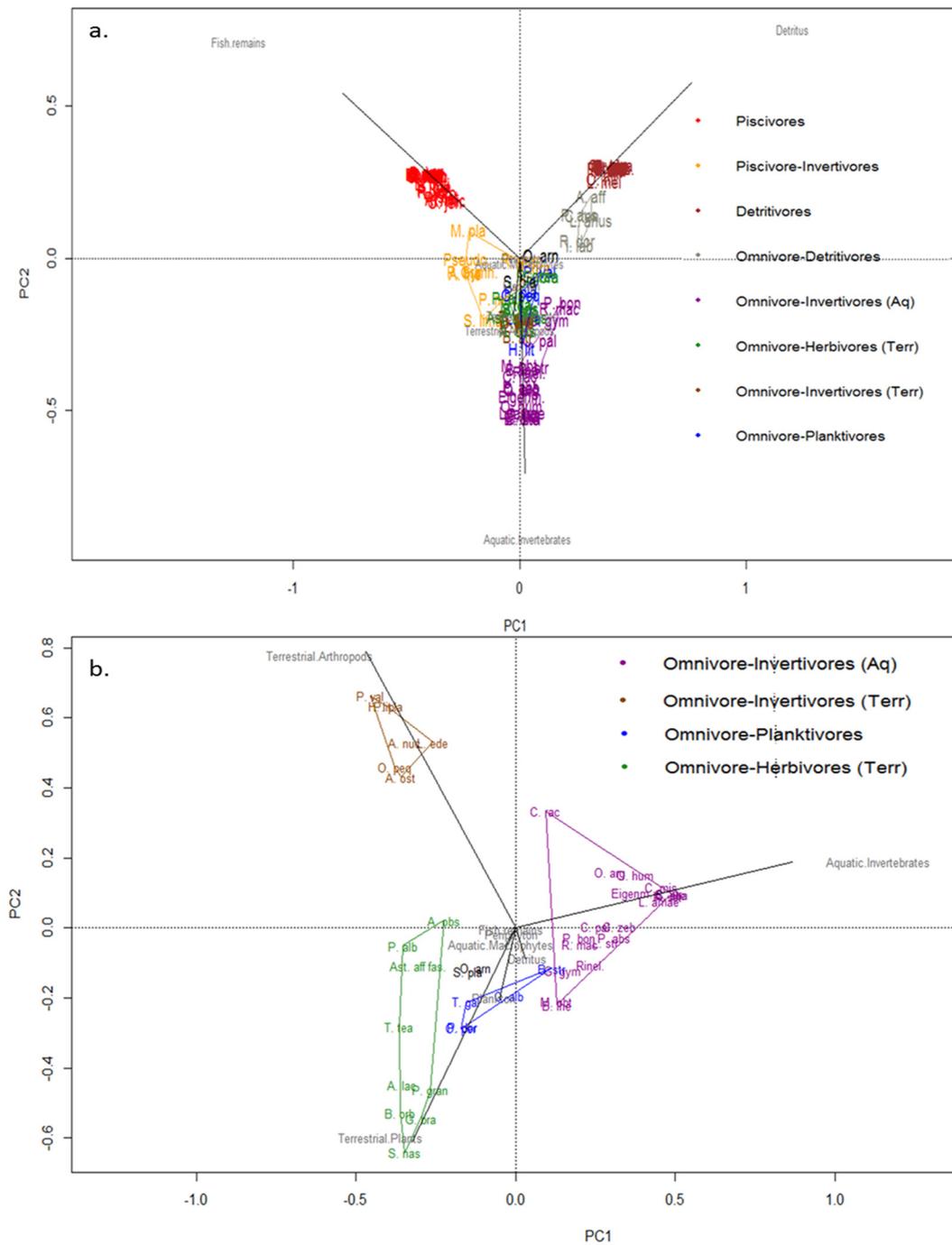


Figure 3. Principal component analysis: (a) showing all fish species assemblages in trophic groups according main food item in diet; PCA axes 1 and 2 explained 40% and 27% of the variance, respectively; (b) PCA (without the piscivore and detritivore groups) showing omnivorous fish specialization and grouped in trophic groups; PCA axes 1 and 2 explained 43% and 24% of the variance, respectively. Each colored polygon represents one trophic group. To see the full name of the species, see Figure 2 and/or Table 1.

The combination of the IRI values of each dietary item (detailed in Table 1) used in the cluster analysis allowed classifying species into four coarse-level trophic groups: Piscivore (32% of the species), detritivore (24% of the species), omnivore-invertivore (aquatic) (20% of the species, being omnivores mostly feeding on aquatic macroinvertebrates) and generalist-omnivore (23% of the species being omnivores mostly feeding on terrestrial material) groups (Figure 2, Table 1). When visualising this

data in principal component analysis (PCA) the separation of this same four broad trophic groups was as clearly evident as in the cluster analysis of Figure 2, with the first two axis explaining 67% of the variation in the data (PC1 = 40% and PC2 = 27%) (Figure 3a). The PERMANOVA test gave strong statistical support to this broad level classification into four groups, showing significant differences in the IRI index value for the multiple dietary items between every group ($F_{3,96} = 58.22$; $P = 0.001$).

Furthermore, data exploration using both PCA and cluster analysis suggested the suitability of increasing the resolution of the four broad trophic groups. For instance, piscivore and detritivore groups could be separated into two groups each (Figures 2 and 3a, Table 1), including the strictly piscivorous and detritivorous groups of species, and those that while feeding mostly on fish and detritus respectively also include other diet items to a lesser extent (Figure 3, Table 1). To perform this finer scale classification a PCA using exclusively the omnivorous groups was made to better resolve and classify them into four trophic subgroups (Figure 3b). In this case, 67% of the variation in the data was explained (PC1 = 43% and PC2 = 24%). The PERMANOVA test also showed consistent statistical support to this finer separation of omnivores into four subgroups ($F_{1,41} = 16.16$; $P = 0.001$).

Altogether, the ordination methods supported the separation into eight trophic groups:

- I. Piscivore: Diet dominated by entire fishes, fish remains, scales and fins.
- II. Piscivore-invertivore: Diet dominated by fishes, fish remains, scales and fins, with inclusion of aquatic macroinvertebrates and terrestrial arthropods.
- III. Detritivore: Diet dominated by detritus.
- IV. Omnivore-detritivore: A combination of vegetal and animal sources, with dominance of detritus.
- V. Omnivore-invertivore (Aquatic): A combination of species with either a diet largely dominated by aquatic macroinvertebrates and generally a minor inclusion of vegetal components.
- VI. Omnivore-planktivore: Combination of vegetal and animal sources, with dominance of planktonic items (mostly zooplankton).
- VII. Omnivore-invertivore (Terrestrial): A combination of species with either a diet largely dominated by terrestrial arthropods and generally a minor inclusion of vegetal components.
- VIII. Omnivore-herbivores (Terrestrial): Diet dominated by terrestrial seeds and fruits, but with minor inclusion of terrestrial arthropods.

Finally, a one-way PERMANOVA performed with all eight subgroups supported the trophic classification, showing significant between each group ($F_{8,91} = 101.42$; $P = 0.001$). Two species were excluded (although appeared related to the Omnivore-planktivore group in the cluster analysis) due to their unique diet: *Otocinclus arnoldi*, that fed mostly on periphyton with minor inclusion of detritus, and *Schizodon platae*, with a diet almost entirely composed of aquatic macrophytes (Table 1).

The trophic composition of the assemblages did not differ significantly between the three river sections in term of relative biomass (PERMANOVA $F_{7,111} = 1.4$, $P = 0.18$), relative abundance (PERMANOVA $F_{7,111} = 1.03$, $P = 0.41$) or relative species richness (PERMANOVA $F_{7,111} = 1.18$, $P = 0.31$) of trophic groups. The three sites in the upper portion of the river were particularly variable in its trophic composition in terms of relative abundance and biomass (Table S1, Figure 4). Moreover, no significant difference in the relative biomass, abundance or species richness of any of the trophic groups was found between the three river sections; the only exception being the relative species richness of the omnivores species feeding on terrestrial invertebrates, which was greater in the middle than in the lower Uruguay River section (ANOVA $F_{2,13} = 12.6$; $P = 0.001$; 6 species in the middle vs. 3 in the lower section).

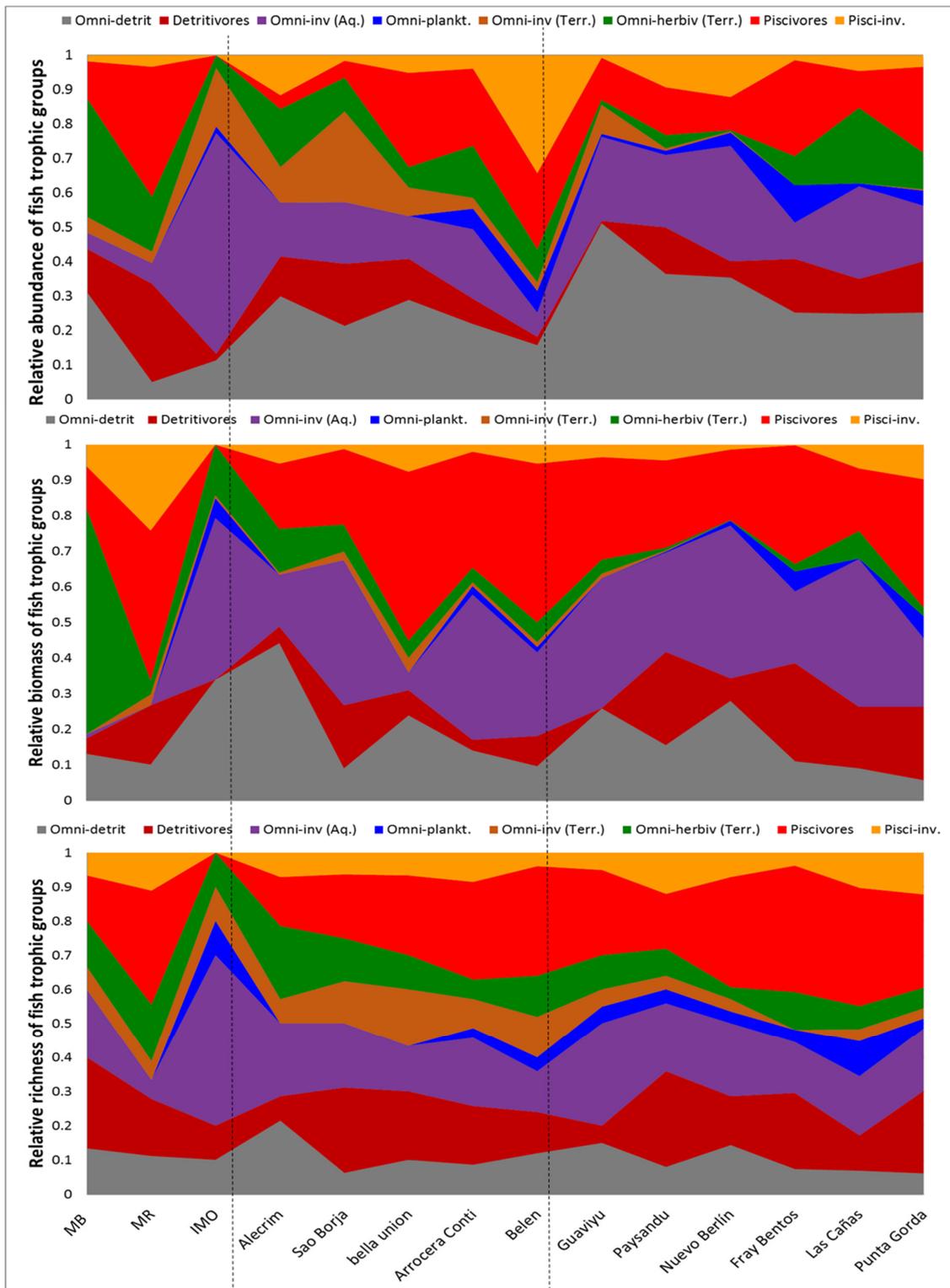


Figure 4. Longitudinal variability in trophic structure of the fish assemblages in sampled locations of Uruguay River from upper (MB, MR, IMO) to middle (Alecrim, Sao Borja, Bella Unión, Isla del Zapallo, Belén) and lower (Guaviyú, Paysandú, Nuevo Berlín, Fray Bentos, Las Cañas and Punta Gorda) river sections. Dashed lines represent the division between river sections. Above: Relative biomass; middle panel: Relative abundance; and below relative richness of each trophic group.

In terms of relative abundance of individuals, the assemblages along the river were generally dominated by omnivore-detritivore ($26 \pm 11\%$ of total abundance, mean and Standard Deviation), followed by the omnivore-invertivore feeding mostly on aquatic prey ($20 \pm 15\%$, mean and SD) and the piscivores ($16 \pm 11\%$, mean and SD). Meanwhile, detritivore and omnivore-herbivore groups represented about 10% of the total abundance each, whereas the remaining trophic groups represented less than 5% of the total abundance (Table S1, Figure 4).

In contrast, both in terms of relative biomass and relative species richness, the trophic structure of the assemblages was clearly dominated by the piscivore group (representing $27 \pm 13\%$ of total biomass and $24 \pm 10\%$ of total richness), followed by the omnivore-invertivore group that feed on aquatic macroinvertebrates (representing $26 \pm 16\%$ of the total biomass and $20 \pm 10\%$ of the total richness). The omnivore-detritivore conformed the third most important group ($18 \pm 11\%$ of total biomass), while the remaining groups represented 10% or less of the total biomass. In terms of relative species richness, omnivore-detritivore groups occupied the third place in importance, representing $20 \pm 10\%$ of all the species present on average. Each of the remaining trophic groups hosted about 10% of the total species number or less (Table S1, Figure 4). Remarkably, the trophic group with less relative biomass, density and species richness was the omnivore-planktivores—composed by five species feeding on copepods, cladocerans and/or ostracods mostly (see Table 1)—present in only one third of the upper and middle river section localities, but being always present in the lower river section.

4. Discussion

A total of one hundred species were recorded in a single sampling campaign comprising 14 localities spread along the main course of Uruguay River. This elevated taxa number illustrates the high biodiversity of the river, especially because this is a 12-h gillnet sampling in each site (in comparison with larger studies), but approximates to the total number of species historically registered for the river [43,165]. Moreover, the species richness seems to be at a similar level than that found for tropical rivers of comparable discharge. For example a study performed within a river stretch of a similar length in the Teles Pires River, located in Central Brazil and with similar characteristics to the Uruguay River (1600 km extension, c.a. 4000 m³/s of average discharge) in a year of sampling, 90 species were collected [82]. Another example is the Miranda River, a tropical river located in Pantanal, Brazil, where 101 species were recorded over two years of sampling [166].

Moreover, the abundance and the movement of migrating species is controlled by seasonality, spatial and temporal environmental variability, and the hydrological regime [167]; therefore, it is not likely that all species that inhabit the main course of the river would be collected at the same time. However, according to previous sampling experience (e.g., [28]) and general literature for the region (e.g., [168,169]) we argue that our sampling was representative of the most common and frequent species in the river.

This study represents the first standardized fish assemblage description published and trophic classification of the species of the entire Uruguay River. Regarding the fish species present registered, it becomes of particular interest to highlight the presence of one exotic invasive fish species that represents a global threat to native biodiversity in the upper Uruguay River: The Nile Tilapia (*Oreochromis niloticus*). This species is one of the most commonly used in freshwater pisciculture production worldwide [170], and often generates great negative ecological consequences, particularly competing with native species [170]. The proliferation of these and other exotic species could affect local biodiversity by predation and competition with native species that share the same trophic niche.

Furthermore, this is the first dietary description for 29 fish species, despite that some of them are of elevated importance in fisheries (e.g., *Luciopimelodus pati*, being one of the most captured species by artisanal-commercial fisheries in the region) [171–173] and aquaculture (e.g., *Hoplias lacerdae* with lack of published field diet studies) (e.g., [174]). The other species with a previously unknown diet are rare species that are not usually collected in large numbers (e.g., *Otocinclus arnoldi* and most of the *Hypostomus* species). All this new information contributes to the knowledge of the trophic structure

of fish assemblage. Moreover, when reviewing literature of the previously studied species, it most generally falls within a similar trophic classification; but one (*Leporinus striatus*) shows contrasting diet differences. *L. striatus* analyzed in this study lie well within the omnivore-invertivore trophic group, with important contribution of aquatic invertebrates (mostly invasive golden mussel, *Limnoperna fortunei*) to its diet. However, previous studies describe the species as an herbivore. This evidence suggest that the trophic classification of this species should be reassigned in the Uruguay River following our study. The reason behind this change might be the contrasting food availability between study sites (Amazon River Basin vs. Uruguay River) after the invasion of the golden mussel into the Uruguay River. The invasive golden mussel is nowadays known to represent a key dietary item in some Anostomid fish species (e.g., *M. obtusidens* and *L. striatus*), formerly classified as herbivorous ([175], González-Bergonzoni et al., in Prep).

Regarding the general trophic classification made here, it must be held in mind that the Uruguay River has a great spatial and temporal variability along its length, which could mean a high intra-specific variability in diet—particularly in the species with feeding plasticity—responding to flood pulses, seasonality, or local habitat conditions (e.g., [176,177]). This kind of spatial and individual size variability was not considered in the current analyses, because the main objective of this study consisted in a broad-scale classification for each species that surpassed local particularities or a particular life stage. Although diet analysis of some rare species that only presented one or few individuals was also performed, those were still kept into the analyses because their diets were sometimes completely unknown in the region. The aspects outlined above must be taken into account if an objective to describe food webs at a fine resolution or at a local level is to be addressed. However, a broad classification of fishes into feeding groups such as this one is an important tool in ecology, allowing comparisons among different environments, river basins or regions, based on fish assemblage structure [178].

The trophic structure of fish assemblages did not generally differ among the three river sections, being the piscivores dominant in terms of relative biomass and richness and the omnivore-detritivore dominant in terms of abundance. This partly reflects the contrasting size structure of species within those trophic groups, being the piscivores usually larger and with higher biomass in the assemblage. Much of the dominance in abundance of the omnivorous-detritivorous group responds to the high frequency and abundance of the *Iheringichthys labrosus* species, sampled along of most of the river length. This ubiquitous species is highly plastic in its diet [40] and digestive morphological features [179], being a constantly dominant species across the entire river.

The observed significantly higher relative species richness of omnivorous species feeding on terrestrial invertebrates towards the middle section of the river may correspond to the dominant environmental characteristics of that zone. In particular, the middle section hosts several large floodplains in which the river channel contacts grasslands and forest areas during floods where terrestrial invertebrates become highly available (e.g., [180]). In this context, it needs to be mentioned that sampling took place during a high river flow scenario, with significant floods, particularly in the middle and lower stretches. Most of the species within this trophic group have morphological adaptations to feed on the water surface (e.g., supra-terminal mouth), where arthropods derived from the land drift in the water surface. This evidence generally agrees with large river theories (e.g. “The flood pulse concept”) in which increased land-water contact increases terrestrial subsidies for fish biomass [180]. Moreover, it matches well with the observed in studies arrayed at diverse scales, where the terrestrial food intake of fish increase whenever the land-water interphase increases, e.g., towards flooded forests (e.g., [181]), or towards stream ecosystems with riparian forests [182]. Thus, this study finding probably remarks that terrestrial carbon input and flow in aquatic ecosystem food webs might be increased in regions with high terrestrial-aquatic habitat connectivity.

The relative importance of trophic groups such as piscivore and omnivore-herbivore did not increase downstream as previously evidenced for smaller fluvial ecosystems (at least at the coarse level defined here) [12–14]. The change in the scale of analysis (large river vs. middle size rivers and streams in the evidence fueling most river theories) may account for the absence of strong changes in the fish

assemblage trophic structure from headwaters to mouth, probably because, even in the upper section, the system may be already large and productive enough to sustain high trophic diversity. However, and remarkably, the omnivorous-planktivorous fish trophic group was far more frequent in the lower than in the middle and upper sections, probably reflecting that the river velocity and turbulent flow decrease downstream as the river widens up allowing establishment of planktonic communities (as postulated by Horwitz 1978, and Vannote 1980 [12,13]).

Several anthropogenic factors may affect fish assemblages, such as the agrochemical inputs from the basin, fisheries, industrial and domestic sewage [183] and habitat fragmentation caused by hydroelectric dams [27,184]. This anthropogenic intervention in freshwater ecosystems typically results in the reduction of local biodiversity and affected community structure, particularly of fish [185,186]. For example, the low species richness and high spatial variability in the relative representation of different trophic groups in the upper Uruguay River might well be attributed to the presence of three hydroelectric dams between sampling sites (being this, a well-known impact of dams) [27,184,187]. Unfortunately, as there is a lack of baseline information on fish trophic structure it became impossible to disentangle the anthropogenic and natural effects driving fish trophic structure along the Uruguay River gradient. In a global scenario of increased anthropogenic pressure to aquatic ecosystems, and particularly of river fragmentation by dam construction [186,188–190] there is an increasing need for the generation of appropriate information about the ecology and biology of fishes, particularly in South America, to achieve better understanding of the ecosystems and improve management plans for the entire continent [34].

This research contributes with basic knowledge that allows interpreting how food webs are structured within this ecosystem, enabling predictions about the roles of particular trophic groups and fish species in the system. Moreover, a proper management of natural resources (such as many of this species that are target for fisheries) demands baseline knowledge on trophic interactions between species, previously inexistent along the entire Uruguay River. Future standardized monitoring programs along the river longitudinal gradient may increase the understanding of these observed patterns across seasons and long temporal scales including the effects of climate variability. Furthermore, in a global scale, the information about trophic classification of fishes generated in this study contributes to the knowledge of ecosystem functioning in this scarcely studied region, and may allow for comparisons with other climate regions.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2073-4441/11/7/1374/s1>, Table S1: Fish assemblage trophic structure along a longitudinal gradient in Uruguay River. Sites are arranged from headwaters to mouth from left to right columns in the table. Values represent the relative abundance / relative biomass (%) of each species and trophic group (as the sum of all species within a group) at each study site. Values are only shown for the species collected in standardized samplings; species presence is marked with "X" in the case of individuals obtained from local fishermen or in previous samplings. The species with * have not been grouped due to unique dietary characteristics, Table S2: Fish species sampled along a longitudinal gradient in the Uruguay River. Taxonomic identification, minimum-maximum standard length (and number of guts analyzed) for each species and site are shown. Sites are arranged from headwaters to mouth from right to left columns in the table. Note that for some species the number of fish is very low and were kept in the analysis for being rare species from which information is highly novel. Use that information with special care.

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