

Isotopic trophic guild structure of a diverse subtropical South American fish community

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Abstract – Characterization of food web structure may provide key insights into ecological function, community or population dynamics and evolutionary forces in aquatic ecosystems. We measured stable isotope ratios of 23 fish species from the Rio Cuareim, a fifth-order tributary of the Rio Uruguay basin, a major drainage of subtropical South America. Our goals were to (i) describe the food web structure, (ii) compare trophic segregation at trophic guild and taxonomic scales and (iii) estimate the relative importance of basal resources supporting fish biomass. Although community-level isotopic overlap was high, trophic guilds and taxonomic groups can be clearly differentiated using stable isotope ratios. Omnivore and herbivore guilds display a broader $\delta^{13}\text{C}$ range than insectivore or piscivore guilds. The food chain consists of approximately three trophic levels, and most fishes are supported by algal carbon. Understanding food web structure may be important for future conservation programs in subtropical river systems by identifying top predators, taxa that may occupy unique trophic roles and taxa that directly engage basal resources.

Key words: carbon; nitrogen; niche; resource; food web

Introduction

Aquatic systems are often defined by the fish species they support. For example, diverse cichlid lineages have defined many tropical ecosystems, particularly the East African rift valley. Economically important lineages (e.g., Salmonidae, Centrarchidae) and large charismatic apex predators characterize many rivers and lakes worldwide. For example, tropical rivers in South America (Amazon basin) support diverse fish communities (Jepsen & Winemiller 2002) and are characterized by a few highly successful lineages (Characidae, Cichlidae, Loricariidae; Albert et al. 2011). Although tropical systems are species rich and niche space appears saturated, some species occupy ecological roles that lack redundancy and are thus extremely important to ecosystem function. For example, the loss of a hyper-abundant detritivore (*Prochilodus mariae*) dramatically alters carbon transport and sediment loads (Taylor et al. 2006). Detritivorous fishes are often abundant and important components of tropical South American food webs.

For example, sucker-mouthed catfishes (Loricariidae) play important functional roles by modifying habitat (Power 1990) and consuming resources that are often poorly available to fishes (e.g., wood, macrophytes; Lujan 2009).

The food web structure of Amazonian streams is often characterized by algal-supported fish biomass, broad carbon range of fish communities (10–14‰ $\delta^{13}\text{C}$) and variable food chain lengths of 2–4 trophic levels (Hamilton et al. 1992; Lewis et al. 2001; Jepsen & Winemiller 2002). Additionally, the omnivore and detritivore trophic guilds are typically diverse (Jepsen & Winemiller 2002). However, subtropical South American rivers are poorly studied compared with Amazonian systems (Winemiller 1989; Hamilton et al. 1992; Lewis et al. 2001; Jepsen & Winemiller 2002, 2007). Subtropical South American drainages support diverse fish assemblages and display comparatively high degrees of endemism and cryptic diversity (Lucena & Kullander 1992; Pialek et al. 2011; Rican et al. 2011). Yet, species boundaries, community composition and ecological

roles of many subtropical South American fishes are poorly known, and our understanding of food web structure in these streams is extremely limited (Zarucki et al. 2010; Serra et al. 2011).

We are not aware of any studies of the food web structure of any subtropical South American streams, although there are analyses of subtropical lakes and estuaries (García et al. 2006, 2007). The Rio de la Plata Basin, the second largest catchment in South America after the Amazon, displays high levels of endemism (35–65%; Pialek et al. 2011; Albert et al. 2011) and supports diverse ichthyofauna. For example, the three primary tributaries, Rio Paraguay, Rio Uruguay and Rio Paraná, support 332, 230 and 330 species, respectively (Reis et al. 2003; Albert et al. 2011). Many Rio de la Plata Basin fishes are believed to be derived from Amazonian lineages (Eigenmann 1906; Eigenmann et al. 1907; Pearson 1937; Reclus 1895; Carvalho & Albert 2011). This system provides a unique opportunity to investigate food web structure in a poorly known subtropical stream with physical and possibly functional attributes similar to temperate latitude streams, but with fish assemblages derived from Amazonian lineages.

We investigated the trophic guild structure of the Rio Cuareim, Uruguay, a major tributary to the Rio Uruguay basin, using stable isotope ratios. Our objectives were to (i) describe the food web structure of the fish community, (ii) compare trophic segregation at community and guild scales (trophic and taxonomic) and (iii) estimate the relative importance of basal carbon sources supporting fish biomass.

Methods

Study site

The La Plata basin is the second largest river in South America and the fifth largest in the world with a 3×10^6 km² catchment area (Brea & Zucol 2011). It extends from southern Uruguay to middle Brazil and comprises tropical and subtropical latitudes (Brea & Zucol 2011) and supports a diverse Gondwanan fish assemblage (Maisley 2000). The Rio Uruguay drainage is the smallest of three main tributaries to the La Plata River, and like most of the La Plata basin, it is supported by an extensive groundwater reservoir (Favetto et al. 2005; Brea & Zucol 2011). The Rio Cuareim drains south-western Brazil and north-western Uruguay and is a major tributary to the middle Rio Uruguay. The surrounding physiographic region is arid, subtropical prairie (Iriondo 1999; Brea & Zucol 2011). The Rio Cuareim is a fifth-order, clear-water piedmont river characterized by cobble substrates and diverse and highly endemic fish communities (Lucena & Kullander 1992; Zarucki et al.

2010; Serra et al. 2011; E. D. Burrell, pers. obs.). For more detailed discussion of the study site, see Burrell (2012).

Study design

We sampled fishes in the upper Rio Cuareim (S 30° 46', W 056° 02') basin using a combination of backpack electro-fishing, seines, cast nets and hook and line sampling. Samples were pooled across three sites along a 15-km reach in the upper basin. Fishes were immediately euthanized and frozen. We lyophilized caudal muscle tissue until dry, ground them into a homogenous powder and packed samples into tin capsules (Costech Analytical Technologies). Aquatic macrophytes (*Hydrilla*) and detritus (leaves) were manually sampled. Terrestrial-derived leaf samples were collected from the substratum and are considered inclusive of associated microbes. Sediment and attached filamentous algae were scrapped from rock surfaces. All basal resources were cleaned of particulate matter using a microscope. Stable isotope ratios were analysed at the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, AZ, USA). Isotope values are written in delta notation, which represent deviation from standards: Pee Dee Belemnite (PDB) limestone and atmospheric nitrogen for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

We used discriminate function analysis (DFA) to determine whether species could be classified into predefined trophic guilds and taxonomic groups (order, family, species) based on their stable isotope ratios. We determined trophic guilds for fishes from dietary references in the literature (Table 1). To estimate the relative importance of basal resources, we estimated the number of trophic transfers that separate each trophic guild from basal resources: herbivores and detritivores (1), omnivores (1.5), invertivores (2) and piscivores (2.5). These values were chosen because generally consumers occupy integer trophic positions, except for omnivores, which feed at multiple trophic levels (Thompson et al. 2007), and thus, they were given an intermediate trophic level. These trophic levels are analogous to other food chains in South American streams (Jepsen & Winemiller 2002). We then corrected consumer isotope ratios based on fractionation rates of 0.5‰ ($\delta^{13}\text{C}$; DeNiro & Epstein 1978) and 2.54‰ ($\delta^{15}\text{N}$; Vanderklift & Ponsard 2003) for each trophic transfer. Owing to assumptions involved with these corrections, we did not attempt to quantify the importance of each basal resource and instead used the spatial relationships in a CN bi-plot to estimate their relative importance. We deposited voucher specimens in the Auburn University Natural History Museum and Learning Center (Auburn, AL, USA).

Table 1. Trophic guild assignment for fish taxa and references used.

Trophic guild	Taxa	Reference
Omnivore	<i>Bryconamericus</i>	Russo et al. 2004
Omnivore	<i>Leporinus</i>	Horeau et al. 1998
Invertivore	<i>Heptapterus</i>	Horeau et al. 1998
Omnivore	<i>Trachelyopterus</i>	Moresco & Bemvenuti 2005
Omnivore	<i>Astyanax</i>	Esteves 1996
Piscivore	<i>Hoplias</i>	Winemiller 1989
Piscivore	<i>Serrasalmus</i>	Winemiller 1989
Omnivore	<i>Rhamdia</i>	Winemiller 1989
Omnivore	<i>Gymnogeophagus</i>	Yafe et al. 2002
Omnivore	<i>Australoheros</i>	Yafe et al. 2002
Piscivore	<i>Oligosarcus</i>	Nunes & Hartz 2006
Detritivore	<i>Prochilodus</i>	Taylor et al. 2006
Herbivore	<i>Hypostomus</i>	Nonogaki et al. 2007
Herbivore	<i>Rineloricaria</i>	Jepsen & Winemiller 2002
Herbivore	<i>Ancistrus</i>	Power 1984, 1990
Piscivore/Invertivore	<i>Crenicichla</i>	Lucena & Kullander 1992

Results

We sampled four basal resources and 23 species of fish (Table 2; Fig. 1). Community-wide bi-plots of fish C and N isotope ratios display relatively large isotopic overlap between most fishes (Fig. 1a). In contrast, discriminate function analysis revealed that fishes can be classified into trophic guilds (70.3% classification success), but was less successful at classifying taxonomic groups (40–58.6% classification success) based on stable isotope ratios (Tables 3 and 4). Trophic guild membership is significantly associated with $\delta^{15}\text{N}$ ratios ($R^2 = 0.58$, $F = 164.33$, $P < 0.0001$; Fig. 2) although herbivores display higher than predicted $\delta^{15}\text{N}$ ratios relative to other guilds (Fig. 2). Large $\delta^{13}\text{C}$ discrepancies within trophic guilds and high overlap between trophic guilds suggest that carbon sources are not useful in identifying fish trophic guilds (Fig. 2).

Approximately 80% of the omnivores were correctly reclassified using stable isotope ratios. Only 20% were classified into the invertivore and herbivore guilds (10% each), demonstrating that, despite the isotopically diverse sources consumed by omnivores, they possess a guild-level isotopic identity. Piscivores and detritivores displayed the highest reclassification success (86% and 100%, respectively). Unexpectedly, high $\delta^{15}\text{N}$ ratios for the herbivore guild resulted in a reduced ability to discriminate herbivores from invertivores (29% of invertivores incorrectly classified as herbivores) and omnivores (25% of herbivores incorrectly classified as omnivores). Course and fine taxonomic groups can also be classified but DFA was less successful at separating them (Table 3). Most species had similar C/N ratios regardless of trophic guild (Table 2); however, *Gymnogeophagus gymnogenys* and *Prochilodus lineatus* display comparatively high C/N ratios and

Table 2. Stable isotope ratios (mean \pm 1 SD) of fishes in the Rio Cuareim, Uruguay. Samples are representative of adult size classes.

Taxa	n	C/N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Piscivore				
<i>Crenicichla missioneira</i>	13	3.17	-19.0 ± 0.6	12.2 ± 0.5
<i>Crenicichla celidochilus</i>	10	3.16	-18.9 ± 0.9	12.9 ± 0.1
<i>Hoplias lacerdae</i>	3	3.18	-18.1 ± 1.1	14.1 ± 0.9
<i>Oligosarcus robustus</i>	2	3.25	-20.6 ± 0.7	13.5 ± 0.5
<i>Serrasalmus spilopleura</i>	2	3.21	-20.4 ± 0.6	13.5 ± 0.1
Invertivore				
<i>Crenicichla scottii</i>	11	3.15	-19.9 ± 0.3	11.7 ± 0.2
<i>Crenicichla minuano</i>	18	3.14	-22.1 ± 0.6	11.4 ± 0.5
<i>Crenicichla lepidota</i>	15	3.17	-20.9 ± 1.3	11.3 ± 0.1
<i>Heptapterus mustelinus</i>	2	3.44	-20.6 ± 0.6	12.2 ± 0.1
<i>Crenicichla tendybaguassu</i>	5	3.17	-18.5 ± 0.5	11.7 ± 0.3
Omnivore				
<i>Gymnogeophagus gymnogenys</i>	7	3.84	-17.2 ± 1.3	9.4 ± 0.7
<i>Gymnogeophagus cf. meridionalis</i>	1	3.18	-18.9	10.9
<i>Gymnogeophagus meridionalis</i>	4	3.18	-20.6 ± 1.1	10.7 ± 0.1
<i>Australoheros scitulus</i>	5	3.19	-18.3 ± 0.6	10.5 ± 0.3
<i>Astyanax</i> sp.	5	3.27	-21.6 ± 0.6	10.8 ± 0.6
<i>Leporinus amae</i>	3	3.11	-19.5 ± 0.5	10.8 ± 0.6
<i>Bryconamericus iheringi</i>	6	3.44	-19.8 ± 1.0	10.5 ± 0.3
<i>Rhamdia quelen</i>	1	3.15	-21.6	10.9
<i>Trachelyopterus galeatus</i>	1	3.20	-22.1	10.8
Herbivore				
<i>Ancistrus taunayi</i>	5	3.24	-25.6 ± 1.5	11.3 ± 0.5
<i>Rineloricaria cf. misionera</i>	3	3.30	-18.0 ± 0.2	11.1 ± 0.4
<i>Hypostomus uruguayensis</i>	1	3.16	-16.7	9.9
Detritivore				
<i>Prochilodus lineatus</i>	2	3.82	-21.9 ± 0.6	8.3 ± 0.5

may be stoichiometrically unique. Three sucker-mouthed catfishes displayed significantly different $\delta^{13}\text{C}$ ratios, which were strongly associated with unique basal resources (Fig. 1).

The $\delta^{13}\text{C}$ range of each trophic guild varied: piscivore (2.5‰), insectivore (3.6‰), omnivore (4.9‰) and herbivore (8.9‰) represent 28, 41, 55 and 100% of the community-wide $\delta^{13}\text{C}$ range (8.9‰), respectively. The detritivore guild is not included because only one species was classified into the guild. Piscivore $\delta^{15}\text{N}$ ratios relative to basal $\delta^{15}\text{N}$ ratios suggest the occurrence of approximately 3 trophic levels (Fig. 1).

On the basis of our estimated fractionation corrections, algae may support most fish biomass (Fig. 3). Macrophyte carbon only appears important to a few species (Fig. 1a) that may consume them directly (Table 2).

Discussion

This study describes the food web structure of a subtropical South American piedmont stream and provides important context for the numerous food web studies of Amazonian rivers (Hamilton et al. 1992; Lewis et al. 2001; Jepsen & Winemiller 2002, 2007). Stable isotope analyses revealed distinct trophic

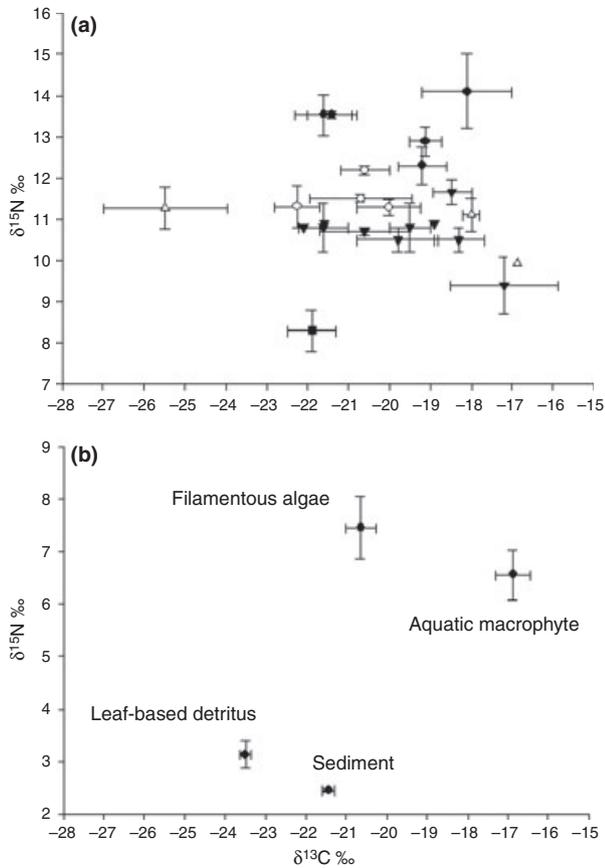


Fig. 1. Stable isotope (mean \pm 1 SD) bi-plot showing the trophic relationships of (a) fishes: piscivores (◆), invertivores (○), omnivores (▼), herbivores (△), detritivores (■); (b) basal resources in the Rio Cuareim, Uruguay.

Table 3. Classification success (%) from discriminate function analysis of trophic guilds (according to the literature) and taxonomic groups using stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Model	Guild	Order	Family	Species
Reclassification success (%)	70.3	58.6	40	51.7

guilds within the fish community and identified important nutrient sources for fish consumers. Several characteristics, such as food chain length, the relative importance of basal resources, and high occurrence of omnivory were analogous to Amazonian rivers.

Piscivores were isotopically distinct from other guilds despite consisting of two functionally different groups. Winemiller (1989) classified *Serrasalmus* (Piranha) as shearers, and *Hoplias* as engulfers based on their feeding modes. In Amazonian systems, these two piscivore guilds were not isotopically distinguishable (Jepsen & Winemiller 2002); however, our data easily separate them by $\delta^{13}\text{C}$ signatures. This could be due to species-level taxonomic differences or possibly due to tropical–subtropical discrepancies in guild structure. *Crenicichla* are diverse in subtropi-

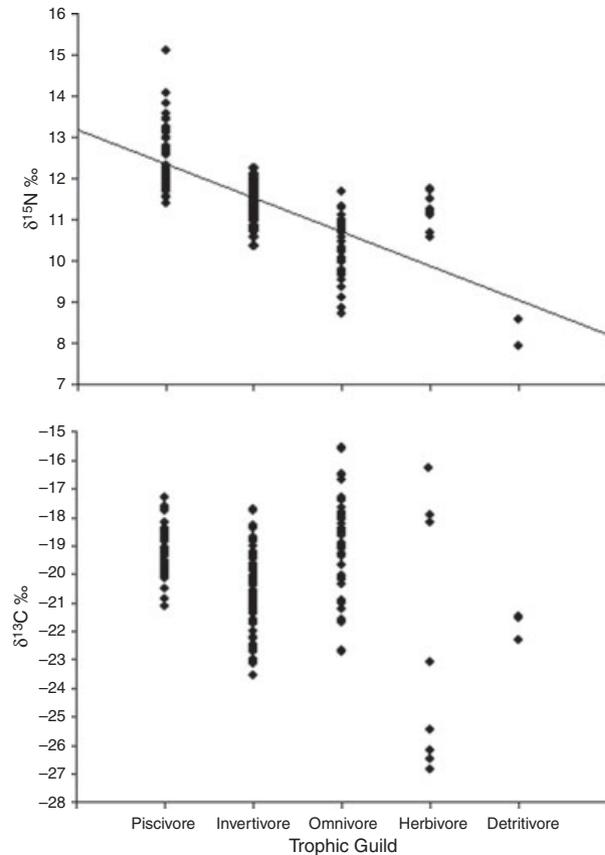


Fig. 2. The isotopic relationship between trophic guild and $\delta^{15}\text{N}$ ratios for fishes in the Rio Cuareim, Uruguay. Each point represents an individual. Guild assignment is based on previous literature and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

cal South American rivers (Pialek et al. 2011) and are often important mesopredators in tropical systems (Reznick et al. 1990; Johansson et al. 2004). We found that six species are split between two trophic guilds (piscivore and invertivore), and $\delta^{13}\text{C}$ ratios vary greatly among species, indicating they may have species-specific trophic roles.

Omnivory may be an adaptive response to fluctuations in resource availability or poor resource predictability (Winemiller 1989; Jepsen & Winemiller 2002). Seasonal fluxes of terrestrial subsidies from floodplains that occur in Amazonian streams (i.e., Winemiller & Jepsen 1998) are unlikely in arid subtropical South America (Iriondo 1999) and may be replaced by seasonal temperature shifts that influence autochthonous resources (e.g., algae, macrophyte biomass). Almost half the species sampled were classified as omnivores, including primarily taxa that display generalist feeding habits in other systems (Esteves 1996; Yafe et al. 2002; Russo et al. 2004). Despite the diverse resources consumed by these taxa, our analyses indicate that the omnivore guild has a distinct isotopic identity. In contrast, omnivores were comparatively less isotopically distinct than

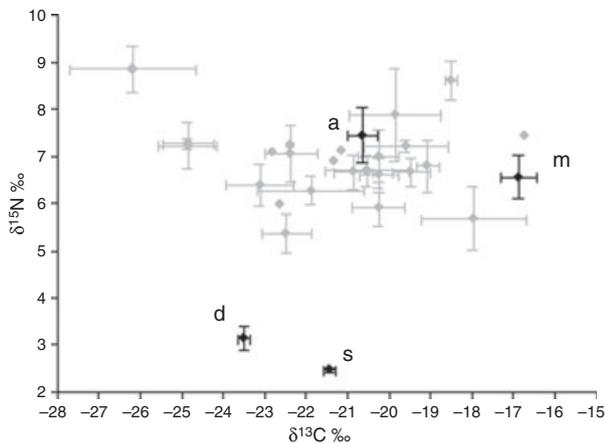


Fig. 3. Stable isotope bi-plot (mean \pm 1 SD) of basal resources: filamentous algae (a), macrophytes (m), terrestrial-derived detritus (d) and sediment (s). Grey-scale points are fishes after correction for fractionation based on an estimated number of trophic transfers: herbivores and detritivores (1), omnivores (1.5), invertivores (2) and piscivores (2.5).

Table 4. Reclassification success of trophic guild membership of fishes in the Rio Cuareim, Uruguay, using discriminate function analysis. Guild membership is based on literature, and predicted guild membership is based on stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Guild	Predicted Guild Membership (%)				
	Piscivore	Invertivore	Omnivore	Herbivore	Detritivore
Piscivore	85.7	14.2	0	0	0
Invertivore	14.5	52.7	3.6	29.1	0
Omnivore	0	10.5	78.9	10.5	0
Herbivore	12.5	0	25	62.5	0
Detritivore	0	0	0	0	100

other trophic guilds in Amazonian food webs (Jepsen & Winemiller 2002).

Herbivores were the least isotopically distinct of all predefined trophic guilds, because of higher than predicted $\delta^{15}\text{N}$ ratios. This guild also consists of the most $\delta^{13}\text{C}$ depleted and enriched species sampled; thus, the guild spans the entire community $\delta^{13}\text{C}$ range. *Hypostomus* and *Rineloricaria* were associated with macrophyte and algal carbon, respectively. *Ancistrus* displayed more negative $\delta^{13}\text{C}$ ratios than any basal resource sampled. Previous studies established *Ancistrus* as herbivorous grazers (Power 1984, 1990), but recent studies suggest they often display more negative $\delta^{13}\text{C}$ ratios than other loricariids and that some species may be detritivorous (Lujan 2009). Thus, the inclusion of *Ancistrus taunayi* in the herbivore guild may be tentative. Sucker-mouthed catfishes may play particularly important roles in subtropical South American streams by directly exploiting a variety of basal resources. Additionally, by exploiting allochthonous resources (e.g., wood, detritus) that are difficult to assimilate relative to

autochthonous resources (Thorp & DeLong 1994), loricariids may be important in nutrient processing.

Algal carbon supports many Amazonian river food webs (Hamilton et al. 1991; Lewis et al. 2001; Jepsen & Winemiller 2007). On the basis of our estimated fractionation corrections, algae may support most fish biomass. However, if the food chain is longer than we estimate, or fractionation rates are higher (i.e., Post 2002), the importance of detritus may be equally or more important. Macrophyte carbon only appears important to a few species that may consume them directly. We did not collect water samples, so we are unsure of the role of particulate organic matter (POM). However, two filter-feeding bivalves have $\delta^{13}\text{C}$ ratios of -31‰ (Burruss 2012), suggesting POM is not an important basal resource to fish biomass.

The Rio Cuareim displays many trophic characteristics analogous to Amazonian rivers including food chain length, well-differentiated trophic guilds and algal-supported consumer biomass (Hamilton et al. 1991; Lewis et al. 2001; Jepsen & Winemiller 2002, 2007). Several subtropical lineages such as *Gymnogeophagus* (Reis & Malabarba 1988) and *Australoheros* (Rican et al. 2011) are broadly omnivorous (Yafe et al. 2002; this study), and thus, subtropical South American food webs may be characterized by high rates of omnivory similar to tropical river food webs (Jepsen & Winemiller 2002). *Crenicichla* are often apex predators (Layman et al. 2005), and through predation pressure, they alter community structure and evolution (Reznick et al. 1990; Johansson et al. 2004). Our data suggest a diverse group of six species may partition their diets, and thus, collectively, *Crenicichla* may exert diverse predation pressures in subtropical South American food webs.

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