



**UFRGS**  
UNIVERSIDADE FEDERAL  
DO RIO GRANDE DO SUL



PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

**INSTITUTO DE BIOCÊNCIAS**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL**

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**ECOLOGIA TRÓFICA E COMPOSIÇÃO DA ICTIOFAUNA EM RIACHOS DA SUB-BACIA  
DO RIO IJUÍ, RS, BRASIL**

PORTO ALEGRE

2020

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DO RIO IJUÍ, RS, BRASIL**

Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Doutor em Biologia Animal.

Área de concentração: Biodiversidade

Orientador(a): Prof<sup>ª</sup> Dr<sup>ª</sup> Clarice Bernhardt Fialho

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Aprovada em \_\_\_\_ de \_\_\_\_\_ de \_\_\_\_.

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*Dedicatória*

*Dedico estes anos da minha vida e  
todo o significado de um doutorado  
às pessoas mais importantes,  
Meus pais e  
Minha Filha, Bibiana,  
meu mais novo, puro e verdadeiro amor.*



*Epigrafe*

*"Cada livro, cada volume que você vê, tem alma. A alma de quem o escreveu, e a alma dos que o leram, que viveram e sonharam com ele." Carlos Ruiz Zafón*

*E assim como os livros: são as teses!*

## *Agradecimentos*

*Eu agradeço a todas as pessoas que contribuíram para tornar essa conquista uma realidade. Agradeço em especial a minha mãe e ao meu pai pelo amor incondicional, pelo apoio e por acreditarem sempre que eu seria capaz. Agradeço pelo carinho e pelas conversas que tiveram comigo, sendo sempre a fonte da força que eu precisei para seguir em frente nos meus objetivos e vencer os obstáculos que encontrei pelo caminho. Agradeço todo o esforço que fizeram para que as coletas de peixes pudessem acontecer, minha mãe organizando a logística do "acampamento" na sala do apartamento e meu pai ajudando a pescar e a coletar os famigerados "sources"... Agradeço a eles todo o amor que representam na minha vida e tudo que até hoje conquistei... Agradeço aos meus pais por quem me tornei e pelo empenho sobre-humano que fizeram para que eu tivesse a oportunidade de estudar até o doutorado...*

*Agradeço a minha irmã e ao meu sobrinho por todo o amor, carinho e torcida neste longo processo... Obrigada Joice, por ajudar com a Bibiana nesta reta final da tese, para que eu pudesse concluí-la... Eu amo vocês e estaremos sempre juntos em todas as fases e conquistas...*

*Agradeço à minha professora e Amiga Clarice, sem a qual esta etapa da minha vida não seria possível. Querida Professora, obrigada por todo o suporte e carinho que você me dedicou durante todos os anos em que frequentei a UFRGS, desde o mestrado. Sem você*

e sem teu apoio eu não teria concluído o mestrado (trabalhando), não teria ingressado no doutorado, não teria grana para as coletas, não teria a coragem necessária para participar do processo seletivo para o sanduíche, não teria conseguido licença do meu trabalho como professora da Educação Básica para viajar, não teria tido onde morar nos meus últimos dias em Porto Alegre, entre tantas outras coisas... Em você encontrei um porto seguro para as minhas angústias acadêmicas e pessoais e encontrei palavras amigas e sábias, proferidas durante um chimarrão, nos momentos em que me encontrei sozinha e perdida... Esperei muitas vezes, ansiosa pelo intervalo após o almoço quando eu mostrava os meus dados e tabelas e conseguíamos conversar sobre tantas coisas... Tive em você um exemplo de chefe e gestora, que valoriza o humano e acredita nas meninas desconhecidas vindas do interior; que compreende que a métrica da meritocracia não é igual para todos e assim, tenta oportunizar, com muito jogo de cintura e com as "armas que tem nas mãos" um pouquinho mais de igualdade entre aqueles que percorrem os corredores do Zoo na UFRGS... Obrigada, professora Clarice pelo exemplo que a Senhora se tornou na minha vida e pela diferença que fez nela. Que a minha filha possa encontrar uma professora como a Senhora, que a ensine que a Universidade precisa ir além da Ciência e que a vida vai além das portas dos laboratórios...

Agradeço ao Professor Malabarba que tantas vezes esclareceu com paciência as minhas inúmeras dúvidas e que indicou os caminhos pelos quais conduzir o meu trabalho, quando eu

*não encontrava explicações possíveis e não sabia como seguir, contestou minhas hipóteses e com isso me fez pensar, aprender sempre mais e crescer...*

*Agradeço ao Professor Winemiller que me acolheu em um país diferente e teve toda a paciência com o meu péssimo inglês, desenhando, literalmente, em uma folha de papel quando eu não conseguia compreender suas explicações... Com o senhor ampliei meus horizontes, expandi meus conhecimentos e aprendi que um cientista renomado também pode ser acessível...*

*Agradeço a todos os meus colegas do Laboratório de Ictiologia da UFRGS que de uma forma ou de outra contribuíram para que esta tese pudesse ser concluída, ajudando nas coletas, nas triagens, nas identificações das espécies, nas análises e em tudo aquilo que perpassa a vida em um laboratório... Muito obrigada! Aprendi com cada um de vocês e cada um de vocês, à sua maneira, me modificou um pouco e deixou sua marca ao longo de toda esta caminhada... Assim como agradeço a todos os colegas com quem convivi e aprendi no Winemiller Aquatic Ecology Lab, mesmo que por um breve período de tempo.*

*Agradeço, a minha filha, que chegou neste último ano, modificou toda a minha vida e trouxe a ela um novo significado. Pensando em você, minha pequenininha linda, encontrei a perseverança necessária para concluir este doutorado. Hoje, você é o que eu tenho de mais precioso em minha vida e é por você que eu dou cada um dos meus passos. Eu te amo*

*Bibiana.*

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## RESUMO

A sub-bacia do rio Ijuí, está inserida na área de drenagem do rio Uruguai que compõe uma das principais bacias hidrográficas da América do Sul e possui grande diversidade de peixes, distribuídos em vários habitats dulcícolas, incluindo os riachos. Estes ambientes, ricos em micro-habitats são de grande importância para a manutenção dos ecossistemas e abrigam espécies de pequeno porte, muitas vezes endêmicas. Conhecer a ictiofauna de riachos da sub-bacia hidrográfica do rio Ijuí, entendendo algumas relações tróficas que ocorrem entre as espécies, consiste no objetivo geral desta tese, que está dividida em quatro capítulos, dos quais são objetivos específicos: 1) avaliar a composição da comunidade e o padrão de distribuição das espécies, testando a hipótese de que a complexidade da comunidade de peixes aumenta da montante em direção à jusante da sub-bacia hidrográfica do rio Ijuí; 2) investigar os hábitos alimentares de *Astyanax paris*, testando a hipótese de que esta espécie modifica suas presas conforme os estágios de seu ciclo de vida (ontogenia); 3) investigar o uso de recursos e a partição de nicho entre espécies de peixes pertencentes às mesmas e diferentes guildas tróficas e às mesmas e diferentes famílias, testando a hipótese de que dentro de uma guilda trófica ou família as espécies de peixes co-ocorrentes apresentam partição de nicho trófico e as sobreposições de nicho são menores entre espécies de diferentes famílias devido ao conservadorismo filogenético do nicho; 4) investigar diferenças nos hábitos alimentares de 15 espécies de Characidae, de cinco gêneros (*Astyanax*, *Bryconamericus*, *Diapoma*, *Hyphessobrycon* e *Piabarchus*) e identificar associações entre a ecologia alimentar dessas espécies e suas características ecomorfológicas, incluindo caracteres do aparato oral, testando a hipótese de que essas espécies diferem no uso dos recursos alimentares e a seleção de itens preferenciais na dieta está relacionada às suas características ecomorfológicas ou caracteres do aparato oral. Para isso, seis riachos da sub-bacia do rio Ijuí foram amostrados ao longo de um ano, com a técnica da pesca elétrica; As relações tróficas foram estudadas através de duas análises complementares: investigação do conteúdo estomacal dos peixes capturados, identificando-se morfológicamente as presas e análises de isótopos estáveis de  $\delta^{13}\text{C}$  e  $\delta^{15}\text{N}$  do tecido muscular dos peixes. Assim, conclui-se que: dos 5029 indivíduos coletados, foram identificadas 55 espécies, 13 famílias e cinco ordens de peixes, com maior riqueza nas áreas à jusante da sub-bacia do rio Ijuí; a espécie *Astyanax paris* comportou-se como um insetívoro nos riachos estudados e alterou gradualmente sua dieta de insetos aquáticos para terrestres, conforme seu desenvolvimento ontogenético; nos estômagos dos peixes onívoros e

invertívoros analisados foram encontrados 18 itens alimentares de origem aquática e 15 de origem terrestre; nas análises de conteúdo estomacal a sobreposição de nicho entre as espécies co-ocorrentes foi baixa na maioria das unidades amostrais e somente durante o verão a sobreposição de nicho foi intermediária; a análise de isótopos estáveis revelou que na maioria das comparações pareadas a porcentagem de sobreposição do espaço isotópico, em relação aos isótopos estáveis de carbono e nitrogênio, foi baixa nos três ambientes amostrados. As espécies de Characidae estudadas apresentaram diferenças entre si em relação aos índices ecomorfológicos; os índices ecomorfológicos associados às habilidades de natação, habitat e captura de alimentos foram os principais responsáveis pelas distâncias ecomorfológicas entre as espécies; os itens alimentares ingeridos pelas espécies de Characidae estavam relacionados às características ecomorfológicas e ao aparato oral destes peixes, principalmente quanto à natação, tamanho da boca e número de dentes.

Palavras-chave: comunidade de peixes; relações tróficas; ontogenia; isótopos estáveis.

## ABSTRACT

The Uruguay River is one of the main hydrographic basins of South America and has a great diversity of fishes, distributed in several freshwaters habitats, including the streams. These environments, rich in microhabitats, are of great importance for the maintenance of ecosystems and harbor small, often endemic, species. Knowing the ichthyofauna of streams in the Ijuí River sub-basin, included in the drainage area of the Uruguay River, understanding some trophic relationships that occur between species, is the general objective of this thesis, which is divided into four chapters, of which specific objectives: 1) to evaluate the community composition and species distribution pattern, testing the hypothesis that the complexity of the fish community increases from the amount downstream of the sub-basin of the Ijuí river, in relation to the streams sampled; 2) to investigate the feeding habits of *Astyanax paris*, testing the hypothesis that this species modifies its prey according to the sequences of the states of its life cycle (ontogeny); 3) to investigate resources use and niche partitioning among fish species belonging to same and different trophic guild and those belonging to the same and different families, testing the hypothesis that within a trophic guild or family the co-occurring fish species present trophic niche partition and niche overlaps are smaller between species from different families due to the phylogenetic conservatism of the niche; 4) to investigate differences in the eating habits of 15 Characidae species of the five genera (*Astyanax*, *Bryconamericus*, *Diapoma*, *Hyphessobrycon* and *Piabarchus*) and to identify associations between the feeding ecology of these species and their ecomorphological characteristics, including oral apparatus characters, testing the hypothesis that these species differ in the use of food resources and the selection of preferred items in the diet is related to their ecomorphological characteristics or characters of the oral apparatus. For this purpose, six streams of the sub-basin of the Ijuí River were sampled over a year, using the technique of electric fishing. The trophic relationships were studied through two complementary analyzes: stomach contents investigation of the captured fish, morphologically identifying the prey and stable isotopes analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of fish muscle tissue. Thus, it was concluded that: of the 5029 individuals collected, 55 species, 13 families and five orders of fish were identified, with greater richness in the areas downstream of the Ijuí sub-basin; the species *Astyanax paris* behaved as an insectivore in the studied streams and gradually changed its diet from aquatic insects to terrestrial, according to its ontogenetic development; in the analyzed omnivorous and invertivorous fishes stomachs were found 18 food items of aquatic origin, 15 of terrestrial



origin; in stomach content analysis, niche overlap among co-occurring species was low in most sampling units and only during the summer niche overlaps were intermediate; the stable isotopes analysis revealed that in most paired comparisons the overlapping percentage of the isotopic space, in relation to the stable isotopes of carbon and nitrogen, in the three sampled environments was low; the species of Characidae studied presented differences among themselves in relation to the ecomorphological indices; the ecomorphological indices associated with swimming, habitat and food capture skills were mainly responsible for ecomorphological distances between species; the food items ingested by the Characidae species were related to the ecomorphological and oral apparatus characteristics of the fish, especially regarding swimming, mouth size and number of teeth.

**Keywords:** fish community; trophic relationships; ontogeny; stable isotopes.

## INTRODUÇÃO<sup>1</sup>

A fauna de peixes da América do Sul é considerada a mais diversa do mundo com estimativas de 9100 espécies entre indivíduos de água doce e ambientes marinhos, representando 27% da ictiofauna mundial (REIS *et al.*, 2016). Para os ambientes dulcícolas continentais somam-se 5160 espécies válidas e na última década mais de 100 espécies novas foram sendo descritas a cada ano (REIS *set al.*, 2016). Estas espécies distribuem-se principalmente entre três complexos de bacias hidrográficas dominantes na América do Sul, sendo elas a Amazônica, a Orinoco e a Paraná-Paraguai também conhecida como La Plata que engloba a área de drenagem da bacia do rio Uruguai (REIS, 2013; REIS *et al.*, 2016).

O rio Uruguai é um dos principais afluentes da bacia do rio de La Plata e estende-se por 2.200 km, com uma área de drenagem de cerca de 365.000 Km<sup>2</sup>, elevando-se na formação da Serra Geral no sul do Brasil e fluindo para o estuário do rio de La Plata entre o Uruguai e a Argentina (DI PERSIA & NEIFF, 1986; CAPPATO & YANOSKY, 2009; ANA, 2016; BERTACO *et al.*, 2016). O rio Uruguai é dividido em três porções, alto Uruguai e a jusante do Salto do Yucumã, médio e baixo Uruguai (DI PERSIA & NEIFF, 1986; BERTACO *et al.*, 2016). O Salto do Yucumã é uma cachoeira longitudinal de 1,8 km de extensão (BERTACO *et al.*, 2016). Os principais afluentes do rio Uruguai são o rio Negro (Uruguai/Brasil), rio Quaraí (Uruguai/Brasil), rio Ibicuí (Brasil) e rio Ijuí (Brasil) (CARVALHO & REIS, 2009). A ictiofauna da bacia de drenagem do rio Uruguai, para o território brasileiro, foi estimada em cerca de 175 espécies descritas e 50 não descritas (MALABARBA *et al.*, 2009), das quais 78 são endêmicas, ocupando uma grande variedade de habitats, incluindo riachos de pequeno porte (BERTACO *et al.*, 2016).

Os riachos estão entre os ambientes que apresentem alta diversidade biológica e grande importância na manutenção da integridade de todo ecossistema (MEYER *et al.*, 2007). Os riachos são conhecidos como ambientes lóticos com um fluxo de água unidirecional que corre da fonte à foz e podem apresentar áreas de inundação não persistentes durante estações chuvosas (ESTEVEES & ARANHA, 1999; UIEDA & CASTRO, 1999). São conhecidos por apresentar grande variedade de micro-habitats devido a gradientes ambientais que variam de corredeiras com rochas e pedras a poções e remansos, somados às diversas variações da vegetação marginal ao longo de sua extensão (ARAUJO LIMA, *et al.*, 1995; ESTEVEES & ARANHA, 1999). Nas regiões sul e sudeste do Brasil podem apresentar altas concentrações

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<sup>1</sup> Formatação conforme as regras NBR 14724, 10520 e 6023 da Associação Brasileira de Normas Técnicas (ABNT).

de oxigênio dissolvido e grandes variações sazonais de temperatura, com influências da geomorfologia da bacia de drenagem sob os componentes abióticos de transparência, pH e condutividade (ARAUJO LIMA, *et al.*, 1995; ESTEVES & ARANHA, 1999).

A estrutura da comunidade de peixes nos riachos se modifica ao longo do espaço e do tempo, e podem ocorrer mais variações entre diferentes partes de um mesmo riacho, que entre diferentes riachos de uma mesma bacia de drenagem, como por exemplo, mudanças na riqueza de espécies ou diversidade de grupos funcionais que se alteram ao longo de um gradiente de cabeceiras (montante) em direção à foz (jusante) (VANNOTE *et al.*, 1980; ARAUJO LIMA, *et al.*, 1995). Os estudos de composição e distribuição de espécies que habitam riachos, bem como as investigações sobre as redes tróficas que elas estabelecem, contribuem, portanto, no entendimento da dinâmica das comunidades e nas estimativas de suscetibilidade dos habitats, sendo úteis na definição de áreas prioritárias para conservação (BAILLY *et al.*, 2016; ROSE *et al.*, 2016).

A ictiofauna de riacho na sub-bacia hidrográfica do rio Ijuí, um dos principais afluentes do rio Uruguai, é o objeto de investigação desta tese, no que se refere à composição da comunidade e relações tróficas estabelecidas. O rio Ijuí está localizado na região nortenoeste do estado do Rio Grande do Sul, com uma drenagem de 10.649,13 Km<sup>2</sup>, abrangendo 20 municípios, na porção do médio Uruguai, no Sul do Brasil (FEPAM, 2016). Os principais rios formadores do rio Ijuí são Ijuzinho, Conceição, Potiribu, Caxambu, Faxinal, Fiúza e Palmeira (FEPAM, 2016). O estudo da alimentação e diversidade dos peixes de riacho da sub-bacia do rio Ijuí foi conduzido com base em coletas de espécimes em seis riachos distribuídos ao longo da sub-bacia, durante um ano de amostragens, através da técnica da pesca elétrica, que está entre as mais adequadas e efetivas para ambientes de água doce (YODER & SMITH, 1998).

Os peixes são componentes fundamentais das redes tróficas aquáticas estabelecidas em ecossistemas de riachos, distribuindo-se em diversos níveis tróficos e sendo determinantes na dinâmica dos micro-habitats que ocupam (VALENTINI *et al.*, 2009). O estudo dos hábitos alimentares das espécies contribui para o entendimento das redes tróficas nos riachos, em como as diferentes estratégias tróficas influenciam a comunidade e como as interações entre os indivíduos desta comunidade afetam o fluxo de energia no ecossistema, influenciando em sua estrutura e funcionalidade (VALENTINI *et al.*, 2009; POMPANON *et al.*, 2012; PENDLETON *et al.*, 2014).

As interações tróficas podem afetar os processos ecossistêmicos quando estresses e perturbações antrópicas modificam essas interações ou ocasionam perda de biodiversidade na comunidade (THÉBAULT & LOREAU, 2003). A supressão de espécies afeta a estrutura de níveis tróficos inferiores e superiores, alterando o fluxo de energia e ocasionando, em algumas situações, extinções secundárias (THÉBAULT & LOREAU, 2003; PENDLETON *et al.*, 2014). Nos ambientes impactados, ou sob influência antrópica como o caso dos riachos do rio Ijuí, conhecer o papel trófico de cada espécie no ecossistema contribui no entendimento da rede trófica e em como as relações ecológicas podem ser afetadas frente à perda de biodiversidade. Para isso, entender o papel de cada espécie na rede trófica implica em conhecer quais recursos são utilizados pelas espécies; quais espécies apresentam maior plasticidade trófica, utilizando-se de recursos diversos e provenientes de fontes variadas; como ocorrem as interações tróficas intra e interespecíficas; entre outros. Estes conhecimentos possibilitam o levantamento de hipóteses sobre a origem dos nutrientes que compõem as teias alimentares aquáticas e sobre a dinâmica das interações ecológicas entre espécies co-ocorrentes.

As dietas das espécies podem ser compreendidas por diversos métodos, entre os quais a identificação morfológica das presas, com auxílio de literatura específica e chaves de identificação dicotômicas (MCCAFFERTY, 1998; MUGNAI *et al.*, 2010; SEGURA *et al.*, 2011), quando se investiga visualmente o conteúdo estomacal dos peixes, com auxílio de lupas ou microscópios (POST, 2002; HARDY *et al.*, 2010; TAGUCHI *et al.*, 2014; WANG *et al.*, 2014). A quantificação dos itens alimentares encontrados nos estômagos é realizada pelo método volumétrico (VO%) (HYNES, 1950) associado à frequência de ocorrência (FO%) (HYSLOP, 1980). No método volumétrico os itens alimentares podem ser quantificados com a contagem do número de quadrados que cada presa ocupa em um papel milimetrado, com a altura fixa em um milímetro. A altura fixa em um milímetro pode ser obtida com ajuda de uma lâmina de microscópio óptico e os itens alimentares são prensados contra a lâmina antes da contagem do número de quadrados, para que não sejam superestimados quando ao volume.

O volume de cada item alimentar quantificado é tratado como um dado de abundância, enquanto o número de vezes que o item alimentar é identificado nos estômagos em relação ao total de itens nos estômagos analisados é tratado como dado de frequência relativa do respectivo item, correspondente ao dado de frequência de ocorrência. (HYNES, 1950; HYSLOP, 1980). Os dados de abundância (volume) e frequência de ocorrência (frequência relativa) podem ser então utilizados para testar se existem possíveis diferenças

inter ou intraespecíficas na alimentação das espécies de peixes, quanto à fatores espaciais, sazonais e ontogenéticos, entre outros. Entre os testes de hipóteses disponíveis e adequados para esses dados biológicos, está a análise de variância multivariada com permutação (permanova), que não exige o pressuposto de normalidade dos dados (ANDERSON, 2001), baseada em uma matriz de distância que usa como medida de dissimilaridade o índice de Bray-Curtis (BORCARD *et al.*, 2011). Esse índice é adequado por aceitar tanto dados de abundância (neste caso, o volume) quando de presença e ausência (neste caso, a frequência de ocorrência) (BORCARD *et al.*, 2011). Os padrões na composição da dieta das espécies de peixes, conforme os fatores testados (intra ou interespecífico, espaciais, sazonais e ontogenéticos, entre outros), podem ser estão visualizados com uma análise de ordenação (BORCARD *et al.*, 2011).

Nos estudos de dieta há necessidade de associação entre os métodos de identificação das presas através do conteúdo estomacal, que nos permitem verificar quem são os componentes das teias alimentares e as análises de isótopos estáveis que fornecem uma visão sobre o fluxo energético na rede trófica e na origem dos nutrientes utilizados pelas espécies (POST, 2002; VALENTINI *et al.*, 2009; HARDY *et al.*, 2010; JO *et al.*, 2014; TAGUCHI *et al.*, 2014; WANG *et al.*, 2014). Técnicas empregando o uso de isótopos estáveis podem fornecer a posição trófica de cada indivíduo na assimilação da energia na teia alimentar e detectar interações ecológicas complexas, como traços de onivoria em um organismo que ocupa posições tróficas diferentes (POST, 2002).

Análises de isótopos estáveis de carbono ( $\delta^{13}\text{C}$ ) e outros elementos podem ser usadas para estimar a assimilação de recursos alimentares pelos consumidores (POST, 2002). A razão isotópica do carbono é particularmente útil porque seu fracionamento trófico é pequeno, em média não mais que 0,5‰, permitindo, portanto, inferências sobre as fontes energéticas (POST, 2002; MANETTA & BENEDITO-CECILIO, 2003; LAYMAN ET AL., 2007; WANG ET AL., 2014). Os isótopos estáveis de carbono podem ser utilizados para distinguir as fontes autotróficas, plantas de via  $\text{C}_3$ ,  $\text{C}_4$  ou CAM, porque entre elas há diferenças na fixação biológica do  $\text{CO}_2$  atmosférico e nos processos de fracionamento bioquímico (MANETTA & BENEDITO-CECILIO, 2003). Nos sistemas onde existem fontes autotróficas variadas (como plantas  $\text{C}_3$  *versus*  $\text{C}_4$ ) com diferenças nos valores de  $\delta^{13}\text{C}$ , o fluxo da energia pode ser indicado pela assinatura isotópica do carbono que possui transferência conservativa ao longo da cadeia, em virtude da baixa taxa de enriquecimento por nível trófico (MANETTA & BENEDITO-CECILIO, 2003; PEREIRA & BENEDITO, 2007). As posições tróficas

verticais, por sua vez, podem ser estimadas baseadas no enriquecimento do isótopo de nitrogênio ( $^{15}\text{N}$ ) do tecido do consumidor em relação aos itens de sua dieta para os quais os níveis tróficos são conhecidos (POST, 2002; WANG *et al.*, 2014; WILLIS *et al.*, 2017). Além disso, utilizando-se valores de  $\delta^{13}\text{C}$  e  $\delta^{15}\text{N}$  é possível estimar, por exemplo, a amplitude e a sobreposição de nicho isotópico das espécies, que pode refletir seu nicho trófico (JACKSON *et al.*, 2011).

O nicho de uma espécie pode ser definido como um hipervolume n-dimensional em que cada ponto corresponde a um estado do meio ambiente que permitiria que uma espécie existisse indefinidamente (HUTCHINSON, 1957). O nicho pode então ser entendido como fundamental, sob uma configuração ótima desse hipervolume potencial de variáveis ambientais, livre de restrições e competidores, considerado como um conjunto de pontos em um espaço n-dimensional abstrato; ou realizado, em que o hipervolume é realmente usado sob essas restrições bióticas (HUTCHINSON, 1957). A amplitude ou largura de nicho, dentro de um modelo espacial, é um importante descritor, definida como a "distância através" do nicho ao longo de uma determinada linha no espaço de nicho (COLWELL & FUTUYMA, 1971). A largura de nicho é usada como uma medida inversa da especialização ecológica, sustentando hipóteses de que quanto maior a especialização da espécie, por exemplo, menor sua amplitude de nicho (COLWELL & FUTUYMA, 1971; SMITH, 1982). Medidas de largura de nicho envolvem a distância entre a distribuição do uso de recursos e a distribuição da disponibilidade de recursos (SMITH, 1982). A sobreposição de nicho, por sua vez, é a região do espaço de nicho compartilhada por dois ou mais nichos, ou seja, o uso conjunto de um ou mais recursos por duas ou mais espécies (COLWELL & FUTUYMA, 1971).

O objetivo geral desta tese consiste, portanto, em conhecer quais as espécies de peixes coexistem nos riachos do rio Ijuí e entender as relações tróficas intra ou interespecíficas que elas estabelecem, bem como o uso e compartilhamento de recursos alimentares. São objetivos específicos:

- Capítulo 1: Avaliar a composição da comunidade de peixes e o padrão de distribuição das espécies em riachos localizados ao longo do gradiente longitudinal (montante-jusante) na sub-bacia hidrográfica do rio Ijuí, afluente do rio Uruguai, pretendendo-se contribuir para o conhecimento da riqueza e abundância de espécies nesta região do sul do Brasil. Hipótese testada: a composição da comunidade de peixes não é homogênea ao longo dos riachos amostrados, e sua complexidade aumenta da montante em direção à jusante (deságue da sub-bacia do rio Ijuí na bacia do rio Uruguai).

- Capítulo 2: Investigar os hábitos alimentares de *Astyanax paris* nos riachos da sub-bacia do rio Ijuí no estado do Rio Grande do Sul, Brasil. Hipótese testada: *A. paris* segue o padrão de outros peixes de água doce neotropicais, modificando suas presas conforme seu crescimento ao longo do seu ciclo de vida (ontogenia).

- Capítulo 3: Investigar o uso de recursos e a partição de nicho entre espécies de peixes co-ocorrentes, pertencentes à mesma e diferente guilda trófica ou família, analisando dados do conteúdo estomacal e isótopos estáveis de  $\delta^{13}\text{C}$  e  $\delta^{15}\text{N}$  em riachos da bacia do rio Uruguai, sub-bacia do rio Ijuí. Hipótese testada: dentro de uma guilda trófica ou família as espécies de peixes co-ocorrentes apresentam partição de nicho trófico e as sobreposições de nicho são menores entre espécies de diferentes famílias.

- Capítulo 4: Investigar diferenças nos hábitos alimentares de 15 espécies de Characidae, de cinco gêneros (*Astyanax*, *Bryconamericus*, *Diapoma*, *Hyphessobrycon* e *Piabarchus*), que coexistem em riachos da bacia do rio Uruguai, sub-bacia do rio Ijuí; buscando compreender suas preferências alimentares e identificar associações entre a ecologia alimentar e características ecomorfológicas, incluindo caracteres do aparato oral. Hipótese testada: essas espécies diferem no uso dos recursos alimentares e a seleção de itens preferenciais na dieta está relacionada às suas características ecomorfológicas ou caracteres do aparato oral. Hipótese testada: a dieta entre espécies do mesmo gênero é mais semelhante do que entre espécies de gêneros diferentes.

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**CAPÍTULO 1: Fishes community composition and patterns of species distribution in Neotropical streams**

Artigo publicado.

Cavalheiro, L. W. & Fialho, C. B. 2020. Fishes community composition and patterns of species distribution in Neotropical streams. *Biota Neotropica*, 20(1):1-13. DOI: <http://dx.doi.org/10.1590/1676-0611-bn-2019-0828>.



## Fishes community composition and patterns of species distribution in Neotropical streams

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CAVALHEIRO, L.W., FIALHO, C.B. **Fishes community composition and patterns of species distribution in Neotropical streams.** *Biota Neotropica*. 20(1): e20190828. <http://dx.doi.org/10.1590/1676-0611-BN-2019-0828>

**Abstract:** The ichthyofauna of streams in the Neotropical region is not yet fully known. This study aims to investigate the ichthyofauna composition of six streams of the Ijuí River sub-basin, Rio Grande do Sul State, inserted in the Uruguay River basin, as to contribute to the knowledge of fishes species richness and distribution in the south of Brazil. Sampling was carried out between July 2015 and May 2016, bimonthly, using the technique of electric fishing to collect the fishes. Spatial variations (per sampled stream) in the ichthyofauna composition were tested with a permutational multivariate analysis of variance. In total, we collected 5,029 individuals from 55 species, 13 families and five orders. From these species, 17 are endemic to the Uruguay River basin. Five species alone represented approximately 70% of the ichthyofauna abundance sampled. Our hypothesis that the fish community composition is not homogeneous along the streams sampled was confirmed and we observed that species complexity increases from the upstream closest area to the downstream according to the river continuum concept.

**Keywords:** *Abundance, Characidae, Heptapteridae, Loricariidae, Richness, Uruguay River basin.*

## Composição da comunidade de peixes e padrões de distribuição de espécies em riachos Neotropiacais

**Resumo:** A ictiofauna de riachos na região Neotropical ainda não é totalmente conhecida. Este estudo objetiva investigar a composição da ictiofauna de seis riachos da sub-bacia do rio Ijuí, estado do Rio Grande do Sul, inseridos na bacia do rio Uruguai, de forma a contribuir no conhecimento da riqueza e distribuição de espécies de peixes no sul do Brasil. A amostragem foi realizada entre julho de 2015 e maio de 2016, bimestralmente, utilizando a técnica da pesca elétrica. Variações espaciais (por riacho amostrado) na composição da ictiofauna foram testadas com uma análise de variância multivariada permutacional. No total, coletamos 5029 indivíduos de 55 espécies, 13 famílias e cinco ordens. Destas espécies, 17 são endêmicas da bacia do rio Uruguai. Cinco espécies sozinhas representaram aproximadamente 70% da abundância da ictiofauna amostrada. Nossa hipótese de que a composição da comunidade de peixes não é homogênea ao longo dos riachos amostrados foi confirmada e observamos que a complexidade das espécies aumenta de áreas à montante em direção à jusante, conforme o conceito do rio contínuo.

**Palavras-chave:** *Abundância, bacia do rio Uruguai, Characidae, Heptapteridae, Loricariidae, Riqueza.*

## Introduction

The ichthyofauna of the Neotropical region comprises 4,475 valid species, and perhaps more than 1,550 undescribed ones (Reis 2013). It is estimated that there are 6,025 species and that this number could be surpassed, overcoming the 8,000 species (Schaefer 1998, Reis 2013). In South America, this ichthyofauna occupies a variety of habitats, from large rivers to small and medium-sized streams, swamps, lagoons, high altitude lakes, among others (Vari & Malabarba 1998, Reis 2013).

Among the habitats occupied by the ichthyofauna, streams are known as lotic environments, with unidirectional water flows from headwaters to mouth and may have non-persistent flooding areas during rainy seasons (Esteves & Aranha 1999, Uieda & Castro 1999). They are known to have a wide variety of mesohabitats due to environmental gradients ranging from rocky riffles and runs to sandy pools and backwaters, in addition to a variety of marginal vegetation in the stream bank (Araújo-Lima et al. 1995, Esteves & Aranha 1999). In southern and southeastern Brazil, the streams may present high dissolved oxygen concentration and large seasonal temperature variation, with influence of drainage basin geomorphology under abiotic components as transparency, pH and conductivity (Araújo-Lima et al. 1995, Esteves & Aranha 1999).

The streams have high biological diversity and great importance in maintaining the integrity of the entire ecosystem (Meyer et al. 2007). These environments frequently present isolated populations of fish, often undescribed, with a high degree of endemism (Langeani et al. 2007, Reis 2013, Vidotto-Magnoni et al. 2015). The assessment of species in these sites contributes, therefore, to the understanding of the distribution of the species already described and to the description of new taxa (Pereira et al. 2014). Studies of species distribution assist in estimating changes in habit susceptibility to anthropogenic impacts that influence the composition of aquatic communities and are useful in the definition of priority areas for conservation (Bailly et al. 2016, Rose et al. 2016).

Freshwater ecosystems are particularly vulnerable to anthropogenic impacts that often promote the proliferation of some populations in the face of the decline, or even the extinction of others (Agostinho et al. 1999, Bailly et al. 2016). In streams, the susceptibility to these impacts may be higher because of the reduced size of these habitats and the sensitivity of microhabitats (Galves et al. 2009, Bonato & Fialho 2016). The fishes community is an indicator of the biological integrity of freshwater systems (Moore et al. 1997) and the knowledge of streams ichthyofauna is an informative tool to propose mitigation measures to these impacts (Vidotto-Magnoni et al. 2015). In the hydrographic region of River Uruguay, Brazil, anthropogenic impacts consist mainly on the environmental degradation in areas of high population and industrial density caused by agricultural activities, by the construction of hydroelectric dams, with the disappearance of lotic environments, and by the constant introduction of exotic species (Malabarba et al. 2009).

The Uruguay River is one of the main tributaries of the La Plata River basin which, in South America, comprehends the second largest drainage system, behind only the Amazonas (Cappato & Yanosky 2009). The Uruguay River has an extension of 2,200 km (ANA 2016) with a drainage area of about 365,000 km<sup>2</sup> (Di Persia & Neiff 1986, Albert & Reis 2011). Its main tributaries are the Negro River, Quaraí River, Ibicuí River and Ijuí River (Carvalho & Reis 2009). The ichthyofauna of the

Uruguay River drainage system comprises about 275 species known; from these, 78 (28%) are endemic (Bertaco et al. 2016).

The “river continuum concept” proposed by Vannote et al. (1980) explains the distribution pattern of fishes fauna following the upstream-downstream gradient. This theory describes the structure and functions of communities along river systems, considering gradients of physical factors, formed by the drainage network, which include energy input, organic matter transport and use by macroinvertebrates functional feeding groups (Vannote et al. 1980). In addition, this concept proposes that community complexity increases from upstream to downstream, with the alteration on the composition of species and trophic guilds being influenced by continuum gradients (Vannote et al. 1980).

This study aims, therefore, to evaluate the composition of the fishes community and the pattern of species distribution in streams located along a longitudinal gradient (upstream-downstream) in the hydrographic sub-basin of the Ijuí River, tributary of Uruguay River, intending to contribute to the knowledge of the richness and abundance of species in this region of the south of Brazil. The hypothesis is that the composition of the fishes community is not homogeneous along the streams sampled, and that its complexity increases from the upstream closest area to the downstream (mouth of the Ijuí River sub-basin in the Uruguay River basin), according to the “river continuum concept”.

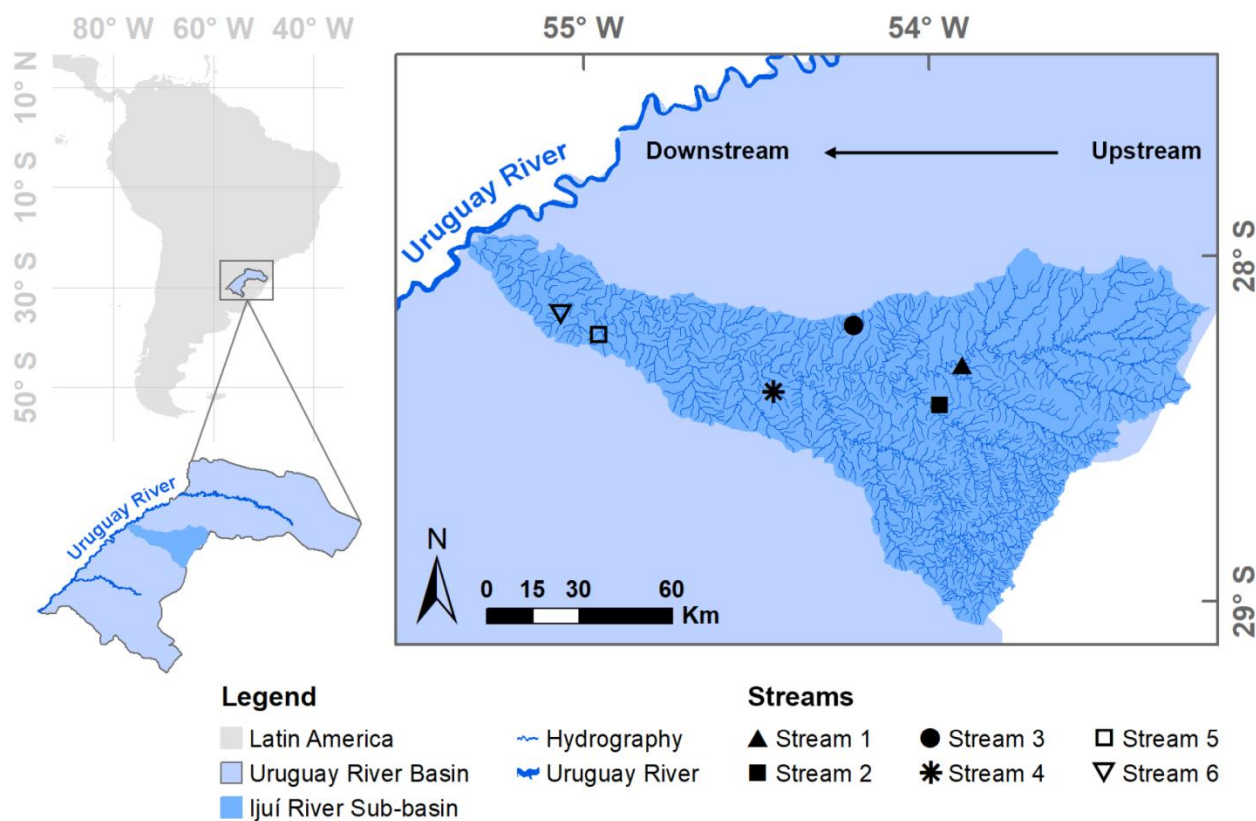
## Material and Methods

Collections were carried out in six streams, located in rural areas of the Ijuí River sub-basin, at the northwest region of the Rio Grande do Sul State, southern Brazil. With a drainage of 10,649.13 Km<sup>2</sup>, it is located in the middle portion of the Uruguay River hydrographic network (FEPAM 2016) (Figure 1). In order to sample different portions of the Ijuí River sub-basin (high, middle and low), chosen streams were distributed along the longitudinal gradient, from upstream to downstream areas, near the mouth of the Ijuí River sub-basin in the Uruguay River (Figure 1). From the sampled streams, two are located in an upper portion of the sub-basin: stream 1 (28°18'58.4"S, 53°54'17.9"W) (Figure 2a) and stream 2 (28°25'56.2"S, 53°58'14.9"W) (Figure 2b); two are in the mid portion: stream 3 (28°12'06.2"S, 54°13'06.9"W) (Figure 2c) and stream 4 (28°23'41.5"S, 54°27'05.9"W) (Figure 2d); and two are in the lower portion: stream 5 (28°13'40.8"S, 54°57'24.8"W) (Figure 2e) and stream 6 (28°10'13.5"S, 55°03'57.4"W) (Figure 2f). Anthropogenic activities developed nearby the streams consist mainly in agriculture (soybean crops) and cattle farming, with swine farming in the corresponding area to the stream 4. The riparian vegetation, next to the streams, is poorly preserved at all sampling sites, corresponding to narrow tree lines running along the streams, often less than 5m width.

Biological samples were collected bimonthly, from July 2015 to May 2016, summing up six capture expeditions for each stream (July, September, and November 2015, and January, March, and May 2016). Fishes were collected using the electric fishing technique, in an extension of 100m in each stream, for the period of an hour. Fieldwork and sampling were carried out under a scientific collection permit (Permit Number 48291-1) issued by the Instituto Chico Mendes de Conservação da Biodiversidade, Ministério do Meio Ambiente, Brasília – Distrito Federal, Brazil. This study was conducted in accordance with protocols approved in their ethical and methodological aspects, for the



## Fishes composition in streams



**Figure 1.** Location of the sampled streams in the Ijuí River sub-basin and its respective position into the Uruguay River hydrographic basin, Brazil.

use of fish, by the Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul, Brazil (Permit Number 35495).

In the field, individuals were anesthetized and euthanized with eugenol 10% (Jenkins et al. 2014) and fixed with formalin 10%. In the laboratory, specimens were selected and identified before being preserved in alcohol 70%. Species identification was made according to criteria of the literature (Buckup & Hahn 2000, Casciotta et al. 2002, Lucena 2007, Ghazzi 2008, Carvalho & Reis 2009, Malabarba et al. 2015) and specialists. The classification and nomenclature followed Eschmeyer et al. (2018) and Betancur-R et al. (2017) for Cichlidae. Voucher specimens were deposited in the ichthyologic collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Brazil. The fish community was described considering the abundance (number of individuals collected) and richness (number of species).

Spatial variations (for each sampled stream) on the ichthyofauna composition were tested using the permutational multivariate analysis of variance (PERMANOVA;  $\alpha < 0.05$ ), based on a dissimilarity matrix constructed with the Bray-Curtis index (Anderson 2001, Anderson et al. 2011, Borcard et al. 2011). Abundance data were standardized using  $\log_{10}(y+1)$  (Legendre & Legendre 1998, Anderson et al. 2011). The Bray-Curtis index was chosen as it considers the abundance data and enables the exclusion of joint absences (Anderson et al. 2011). This decision was made because we did not consider two samples to be more similar due to the sharing of absence of a particular species, since we do not have *a priori* information if the species does not actually exist in the local, or was simply not captured (Anderson et al. 2011). The pattern

of species spatial distribution, if identified with the PERMANOVA, was visualized with a principal coordinates analysis (PoCA), using a dissimilarity matrix made with the Bray-Curtis index (Legendre & Legendre 1998, Borcard et al. 2011). In the PCoA graph presenting the species composition along the sampled streams, only those species that contributed with a minimum of 10% of the explanation of the data distribution (eigenvectors  $\geq \pm 0.10$ ) were shown, for the first two axis, in order to improve the visualization of distribution patterns and avoid visual pollution. In the PCoA graph presenting the distribution of fish families, all species were shown. Statistical tests were carried out using R Project for Statistical Computing software, version 3.4.1. with the Vegan statistical package, version 2.4-5 (Oksanen et al. 2017).

## Results

The ichthyofauna found in the six sampled streams in the Ijuí River basin is distributed within five orders, 13 families, 33 genera and 55 species, totaling 5,029 individuals sampled (Table 1). The orders Characiformes and Siluriformes presented five families each, while Cichliformes, Gymnotiformes and Synbranchiformes were represented by a single family. The order Siluriformes was the most abundant in number of collected individuals (3,051 specimens), representing 60.68% of the total sampled, distributed within 17 genera. Characiformes presented the highest richness (23 species) and the second highest abundance (36.85% of individuals collected), comprised by 11 genera. Cichliformes had eight species and 1.25% of the total abundance,





**Figure 2.** Sampling sites in the streams of the Ijuí River sub-basin, Brazil. Upper portion (upstream): (a) Stream 1 and (b) Stream 2; mid portion (midstream): (c) Stream 3 and (d) Stream 4; lower portion (downstream): (e) Stream 5 and (f) Stream 6.



Fishes composition in streams

Table 1. List of occurrence and abundance of species of the ichthyofauna sampled in six streams in the Ijuí River sub-basin, Brazil. a Species endemic to the Uruguay River basin.

| Taxa  | Upper portion |          |          | Mid portion |          |          | Lower portion |          |          | Total | % of total | Voucher  |
|---|---------------|----------|----------|-------------|----------|----------|---------------|----------|----------|-------|------------|--|
|   | Stream 1      | Stream 2 | Stream 3 | Stream 4    | Stream 5 | Stream 6 | Stream 1      | Stream 2 | Stream 3 |       |            |  |
| <b>CHARACIFORMES</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <b>Characidae</b>   |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Asytanax abramis</i> (Jenyns 1842)   |               |          |          |             | 4        | 19       |               |          |          | 23    | 0.46       | UFRGS 22179; 22180; 22182; 22187; 22373  |
| <i>Asytanax aramburui</i> Protogino, Miquelarena & López 2006                   |               |          |          | 4           | 4        | 11       |               |          |          | 15    | 0.3        | UFRGS 21981; 21985; 21997; 21998   |
| <i>Asytanax eigenmanniorum</i> (Cope 1894)                                      |               |          |          | 3           | 1        | 1        |               |          |          | 4     | 0.08       | UFRGS 21967; 21993   |
| <i>Asytanax lacustris</i> (Lütken 1875)   | 12            | 41       | 2        | 2           | 13       | 81       |               |          |          | 151   | 3          | UFRGS 21968; 21969; 21970; 21974; 21984; 21991; 21995; 22002; 22076; 22178; 22181; 22183; 22184; 22185; 22186; 22188; 22189; 22190; 22191; 22192; 22193; 22194; 22372; 22374 |
| <i>Asytanax laticeps</i> (Cope 1894)  |               |          | 7        | 1           |          |          |               |          |          | 8     | 0.16       | UFRGS 21971; 21976; 21987; 21992   |
| <i>Asytanax ojiara</i> Azpelicueta & Garcia 2000                                | 1             | 12       | 1        |             |          |          |               |          |          | 14    | 0.28       | UFRGS 22473; 22477; 22723; 22724; 22725; 22726   |
| <i>Asytanax paris</i> Azpelicueta, Almirón & Casciotta 2002                     |               |          | 7        |             |          |          |               |          |          | 20    | 0.4        | UFRGS 21927; 21928; 21929  |
| <i>Asytanax saguazu</i> Casciotta, Almirón & Azpelicueta 2003                   |               |          |          | 5           | 15       |          |               |          |          | 20    | 0.4        | UFRGS 21919; 21980; 21982; 21986; 21988  |
| <i>Asytanax</i> sp.   |               |          |          | 1           | 7        |          |               |          |          | 8     | 0.16       | UFRGS 21972; 21990; 21994  |
| <i>Asytanax xiru</i> Lucena, Castro & Bertaco 2013                              |               | 2        | 1        | 2           | 7        |          |               |          |          | 12    | 0.24       | UFRGS 21975; 21983; 21989; 21999; 22000; 22001; 22003  |
| <i>Bryconamericus iheringii</i> (Boulenger 1887)                                | 3             | 75       | 21       | 18          | 98       | 125      |               |          |          | 340   | 6.76       | UFRGS 22478; 22481; 22544; 22702; 25454; 25456   |
| <i>Bryconamericus uporas</i> Casciotta, Azpelicueta & Almirón 2002 <sup>a</sup> | 9             | 5        | 34       | 41          | 1        | 9        |               |          |          | 99    | 1.97       | UFRGS 22479; 22480; 22703; 22713; 22714; 25449   |
| <i>Diapoma uruguayense</i> (Messner 1962) <sup>a</sup>                          |               |          |          |             | 3        |          |               |          |          | 3     | 0.06       | UFRGS 22474  |
| <i>Galeocharax humeralis</i> (Valenciennes 1834)                                |               |          |          | 1           |          |          |               |          |          | 1     | 0.02       | UFRGS 25405  |
| <i>Hyphessobrycon luetkenii</i> (Boulenger 1887)                                |               |          |          | 1           | 9        |          |               |          |          | 10    | 0.2        | UFRGS 22475; 22476   |
| <i>Hyphessobrycon togoi</i> Miquelarena & López 2006                            |               |          | 1        |             |          |          |               |          |          | 1     | 0.02       | UFRGS 22472  |
| <i>Oligosarcus</i> sp.  |               |          |          |             | 2        |          |               |          |          | 2     | 0.04       | UFRGS 25450  |
| <i>Piabarchus stramineus</i> (Eigenmann 1908)                                   | 1             |          |          | 47          |          |          |               |          |          | 60    | 1.19       | UFRGS 22699; 22704; 22715  |
| <b>Crenuchidae</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Characidium pterostictum</i> Gomes 1947                                      | 10            | 68       | 162      | 196         | 328      | 207      |               |          |          | 971   | 19.31      | UFRGS 24564; 24565; 24566; 25425; 25426; 25427   |
| <i>Characidium tenue</i> (Cope 1894)  |               |          | 5        |             |          |          |               |          |          | 5     | 0.1        | UFRGS 25385; 25397   |

Continuation Table 1.

| Taxa   | Upper portion |          |          | Mid portion |          |          | Lower portion |          |          | Total | % of total | Voucher  |
|--|---------------|----------|----------|-------------|----------|----------|---------------|----------|----------|-------|------------|--|
|  | Stream 1      | Stream 2 | Stream 4 | Stream 3    | Stream 4 | Stream 5 | Stream 6      | Stream 5 | Stream 6 |       |            |  |
| <b>Curimatidae</b>   |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Steindachnerina biornata</i> (Braga & Azpelicueta 1987)                         |               | 1        |          |             |          |          |               |          |          | 1     | 0.02       | UFRGS 25460  |
| <b>Erythrinidae</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Hoplias malabaricus</i> (Bloch 1794)  |               | 2        |          |             | 2        | 1        |               |          |          | 5     | 0.1        | UFRGS 25355  |
| <b>Parodontidae</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Apareiodon affinis</i> (Steindachner 1879)                                      |               |          |          |             | 77       | 3        |               |          |          | 80    | 1.59       | UFRGS 25363; 25367   |
| <b>SILURIFORMES</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <b>Callichthyidae</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Corydoras longipinnis</i> Knaack 2007   |               | 94       |          |             |          |          |               |          |          | 94    | 1.87       | UFRGS 22177; 25433; 25452                                    |
| <b>Heptapteridae</b>   |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Cetopsorhamdia iheringi</i> Schubart & Gomes 1959                               | 20            |          |          |             |          |          |               |          |          | 20    | 0.4        | UFRGS 25402; 25409   |
| <i>Heptapterus mandimbusu</i> Aguilera, Benitez, Terán, Alonso & Miranda 2017      | 23            |          |          | 66          |          |          |               |          |          | 90    | 1.79       | UFRGS 25357; 25366; 25373; 25408                             |
| <i>Heptapterus mustelinus</i> (Valenciennes 1835)                                  | 145           | 358      |          | 69          | 115      | 186      | 214           |          |          | 1087  | 21.61      | UFRGS 21107; 21955; 25434; 25435; 25436; 25437; 25438; 25447 |
| <i>Heptapterus</i> sp1   | 23            |          |          |             |          | 2        |               |          |          | 23    | 0.46       | UFRGS 25400; 25401; 25404; 25455                             |
| <i>Rhamdella longiuscula</i> Lucena & da Silva 1991 <sup>a</sup>                   |               |          |          |             |          |          |               | 2        |          | 2     | 0.04       | UFRGS 25362  |
| <i>Rhamdia</i> aff. <i>quelen</i> (Quoy & Gaimard 1824)                            | 21            | 22       |          | 7           | 11       | 19       | 10            |          |          | 90    | 1.79       | UFRGS 25440; 25441; 25442; 25443; 25444; 25448; 25451        |
| <b>Loricariidae</b>  |               |          |          |             |          |          |               |          |          |       |            |  |
| <i>Ancistrus taunayi</i> Miranda Ribeiro 1918 <sup>a</sup>                         | 101           | 198      |          | 119         | 132      | 115      | 35            |          |          | 700   | 13.92      | UFRGS 25350; 25358; 25364; 25371; 25372; 25375; 25403        |
| <i>Eurycheilichthys pantherinus</i> (Reis & Schaefer 1992) <sup>a</sup>            |               |          |          | 3           |          |          |               |          |          | 3     | 0.06       | UFRGS 21811; 21978   |
| <i>Hemiancistrus fuliginosus</i> Cardoso & Malabarba 1999                          | 84            | 31       |          | 11          | 57       | 44       | 43            |          |          | 270   | 5.37       | UFRGS 25360; 25361; 25370; 25391; 25395; 25396; 25459        |
| <i>Hisonotus aky</i> (Azpelicueta, Casciotta, Almirón & Koerber 2004) <sup>a</sup> |               |          |          | 2           | 4        |          | 2             |          |          | 8     | 0.16       | UFRGS 25381; 25382; 25383                                    |
| <i>Hypostomus commersoni</i> (Valenciennes 1836)                                   | 3             | 10       |          |             |          | 5        | 4             |          |          | 22    | 0.44       | UFRGS 25354; 25410   |
| <i>Pareiorhaphis hystrix</i> (Pereira & Reis 2002)                                 | 45            | 7        |          | 120         | 179      | 1        |               |          |          | 352   | 7          | UFRGS 25359; 25369; 25374; 25392                             |
| <i>Pareiorhaphis</i> sp. <sup>a</sup>  | 1             |          |          |             |          |          |               |          |          | 1     | 0.02       | UFRGS 21977  |
| <i>Rimeloricaria reisi</i> Ghazzi 2008 <sup>a</sup>                                | 2             |          |          |             |          |          |               |          |          | 2     | 0.04       | UFRGS 25353; 25412   |
| <i>Rimeloricaria sanga</i> Ghazzi 2008 <sup>a</sup>                                | 1             | 31       |          | 5           | 6        | 3        | 16            |          |          | 62    | 1.23       | UFRGS 25418; 25419; 25420; 25421                             |

Fishes composition in streams

| Taxa   | Upper portion |          |          | Mid portion |          |          | Lower portion |          |          | Total | % of total | Voucher |          |          |  |
|--|---------------|----------|----------|-------------|----------|----------|---------------|----------|----------|-------|------------|---------|----------|----------|--|
|  | Stream 1      | Stream 2 | Stream 3 | Stream 4    | Stream 5 | Stream 6 | Stream 1      | Stream 2 | Stream 3 |       |            |         | Stream 4 | Stream 5 | Stream 6   |
| <i>Rineloricaria stellata</i> Ghazzi 2008 <sup>a</sup>                           |               |          | 12       |             |          |          |               |          |          |       |            |         | 12       | 0.24     | UFRGS 25416; 25417   |
| <i>Rineloricaria zaina</i> Ghazzi 2008 <sup>a</sup>                              | 13            | 7        | 8        | 3           | 1        |          |               |          |          |       |            |         | 32       | 0.64     | UFRGS 25413; 25414; 25415  |
| <b>Pseudopimelodidae</b>   |               |          |          |             |          |          |               |          |          |       |            |         | 97       | 1.93     |  |
| <i>Microglanis malabarbai</i> Bertaco & Cardoso 2005 <sup>a</sup>                | 27            |          | 41       | 15          | 11       | 3        |               |          |          |       |            |         | 97       | 1.93     | UFRGS 20253; 20254; 25376; 25380; 25387; 25388; 25389; 25390; 25394  |
| <b>Trichomycteridae</b>  |               |          |          |             |          |          |               |          |          |       |            |         | 85       | 1.69     |  |
| <i>Ituglanis</i> sp.   | 2             |          |          |             |          |          |               |          |          |       |            |         | 2        | 0.04     | UFRGS 21920; 21921   |
| <i>Scleronema</i> sp. <sup>a</sup>   |               | 1        |          | 6           | 38       | 16       |               |          |          |       |            |         | 61       | 1.21     | UFRGS 21958; 21959; 21961; 21962; 21963; 21964; 21965; 21966; 21973; 21979; 22579; 22583; 22584; 22585; 22586; 22587; 22588; 22589 |
| <i>Trichomycterus perkos</i> Datovo, Carvalho & Ferrer 2012                      | 4             |          | 18       |             |          |          |               |          |          |       |            |         | 22       | 0.44     | UFRGS 25377; 25378; 25379; 25393; 25399; 25422; 25423; 25424   |
| <b>GYMNOTIFORMES</b>   |               |          |          |             |          |          |               |          |          |       |            |         | 39       | 0.78     |  |
| <b>Gymnotidae</b>  |               |          |          |             |          |          |               |          |          |       |            |         | 39       | 0.78     |  |
| <i>Gymnotus cuia</i> Craig, Malabarba, Crampton & Albert 2018                    |               | 33       | 4        | 1           | 1        |          |               |          |          |       |            |         | 39       | 0.78     | UFRGS 25429; 25445; 25446  |
| <b>CICHLIFORMES</b>  |               |          |          |             |          |          |               |          |          |       |            |         | 63       | 1.25     |  |
| <b>Cichlidae</b>   |               |          |          |             |          |          |               |          |          |       |            |         | 63       | 1.25     |  |
| <i>Crenicichla hadrostroma</i> Lucena 2007 <sup>a</sup>                          | 1             |          |          |             |          |          |               |          |          |       |            |         | 1        | 0.02     | UFRGS 25458  |
| <i>Crenicichla lepidota</i> Heckel 1840  | 1             |          | 1        |             | 3        | 1        |               |          |          |       |            |         | 6        | 0.12     | UFRGS 25356; 25384; 25406; 25407   |
| <i>Crenicichla missionera</i> Lucena & Kullander 1992 <sup>a</sup>               | 3             |          |          |             | 2        | 2        |               |          |          |       |            |         | 7        | 0.14     | UFRGS 25351; 25431   |
| <i>Crenicichla scottii</i> (Eigenmann 1907) <sup>a</sup>                         |               |          | 1        | 2           | 4        | 7        |               |          |          |       |            |         | 14       | 0.28     | UFRGS 25457  |
| <i>Crenicichla</i> sp.   |               |          |          |             |          | 3        |               |          |          |       |            |         | 3        | 0.06     |  |
| <i>Crenicichla tendybaguassu</i> Lucena & Kullander 1992                         | 1             |          |          |             |          |          |               |          |          |       |            |         | 1        | 0.02     | UFRGS 21996  |
| <i>Geophagus brasiliensis</i> (Quoy & Gaimard 1824)                              | 2             | 12       |          |             |          |          |               |          |          |       |            |         | 14       | 0.28     | UFRGS 25368; 25386; 25432; 25439; 25461  |
| <i>Gymnogeophagus constellatus</i> Malabarba, Malabarba & Reis 2015 <sup>a</sup> |               |          |          |             | 3        | 14       |               |          |          |       |            |         | 17       | 0.34     | UFRGS 25453  |
| <b>SYNBRANCHIFORMES</b>  |               |          |          |             |          |          |               |          |          |       |            |         | 22       | 0.44     |  |
| <b>Synbranchidae</b>   |               |          |          |             |          |          |               |          |          |       |            |         | 22       | 0.44     |  |
| <i>Synbranchus marmoratus</i> Bloch 1795   | 16            |          | 1        |             | 4        | 1        |               |          |          |       |            |         | 22       | 0.44     | UFRGS 25352; 25365; 25398; 25411; 25428; 25430   |
| <b>Total</b>   |               |          | 575      | 1010        | 864      | 650      | 1032          | 898      |          |       |            |         | 5029     |          |  |

followed by Gymnotiformes and Synbranchiformes, with one species each, and 0.78% and 0.44% of the total number of collected specimens, respectively (Table 1). From the 55 fish species collected, 17 are endemic to the Uruguay River hydrographic basin and no exotic species were collected (Table 1).

Characidae had the highest number of species recorded, 18, followed by Loricariidae, Cichlidae, Heptapteridae, and Trichomycteridae, with 11, eight, six and three, respectively. In relation to the total of individuals captured, the most representative families were Loricariidae (29.11%), Heptapteridae (26.09%), Crenuchidae (19.41%) and Characidae (15.73%). The species with the highest number of individuals collected were *Heptapterus mustelinus* (Valenciennes 1835) (21.61%), *Characidium pterostictum* Gomes 1947 (19.31%), *Ancistrus taumayi* Miranda Ribeiro 1918 (13.92%), *Bryconamericus iheringii* (Boulenger 1887) (7.00%) and *Pareiorhaphis hystrix* (Pereira & Reis 2002) (6.76%), representing together approximately 70% of the ichthyofauna abundance. The abundance of the other species was inferior to 6% for each taxon (Table 1).

The distribution of species and the representativity of families were not homogenous throughout the altitudinal gradient of the Ijuí River sub-basin (Figure 3-4). A pattern of spatial variation on the ichthyofauna composition was detected, with differences in richness and species abundance from upstream (upper portion of the sub-basin) to downstream areas, near the mouth in the Uruguay River (sub-basin lower portion) according to PERMANOVA results (Df: 5, pseudo-F: 10.29, R<sup>2</sup>: 0.63, p: 0.0001), which indicates that species distribution does not occur randomly. The streams were more similar to each other regarding the ichthyofauna composition, according to the geographical location along the sub-basin (upper, mid, and lower portion) (Figure 3). Species richness varied between sampled streams, detecting a higher number of species in the lower portion of the sub-basin: 34 in stream 6 and 31 in stream 5. In the sub-basin mid portion, stream 3 and stream 4 presented 23 and 21 species, respectively, while in the upper portion were recorded 28 species in the stream 1 and 20 in the stream 2.

The most abundant species although appearing in all sampled sites, contributed to the segregation of the streams in the Principal Coordinates Analysis (Table 2; Figure 3). *Ancistrus taumayi* and *H. mustelinus* were associated with the upper portion of the sub-basin (streams 1 and 2), *P. hystrix* was associated to the mid portion (streams 3 and 4), while *B. iheringii* and *C. pterostictum* were linked to the stream in the lower areas (streams 5 and 6). Less abundant species also contributed to this segregation, the most important being, according to the PCoA eigenvectors (Table 2): *Corydoras longipinnis* Knaack 2007, Callichthyidae family, recorded only in the upper portion of the sub-basin, with 92 individuals collected in the stream 2, and *Gymnotus cuiia* Craig, Malabarba, Crampton & Albert 2018, with approximately 85% of the individuals collected in this same location; *Bryconamericus uporas* Casciotta, Azpelicueta & Almirón, 2002 and *Microglanis malabarbai* Bertaco & Cardoso, 2005, with 76% and 58%, respectively, of individuals collected in the mid portion of the sub-basin (streams 3 and 4); and *Scleronema* sp., with 89% of the specimens collected in the lower portion (stream 5) (Figure 3).

A pattern in the representativity, abundance, and number of species and families in Characiformes, Siluriformes and Cichliformes is observed in relation to the second axis of PCoA (Figure 4). Siluriformes richness was higher in the upper portion of the Ijuí River sub-basin

(streams 1 and 2), with 18 out of 22 collected species occurring in the area, from which six have been exclusive to it (considering only this study data). Stream 1 (upper portion) presented the highest richness of Siluriformes (16 species) and the highest number of this order taxa with exclusive occurrence, namely: *Cetopsorhamdia iheringi* Schubart & Gomes 1959; *Pareiorhaphis* sp.; *Rineloricaria reisi* Ghazzi 2008; *Ituglanis* sp.; and Heptapteridae (identified only at family level). Siluriformes richness declined along the sub-basin, with 14 species recorded in the mid portion (streams 3 and 4) and 13 in the lower portion (streams 5 and 6) of Ijuí River (Figure 4).

The highest representativity of the Characiformes order occurred within the Characidae family, in the lower portion of the sub-basin (streams 5 and 6). Of the 18 species captured, 15 occurred in this area and eight were recorded exclusively for these two sampled streams (data from this study only). Likewise, the Cichliformes of the Cichlidae family are associated with the lower portion of the sub-basin, where their greatest abundance appeared (streams 5 and 6) (Figure 4).

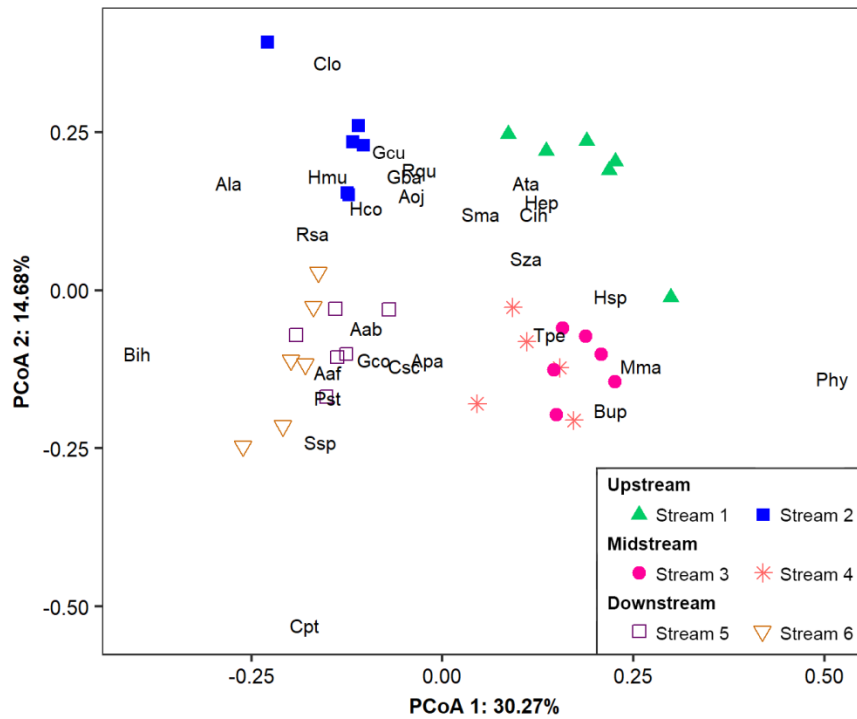
## Discussion

The species richness found in the streams of the Ijuí River sub-basin follows the pattern of freshwater fishes in the Neotropical region, with Characiformes and Siluriformes as the richest orders in number of species (Lowe-McConnell 1999, Malabarba & Malabarba 2014). Our hypothesis that the fish community composition is not homogeneous along the streams sampled was confirmed and we observed that species complexity increases from the upstream closest area to the downstream according to the river continuum concept. The latitudinal variation of the richness within the Ijuí River sub-basin, smaller in the upstream streams (closer to the headwaters of the sub-basin), increasing towards the mouth in Uruguay River (streams 5 and 6), is an expected pattern, according to the "river continuum concept" proposed by Vannote et al. (1980). Although, upstream and midstream areas present virtually the same (or higher) number of species, the richness has increased considerably towards the streams located in the lower portion of the basin (downstream) and we believe this is due to the influence of the Uruguay River, located very close to streams 5 and 6. According to the river continuum concept, the complexity of community structure and function increases along a river system as the increases of the complexity of the physical gradients dynamics formed by a drainage network (Vannote et al. 1980). Furthermore, the three streams with the smallest longitude (streams 1, 3 and 6) in relation to the correspondent streams (streams 2, 4 and 5), which occupy the same portion in the sub-basin (upper, mid, and lower) presented a higher number of species, respectively.

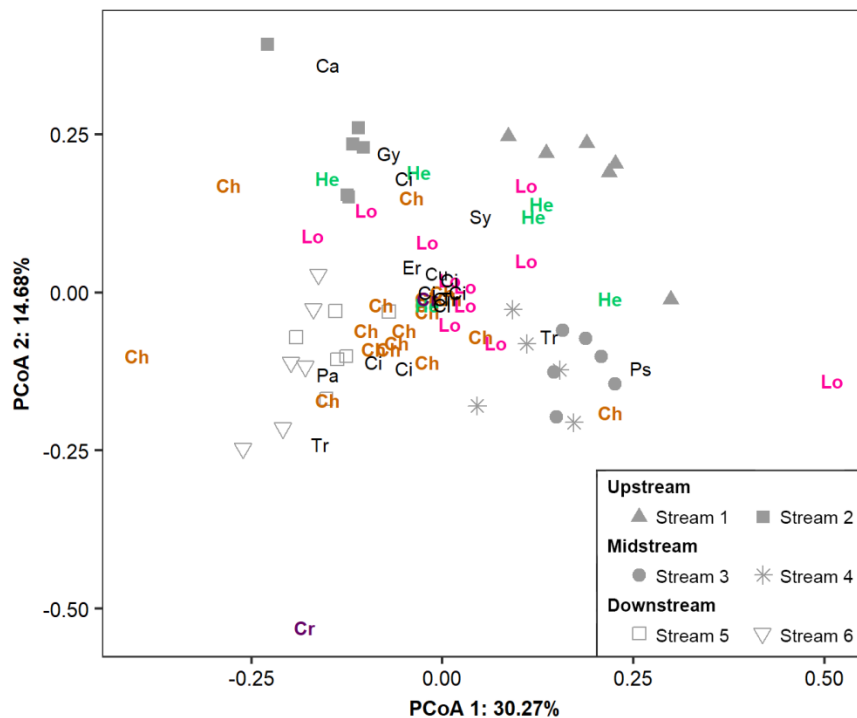
The knowledge about the influence of the global longitudinal gradient on the distribution of species richness is well established and, for freshwater fishes, remains the same even in anthropomorphized habitats, such as in large spatial reservoirs, although this distribution is better explained by the overlapping of factors, rather than a single hypothesis (Brown 2014, Bailly et al. 2016). For freshwater fishes, the species richness tends to decrease within the latitude and increase along the longitudinal fluvial gradients (Osborne & Lewis 1992, Ibañez et al. 2009, Bailly et al. 2016) (same pattern found in our samplings). The further away from the headwaters, within a hydrographic basin, the greater the species richness, as new species are added downstream more easily



Fishes composition in streams



**Figure 3.** Principal Coordinates Analysis (PCoA) of the composition of species sampled in the upper (streams 1 and 2), mid (streams 3 and 4), and lower portion (streams 5 and 6) of the Ijuí River sub-basin, Brazil. Abbreviations list of species is in Table 2.



**Figure 4.** Principal Coordinates Analysis (PCoA) of the composition of species, indicating the representativeness of families, sampled in the upper (streams 1 and 2), mid (streams 3 and 4), and lower portion (streams 5 and 6) of the Ijuí River sub-basin, Brazil. The four most abundant are highlighted by bold typing: Ch: Characidae; Cr: Crenuchidae; Cu: Curimatidae; Er: Erythrinidae; Pa: Parodontidae; Ca: Callichthyidae; He: Heptapteridae; Lo: Loricariidae; Ps: Pseudopimelodidae; Tr: Trichomycteridae; Gy: Gymnotidae; Ci: Cichlidae; Sy: Synbranchidae.

**Table 2.** Eigenvalues and eigenvectors from the Principal Coordinates Analysis (PCoA) of the composition of species sampled in six streams of the Ijuí River sub-basin, Brazil.

|   |              | PCoA 1 | PCoA 2 |
|---|--------------|--------|--------|
| Eigenvalue  |              | 1.31   | 0.63   |
| Proportion Explained  |              | 30.27  | 14.68  |
| Cumulative Proportion   |              | 30.27  | 44.95  |
| Taxa  | Abbreviation | PCoA 1 | PCoA 2 |
| <b>CHARACIFORMES</b>  |              |        |        |
| <b>Characidae</b>   |              |        |        |
| <i>Astyanax abramis</i> (Jenyns 1842)   | Aab          | -0.10  | -0.06  |
| <i>Astyanax aramburui</i> Protogino, Miquelarena & López 2006                 | Aar          | -0.07  | -0.09  |
| <i>Astyanax eigenmanniorum</i> (Cope 1894)                                    | Aei          | -0.02  | -0.02  |
| <i>Astyanax lacustris</i> (Lütken 1875)                                       | Ala          | -0.28  | 0.17   |
| <i>Astyanax laticeps</i> (Cope 1894)  | Alat         | 0.05   | -0.07  |
| <i>Astyanax ojiara</i> Azpelicueta & Garcia 2000                              | Aoj          | -0.04  | 0.15   |
| <i>Astyanax paris</i> Azpelicueta, Almirón & Casciotta 2002                   | Apa          | -0.02  | -0.11  |
| <i>Astyanax saguazu</i> Casciotta, Almirón & Azpelicueta 2003                 | Asa          | -0.09  | -0.09  |
| <i>Astyanax</i> sp.   | Asp          | -0.05  | -0.06  |
| <i>Astyanax xiru</i> Lucena, Castro & Bertaco 2013                            | Axi          | -0.08  | -0.02  |
| <i>Bryconamericus iheringii</i> (Boulenger 1887)                              | Bih          | -0.40  | -0.10  |
| <i>Bryconamericus uporas</i> Casciotta, Azpelicueta & Almirón 2002            | Bup          | 0.22   | -0.19  |
| <i>Diapoma uruguayense</i> (Messner 1962)                                     | Dur          | -0.02  | -0.03  |
| <i>Galeocharax humeralis</i> (Valenciennes 1834)                              | Gum          | 0.00   | 0.00   |
| <i>Hyphessobrycon luetkenii</i> (Boulenger 1887)                              | Hyl          | -0.06  | -0.08  |
| <i>Hyphessobrycon togoi</i> Miquelarena & López 2006                          | Hto          | 0.01   | -0.01  |
| <i>Oligosarcus</i> sp.  | Osp          | -0.02  | -0.01  |
| <i>Piabarchus stramineus</i> (Eigenmann 1908)                                 | Pst          | -0.15  | -0.17  |
| <b>Crenuchidae</b>  |              |        |        |
| <i>Characidium pterostictum</i> Gomes 1947                                    | Cpt          | -0.18  | -0.53  |
| <i>Characidium tenue</i> (Cope 1894)  | Cte          | -0.02  | -0.01  |
| <b>Curimatidae</b>  |              |        |        |
| <i>Steindachnerina biornata</i> (Braga & Azpelicueta 1987)                    | Sbi          | -0.01  | 0.03   |
| <b>Erythrinidae</b>   |              |        |        |
| <i>Hoplias malabaricus</i> (Bloch 1794)                                       | Hom          | -0.04  | 0.04   |
| <b>Parodontidae</b>   |              |        |        |
| <i>Apareiodon affinis</i> (Steindachner 1879)                                 | Aaf          | -0.15  | -0.13  |
| <b>SILURIFORMES</b>   |              |        |        |
| <b>Callichthyidae</b>   |              |        |        |
| <i>Corydoras longipinnis</i> Knaack 2007                                      | Clo          | -0.15  | 0.36   |
| <b>Heptapteridae</b>  |              |        |        |
| <i>Cetopsorhamdia iheringi</i> Schubart & Gomes 1959                          | Cih          | 0.12   | 0.12   |
| <i>Heptapterus mandimbusu</i> Aguilera, Benitez, Terán, Alonso & Mirande 2017 | Hsp          | 0.22   | -0.01  |
| <i>Heptapterus mustelinus</i> (Valenciennes 1835)                             | Hmu          | -0.15  | 0.18   |
| <i>Heptapterus</i> sp1  | Hep          | 0.13   | 0.14   |

## Fishes composition in streams

Continuation Table 2.

|   |              | PCoA 1 | PCoA 2 |
|---|--------------|--------|--------|
| Eigenvalue  |              | 1.31   | 0.63   |
| Proportion Explained  |              | 30.27  | 14.68  |
| Cumulative Proportion   |              | 30.27  | 44.95  |
| Taxa  | Abbreviation | PCoA 1 | PCoA 2 |
| <i>Rhamdella longiuscula</i> Lucena & da Silva 1991                   | Rlo          | -0.02  | -0.02  |
| <i>Rhamdia aff. quelen</i> (Quoy & Gaimard 1824)                      | Rqu          | -0.03  | 0.19   |
| <b>Loricariidae</b>   |              |        |        |
| <i>Ancistrus taunayi</i> Miranda Ribeiro 1918                         | Ata          | 0.11   | 0.17   |
| <i>Eurycheilichthys pantherinus</i> (Reis & Schaefer 1992)            | Epa          | 0.03   | -0.02  |
| <i>Hemiancistrus fuliginosus</i> Cardoso & Malabarba 1999             | Hfu          | -0.02  | 0.08   |
| <i>Hisonotus aky</i> (Azpelicueta, Casciotta, Almirón & Koerber 2004) | Hak          | 0.01   | -0.05  |
| <i>Hypostomus commersoni</i> (Valenciennes 1836)                      | Hco          | -0.10  | 0.13   |
| <i>Pareiorhaphis hystrix</i> (Pereira & Reis 2002)                    | Phy          | 0.51   | -0.14  |
| <i>Pareiorhaphis</i> sp.  | Psp          | 0.01   | 0.02   |
| <i>Rineloricaria reisi</i> Ghazzi 2008                                | Rre          | 0.03   | 0.01   |
| <i>Rineloricaria sanga</i> Ghazzi 2008                                | Rsa          | -0.17  | 0.09   |
| <i>Rineloricaria stellata</i> Ghazzi 2008                             | Rst          | 0.07   | -0.08  |
| <i>Rineloricaria zaina</i> Ghazzi 2008                                | Sza          | 0.11   | 0.05   |
| <b>Pseudopimelodidae</b>  |              |        |        |
| <i>Microglanis malabarbai</i> Bertaco & Cardoso 2005                  | Mma          | 0.26   | -0.12  |
| <b>Trichomycteridae</b>   |              |        |        |
| <i>Ituglanis</i> sp.  | Isp          | 0.01   | -0.01  |
| <i>Scleronema</i> sp.   | Ssp          | -0.16  | -0.24  |
| <i>Trichomycterus perkos</i> Datovo, Carvalho & Ferrer 2012           | Tpe          | 0.14   | -0.07  |
| <b>GYMNOTIFORMES</b>  |              |        |        |
| <b>Gymnotidae</b>   |              |        |        |
| <i>Gymnotus cuiá</i> Craig, Malabarba, Crampton & Albert 2018         | Gcu          | -0.07  | 0.22   |
| <b>CICHLIFORMES</b>   |              |        |        |
| <b>Cichlidae</b>  |              |        |        |
| <i>Crenicichla hadrostigma</i> Lucena 2007                            | Cha          | 0.02   | 0.00   |
| <i>Crenicichla lepidota</i> Heckel 1840                               | Cle          | 0.00   | -0.01  |
| <i>Crenicichla missioneira</i> Lucena & Kullander 1992                | Cmi          | 0.00   | -0.02  |
| <i>Crenicichla scottii</i> (Eigenmann 1907)                           | Csc          | -0.05  | -0.12  |
| <i>Crenicichla</i> sp.  | Csp          | -0.02  | 0.00   |
| <i>Crenicichla tendybaguassu</i> Lucena & Kullander 1992              | Cten         | 0.01   | 0.02   |
| <i>Geophagus brasiliensis</i> (Quoy & Gaimard 1824)                   | Gba          | -0.05  | 0.18   |
| <i>Gymnogeophagus constellatus</i> Malabarba, Malabarba & Reis 2015   | Gco          | -0.09  | -0.11  |
| <b>SYNBRANCHIFORMES</b>   |              |        |        |
| <b>Synbranchidae</b>  |              |        |        |
| <i>Synbranchus marmoratus</i> Bloch 1795                              | Sma          | 0.05   | 0.12   |

than species of headwaters are lost (Osborne & Lewis, 1992). Therefore, a stream fish community structure changes over time and space, and more changes may occur between different parts of the same stream than between different streams in the same drainage basin, in some cases, such as changes on species richness or diversity of functional groups that change along a headwaters (upstream) toward the mouth (downstream) gradient (Vannote et al. 1980, Araújo-Lima et al. 1995).

Stream 1, upper portion of the sub-basin, presented more species than the streams in the mid portion (streams 3 and 4), becoming an exception to the pattern of longitudinal distribution found for the species richness. We believe this result has been influenced by the size of the stream (wider and with a greater water flow than the others) and by the proximity of the sampling site to the stream discharge into a larger river (about 200 meters), the Ijuí River, the main river of the sub-basin. In addition, information available in the literature indicates size, volume, flow speed and diversity of habitats, among others, as factors known to influence the pattern of ichthyofauna richness distribution (Winemiller 1983, Tejerina-Garro et al. 2005, Ibañez et al. 2009, Bailly et al. 2016). The characteristics of this stream could also be responsible for the association of Siluriformes to the upper portion of the Ijuí River sub-basin, in relation to the representativeness of the families Heptapteridae and Loricariidae.

Regarding the conservation status of the species, *Crenicichla hadrostroma* Lucena 2007, *Microglanis malabarbai* Bertaco & Cardoso 2005 and *Trichomycterus perkos* Datovo, Carvalho & Ferrer 2012 are included in the list of threatened species, officially recognized by the 51.797 act of September 8, 2014, state of Rio Grande do Sul, and classified as “near threatened” (category VI), according to the criteria defined by the International Union for Conservation of Nature (IUCN) (FZB 2014). The other species captured appear as “least concern” (FZB 2014), or there is no information about the status of conservation due to the species description be posterior to the act publishing. Another reason for the lack of information is the existence of possible new species, like *Heptapterus* sp1, *Pareiorhaphis* sp., *Ituglanis* sp. and *Scleronema* sp., identified only to the genre level (Buckup 1988, Malabarba et al. 2013, J. Ferrer 2017, oral communication, Universidade Federal do Rio Grande do Sul). Therefore, we understand that studies like this contribute to the knowledge of the biological diversity of the south of Brazil, bringing complementary information about richness and abundance of endemic, threatened or of large distribution, grounding future research that could contribute to the conservation of fish biodiversity in Neotropical streams.

## Acknowledgements

The authors would like to thank: the colleagues of the Ichthyology Lab at the Universidade Federal do Rio Grande do Sul for helping and companionship in fieldwork; Júlia Giora, Juliano Ferrer, Priscilla C. Silva, Rafael Angrizani and Tiago P. Carvalho for helping with species identification. The first author thank a PHD scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

## Author Contributions

Laísa W. Cavalheiro: Substantial contribution in the concept and design of the study;

Clarice B. Fialho: Substantial contribution in the concept and design of the study.

## Conflicts of interest

The author declare that they have no conflict of interest related to the publication of this manuscript.

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Received: 21/06/2019

Revised: 24/10/2019

Accepted: 24/10/2019

Published online: 09/12/2019

**CAPÍTULO 2: Ontogeny of feeding by *Astyanax paris* in streams of the Uruguay River Basin, Brazil**

Artigo publicado.

Cavalheiro, L. W. & Fialho, C. B. 2019. Ontogeny of feeding by *Astyanax paris* in streams of the Uruguay River Basin, Brazil. *Animal Biodiversity and Conservation*, 42(1):9-18. DOI: <https://doi.org/10.32800/abc.2019.42.0009>

# Ontogeny of feeding by *Astyanax paris* in streams of the Uruguay River Basin, Brazil

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Cavalheiro, L. W., Fialho, C. B., 2019. Ontogeny of feeding by *Astyanax paris* in streams of the Uruguay River Basin, Brazil. *Animal Biodiversity and Conservation*, 42.1: 9–18, <https://doi.org/10.32800/abc.2019.42.0009>

## Abstract

*Ontogeny of feeding by Astyanax paris in streams of the Uruguay River Basin, Brazil.* We studied the ontogeny of feeding by *Astyanax paris*, an insectivorous characid fish from streams of the Uruguay River Basin in southern Brazil. Size-based differences in diet composition were evaluated using permutational multivariate analysis of variance (PERMANOVA). Six streams surveyed over twelve months yielded twenty specimens for analysis of stomach contents. Smaller individuals (SL  $\leq$  25 mm) consumed mainly aquatic insects. As body size increased, there was a gradual shift to a diet dominated by terrestrial insects. Ontogeny of feeding habitats thus changes the species' position in stream food webs.

Key words: Characiformes, Diet, Insectivorous, Freshwater fish

## Resumen

*Ontogenia de la alimentación de Astyanax paris en los arroyos de la cuenca fluvial del río Uruguay, en Brasil.* Estudiamos la ontogenia de la alimentación de *Astyanax paris*, un pez carácido insectívoro de los arroyos de la cuenca del río Uruguay, en el sureste de Brasil. Las diferencias de la composición de la dieta en función del tamaño se analizaron mediante el análisis de varianza multivariante con permutaciones (PERMANOVA). Se muestrearon seis arroyos durante 12 meses y se obtuvieron 20 especímenes para analizar el contenido del estómago. Los individuos más pequeños (longitud estándar  $\leq$  25 mm) consumieron principalmente insectos acuáticos. A medida que aumentaba el tamaño corporal, se pasaba gradualmente a una dieta compuesta principalmente por insectos terrestres. En consecuencia, la ontogenia de los hábitats de alimentación cambia la posición de las especies en las redes tróficas de los arroyos.

Palabras clave: Caraciformes, Dieta, Insectívoro, Peces de agua dulce

Received: 18 XII 17; Conditional acceptance: 05 III 18; Final acceptance: 10 IV 18

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## Introduction

Fish are important components of stream food webs and have been shown to influence ecosystem dynamics (Vanni, 2010; Rodríguez–Lozano et al., 2016). Studies of fish feeding habits have shown how trophic strategies can affect intraspecific and interspecific interactions and energy flux through ecosystems (Pompanon et al., 2012; Pendleton et al., 2014).

The differential use of food resources is a well-known intraspecific strategy to avoid trophic niche overlap between juveniles and adults in several freshwater fish species (Bonato and Fialho, 2014; Cavalheiro and Fialho, 2016; Dala–Corte et al., 2016). Some species may therefore concentrate on different food resources at different stages of their development (Rudolf and Lafferty, 2011). The shift from soft-bodied, small prey to large and difficult-to-swallow prey is a common pattern among fish and reduces intraspecific competition for food resources (Russo et al., 2014).

Ontogenetic niche shifts are the key to the functional variation among the life history stages in a population (Rudolf and Rasmussen, 2013). In practice, a species' taxonomic identity alone is not sufficient to *a priori* predict its ecological interactions. Additional information on its biology should also be collected because fish are known for their high phenotypic plasticity in life–history traits, including body shape and trophic morphology in response to different food types (Kerschbaumer et al., 2011; Rudolf et al., 2014; Karjalainen et al., 2016). In this context, studies of diet variation in relation to modifications in body size are essential not only to characterize species as generalists or specialists, but also to identify their trophic strategies. According to Rudolf and Lafferty (2011), major challenges in studying trophic nets lie in determining the different functional roles within species and integrating such information into their trophic identity. Studies addressing the ecological relationships below the species level are therefore necessary to better understand natural communities.

Ontogenetic development in fish affects morphological structures associated with feeding, thus allowing different sized individuals to consume different sized prey. Larger individuals often consume larger prey to maximize energy consumption (Keppeler et al., 2014). The trophic strategy of shifting diet composition according to ontogenetic changes allows smaller, less competitive fish to explore several food resources until they reach a size where they can compete with larger individuals of the same, or other, species (Russo et al., 2014).

The genus *Astyanax*, the most speciose of the family Characidae, currently contains 158 valid species distributed in rivers from southern USA to Argentina, including the Uruguay River basin (Lima et al., 2003; Eschmeyer et al., 2016). In the Uruguay River basin, there are 13 valid species of the genus *Astyanax*, including *A. paris* Azpelicueta, Almirón and Casciotta, 2002 (Lucena et al., 2013b). This species was originally described from Fortaleza and Yabotí–Miní streams, both tributaries of the Yabotí–Guazú

River, Upper Uruguay River in Misiones province, Argentina (Azpelicueta et al., 2002). *Astyanax paris* was considered endemic to locality (Lima et al., 2003; López et al., 2003; Liotta, 2005) until it was recorded in Upper Uruguay in the Brazilian state of Santa Catarina (Bertaco et al., 2016).

The taxonomy and distribution of *Astyanax* species have been relatively well studied in the Uruguay River basin (Azpelicueta and Garcia, 2000; Bertaco and Malabarba, 2001; Azpelicueta et al., 2002; Casciotta et al., 2003; Bertaco and Lucena, 2010; Lucena et al., 2013a, 2013b; Bertaco et al., 2016). However, no information on the diet or any ecological data of *A. paris* is available in the literature so far. This paper thus increases understanding of the species' biology and ecology in relation to how different age classes consume different food resources. Other species of *Astyanax* are considered generalists, such as *A. aff. fasciatus* (Cuvier, 1819), *A. eigenmanniorum* (Cope, 1894), *A. lacustris* (Lütken, 1875) and *A. intermedius* Eigenmann, 1908 in Tibagi River basin, Brazil (Bennemann et al., 2005) and *A. lacustris* in Maquiné River, Brazil (Vilella et al., 2002). Omnivory has been reported for *A. bifasciatus* Garavello and Sampaio, 2010, *A. dissimilis* Garavello and Sampaio, 2010 (Neves et al., 2015), and *A. lacustris* in Iguazú River basin, Brazil (Cassemiro et al., 2002). *Astyanax eigenmanniorum* has been considered herbivorous in Lago del Fuerte Dam, Argentina (Grosman, 1999).

This study aimed to investigate the feeding habits of *A. paris* from streams of the Ijuí River sub-basin in the state of Rio Grande do Sul. Hypothesis tested: *A. paris* follows the pattern of other freshwater neotropical fishes, modifying prey according to the sequences of life cycle states (ontogeny).

## Material and methods

### Study area

The Uruguay River drains an area of about 365,000 km<sup>2</sup> and extends 1,838 km from the Serra Geral in southern Brazil to La Plata River estuary in Uruguay/Argentina (Di Persia and Neiff, 1986; Cappato and Yanosky, 2009; Bertaco et al., 2016). The basin can be divided into upper, middle, and lower courses (Bertaco et al., 2016). The river's main tributaries are the Negro (Uruguay/Brazil), Quaraí (Uruguay/Brazil), Ibicuí (Brazil), and Ijuí (Brazil) Rivers (Carvalho and Reis, 2009). The Ijuí River is a tributary of the upper portion of the Uruguay River basin in the north–northwestern state of Rio Grande do Sul. It has a drainage area of 10,649.13 km<sup>2</sup> extending over 20 municipalities. Surveys were carried out at six streams along Ijuí River, from near its headwaters to near its confluence with the Uruguay River (Três Negrinhos: 28.432277778°S, 53.970805556°W; Nock: 28.316222222°S, 53.904972222°W; Santa Bárbara: 28.201722222°S, 54.218583333°W; Ibicuí: 28.394861111°S, 54.451638889°W; Araçá: 28.228°S, 54.956888889°W; Lajeado Grande: 28.170416667°S, 55.065944444°W).

## Surveys

We carried out surveys at each point bimonthly over one year, from July 2015 to May 2016. Fish were captured by the electric fishing technique along a 100 m stretch in each stream, with a sampling effort of one hour per site. In the field, individuals were anaesthetized and euthanized with 10% eugenol (Chair et al., 2014) and fixed with 10% formalin. In the laboratory, specimens were identified according to taxonomic literature (Azpelicueta et al., 2002; Lucena et al., 2013b).

Specimens were measured (Standard length, SL in mm) and dissected for diet examination. Voucher specimens were deposited in the fish collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (vouchers: UFRGS 21927, 21928, 21929). Fieldwork and sampling were carried out under a scientific collection permit (Permit Number 48291–1) issued by the Instituto Chico Mendes de Conservação da Biodiversidade, Ministério do Meio Ambiente, Brasília–Federal District, Brazil.

Stomach contents were analyzed under a dissecting microscope and identified according to the standard taxonomic references (McCafferty, 1998; Mugnai et al., 2010; Segura et al., 2011). Food items were quantified by the volumetric method (VO%) (Hynes, 1950), associated with the frequency of occurrence (FO%) (Hyslop, 1980).

## Data analysis

Changes in the diet according to the sampling site and intraspecific ontogenetic influences on the diet composition of *A. paris* were tested with permutational multivariate analysis of variance (permanova;  $\alpha < 0.05$ ) (Anderson, 2001), based on a Bray–Curtis dissimilarity matrix (Borcard et al., 2011). The Bray–Curtis index was used to construct the dissimilarity matrix as it considers data both of presence/absence and of abundance (Borcard et al., 2011). To assess possible ontogenetic variations, specimens were arbitrarily divided into three body size categories: small (SL  $\leq 25$  mm;  $n = 10$ ), medium (SL 25 to 51.5 mm;  $n = 4$ ), and large (SL  $\geq 51.5$  mm;  $n = 6$ ). These three categories were determined according to the grouping in small, medium and large fish, of standard length classes defined by the Sturges' rule using the equation:

$$h = (X - x) / (1 + 3.222 * \log(n))$$

where:  $h$  = class interval;  $X$  = maximum standard length;  $x$  = minimum standard length;  $n$  = number of individuals (Sturges, 1926). A canonical analysis of principal coordinates (CAP) was used to compare diet composition in relation to standard length size classes (Legendre and Anderson, 1999). This method of ordering was chosen because of the possibility to apply a distance matrix between objects (the Bray–Curtis metrics), because this enables assessment of the relationships between the principal coordinates

(dietary data) and variables (size categories) by redundancy analysis (RDA), and because it performs a permutation test that does not depend on the usual assumptions of data normality (Legendre and Anderson, 1999). The analysis of variance (ANOVA) with permutation tests was used to test the significance of the ordering analysis and its respective axis and terms ( $\alpha < 0.05$ ) (Legendre and Anderson, 1999).

The indicator value index (IndVal) with randomization (Borcard et al., 2011) was used to determine whether any food items were associated with particular body size categories of *A. paris*. IndVal compares abundances and relative frequencies of food items in the diet of the studied groups (Cardoso et al., 2013). The statistical significance of such associations of food items and body size categories is confirmed by a permutation test (De Caceres, 2013). The higher the IndVal (Stat), the higher the association between a given food item and a specific group (De Caceres, 2013). Components A (comp A) and B (comp B) in the test vary from 0–1, and respectively indicate the probability of a food item being restricted to a given group and the probability of all sampled stomachs of a given group containing that food item (De Caceres, 2013).

Statistical tests were carried out using R Project for Statistical Computing software, version 3.4.1. PERMANOVA, CAP, and ANOVA analyses were implemented in the statistical package Vegan, version 2.4–5 (Oksanen et al., 2017), whereas IndVal test was conducted done in the package Indicspecies, version 1.7.6 (De Caceres and Legendre, 2009).

## Results

Twenty specimens of *A. paris* were collected (13 at Lajeado Grande and seven at Ibicuá). They measured between 21.9 and 80.5 mm in standard length. The diet was composed of 20 food items, classified according to their characteristics, origins, and relevance (table 1). The species presented an insectivorous feeding habit with insects making up 94% of the volume of items consumed. This pattern did not vary between the two sampled streams (PERMANOVA;  $F = 0.97$ ,  $R^2 = 0.04$ ,  $p = 0.51$ ).

This study reports the first occurrence of *A. paris* in Rio Grande do Sul, thus extending its geographical distribution to the Medium Uruguay River Basin (fig. 1). The species was captured at two of the six sampled streams, namely, Ibicuá (28.394861111°S, 54.451638889°W municipality of Vitória das Missões) and Lajeado Grande (28.170416667°S, 55.065944444°W municipality of Dezesseis de Novembro; fig. 2). Both these streams are 1–1.5 m deep and have strong currents. Ibicuá stream is narrower, with muddy dark water and small stones on bottom (fig. 2A). Lajeado Grande stream is the widest. It has clear water and a rocky bottom with flat slippery stones (fig. 2B).

The diet of *A. paris* is affected by ontogeny (PERMANOVA;  $F = 3.68$ ,  $R^2 = 0.30$ ,  $p = 0.0007$ ). There is a marked shift in the species' diet as it grows. The stomach contents of small specimens (SL  $\leq 25$  mm) consisted of 69.78% (VO) aquatic insects and 28.97%



Table 1. Indicator values (IndVal) of food items consumed by standard length size classes (SL) of *Astyanax paris*. Small: SL  $\leq$  25 mm; medium: SL 25 to 51.5 mm; large: SL  $\geq$  51.5 mm. The components A (Comp A) and B (Comp B) in the test vary from 0–1, and respectively indicate the probability of a food item being restricted to a given group and the probability of all sampled stomachs of a given group containing that food item. The Stat (test statistic) is the association between a given food item and a specific group. \*  $\alpha < 0.05$ .

Tabla 1. Valores del indicador (IndVal) de los alimentos consumidos por clase de longitud estándar (LE) de *Astyanax paris*. Pequeña: LE  $\leq$  25 mm; mediana: LE 25 a 51,5 mm; y grande: LE  $\geq$  51,5 mm. Los componentes A (Comp A) y B (Comp B) de la prueba se sitúan entre 0 y 1, e indican, respectivamente, la probabilidad de que un alimento esté limitado a un grupo determinado y la probabilidad de que dicho alimento se encuentre en todos los estómagos analizados. La Stat (prueba estadística) es la asociación entre un alimento determinado y un grupo específico. \*  $\alpha < 0,05$ .

| Food item                        | Comp A | Comp B | Stat | p-value |
|----------------------------------|--------|--------|------|---------|
| <b>Small</b>                     |        |        |      |         |
| Aquatic Diptera                  | 1.00   | 0.10   | 0.32 | 1.00    |
| <b>Medium</b>                    |        |        |      |         |
| Aquatic Plecoptera               | 0.64   | 0.75   | 0.69 | 0.10    |
| Plant fragments                  | 0.81   | 0.50   | 0.64 | 0.07    |
| Fragments of terrestrial insects | 0.73   | 0.50   | 0.61 | 0.19    |
| Aquatic Acarina                  | 1.00   | 0.25   | 0.50 | 0.20    |
| <b>Large</b>                     |        |        |      |         |
| Terrestrial Hymenoptera          | 0.98   | 1.00   | 0.99 | 0.0001* |
| Terrestrial Coleoptera           | 0.93   | 0.33   | 0.56 | 0.14    |
| Terrestrial Araneae              | 1.00   | 0.17   | 0.41 | 0.49    |
| Terrestrial Lepidoptera larvae   | 1.00   | 0.17   | 0.41 | 0.49    |
| Aquatic Odonata                  | 1.00   | 0.17   | 0.41 | 0.49    |
| Terrestrial Odonata              | 1.00   | 0.17   | 0.41 | 0.49    |
| Terrestrial Orthoptera           | 1.00   | 0.17   | 0.41 | 0.49    |
| <b>Small and medium</b>          |        |        |      |         |
| Aquatic Ephemeroptera            | 1.00   | 0.71   | 0.85 | 0.02*   |
| Aquatic Diptera                  | 1.00   | 0.36   | 0.60 | 0.33    |
| Fragments of aquatic insects     | 1.00   | 0.36   | 0.60 | 0.46    |
| Seeds                            | 1.00   | 0.14   | 0.38 | 0.84    |
| <b>Small and large</b>           |        |        |      |         |
| Terrestrial Hemiptera            | 1.00   | 0.25   | 0.50 | 0.75    |
| Terrestrial Coleoptera           | 1.00   | 0.13   | 0.35 | 1.00    |
| <b>Medium and large</b>          |        |        |      |         |
| Aquatic Trichoptera              | 1.00   | 0.30   | 0.55 | 0.29    |
| Fish scales                      | 1.00   | 0.20   | 0.45 | 0.47    |

(VO) of terrestrial insects. Medium-size specimens consumed 46.56% (VO) of aquatic and 42.11% (VO) of terrestrial insects. Large specimens mainly consumed (VO = 91.81%) terrestrial insects, with aquatic insects representing only 2.7% (VO) of the stomach contents.

Other prey items were consumed only occasionally or in low numbers. Aquatic ticks (Acarina) were found

in the stomach of a medium-size specimen only, corresponding to 0.4% (VO) of prey consumed by fish in this group size. Similarly, terrestrial spiders (Araneae) were found in the stomach of only one large specimen. Plant items (fragments and seeds) were found in the stomach of one small specimen (VO = 1.25%), in the stomach of two medium-size specimens

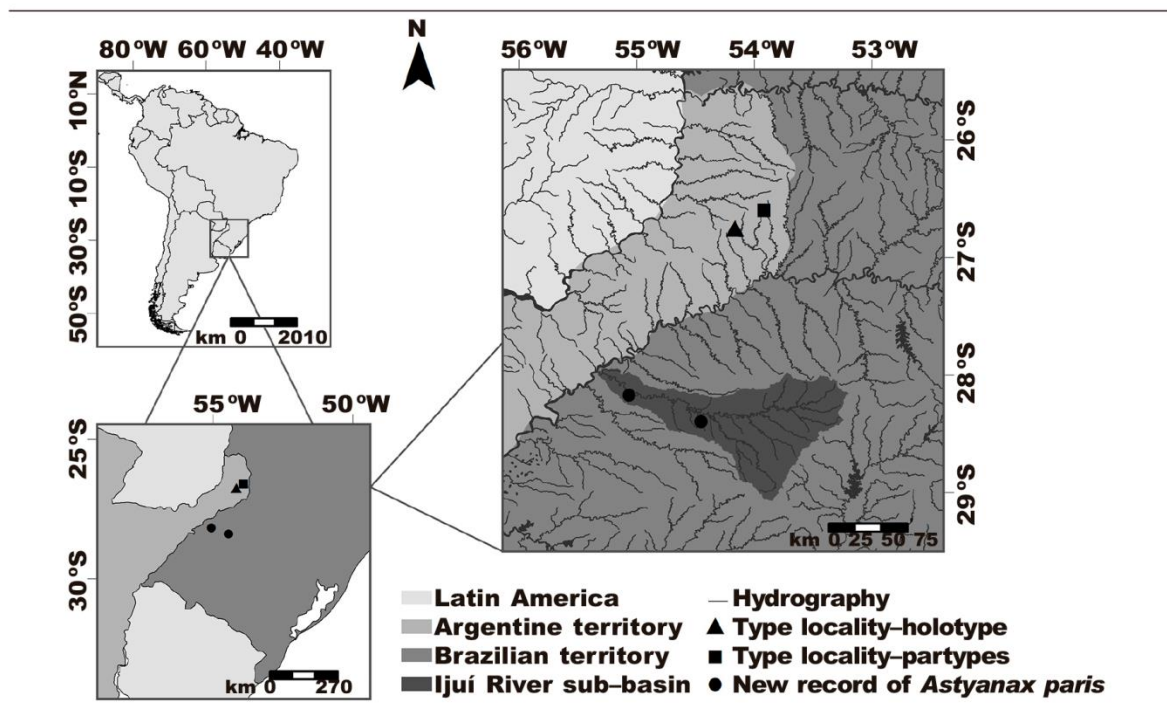


Fig. 1. Records of *Astyanax paris* in Argentinean and Brazilian regions, with indication of the species' type locality (Azpelicueta et al., 2002) and new records from Ijuí River sub-basin, Rio Grande do Sul.

Fig. 1. Registros de *Astyanax paris* en las regiones de Argentina y Brasil, con indicación de la localidad tipo de la especie (Azpelicueta et al., 2002) y nuevos registros de la subcuenca del río Ijuí, en Rio Grande do Sul.

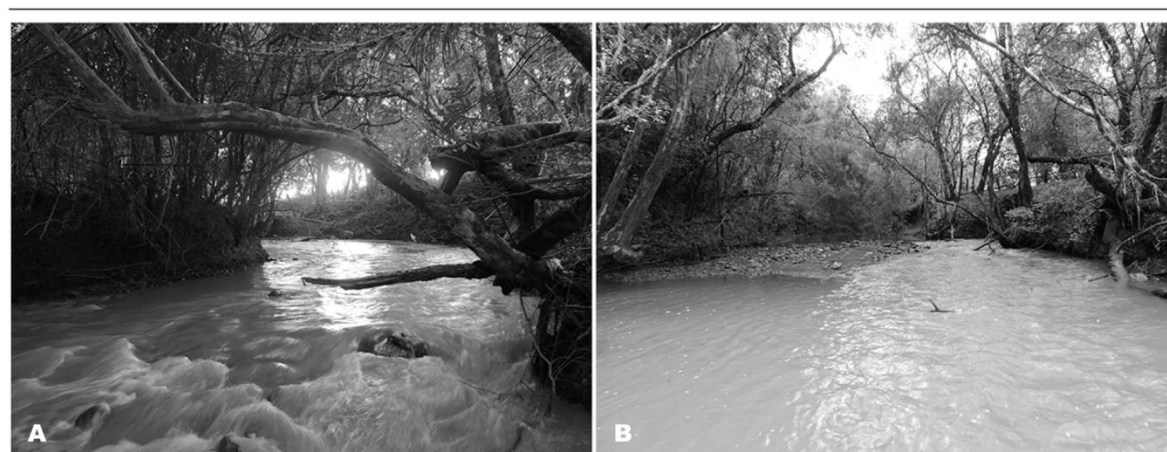


Fig. 2. Localities of collection of *Astyanax paris* in Ijuí River sub-basin, Rio Grande do Sul, Brazil. Ibicuá stream, municipality of Vitória das Missões (A), Lajeado Grande stream, municipality of Dezesseis de Novembro (B).

Fig. 2. Localidades de recogida de *Astyanax paris* en la subcuenca del río Ijuí, en Rio Grande do Sul, Brasil. Arroyo Ibicuá, municipio de Vitória das Missões (A), arroyo Lajeado Grande, municipio de Dezesseis de Novembro (B).



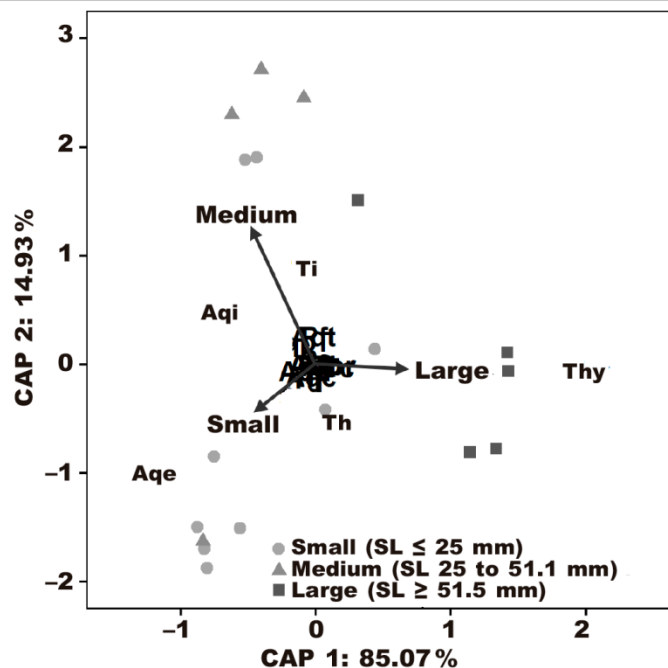


Fig. 3. Canonical analysis of principal coordinates (CAP) of food composition of *Astyanax paris* from Ijuí River sub-basin, Rio Grande do Sul, Brazil: Ac, aquatic Acarina; Ar, terrestrial Araneae; Aqc, aquatic Coleoptera; Tc, terrestrial Coleoptera; Aqd, aquatic Diptera; Td, terrestrial Diptera; Aqe, aquatic Ephemeroptera; Th, terrestrial Hemiptera; Thy, terrestrial Hymenoptera; Tll, terrestrial Lepidoptera larvae; Aqo, aquatic Odonata; To, terrestrial Odonata; Tor, terrestrial Orthoptera; Aqp, aquatic Plecoptera; Aqt, aquatic Trichoptera; Aqi, fragments of aquatic insects; Ti, fragments of terrestrial insects; Sc, scales; Pf, plant fragments; Se, seeds.

Fig. 3. Análisis canónico de las coordinadas principales (CAP) de la composición de la dieta de *Astyanax paris* de la subcuenca del río Ijuí, en Rio Grande do Sul, Brasil: Ac, ácaros acuáticos; Ar, individuos del orden Araneae terrestres; Aqc, coleópteros acuáticos; Tc, coleópteros terrestres; Aqd, dípteros acuáticos; Td, dípteros terrestres; Aqe, efemerópteros acuáticos; Th, hemípteros terrestres; Thy, himenópteros terrestres; Tll, larvas terrestres de lepidópteros; Aqo, odonatos acuáticos; To, odonatos terrestres; Tor, ortópteros terrestres; Aqp, plecópteros acuáticos; Aqt, tricópteros acuáticos; Aqi, fragmentos de insectos acuáticos; Ti, fragmentos de insectos terrestres; Sc, escamas; Pf, fragmentos vegetales; Se, semillas.

(VO = 9.31%), and in that of one large specimen (VO = 3.60%). Fish scales were found in the stomach of one medium-size specimen (VO = 2.02%) and in one large (VO = 1.17%) specimen.

The Canonical Analysis of Principal coordinates ( $F = 3.58$ ,  $p = 0.0009$ ) showed a standard length segregation of populations, especially in relation to the first axis ( $F = 6.12$ ,  $p = 0.0001$ ). This is further evidence of the shift in species diet from aquatic to terrestrial insects, mainly Ephemeroptera and Hymenoptera (fig. 3). These prey items are indicators of the species diet, as shown by IndVal within the 20 food items identified in this study (table 1).

Aquatic Ephemeroptera is an indicator of small and medium-size specimens (Stat = 0.84,  $p = 0.02$ ). This prey item has both a probability to occur in most stomachs of (comp B from IndVal = 0.71), and was restricted to (comp A from IndVal = 1.00) small and medium-size specimens. Large specimens did

not consume Aquatic Ephemeroptera. In contrast, terrestrial Hymenoptera is a strong indicator of large specimens (Stat = 0.99,  $p = 0.0001$ ). Hymenoptera was restricted to large size class and was also predated by all analyzed individuals (comp B from IndVal = 1.00) (table 1).

## Discussion

The fact the of *A. paris* was caught in two capture events and occurred in two streams, despite a year of intense sampling, suggests it has a low population size throughout the Ijuí River sub-basin and that it is naturally rare or extremely difficult to capture. This hypothesis is supported by the lack of previous records of *A. paris* in Rio Grande do Sul even though the ichthyofauna from Brazil's portion of the Uruguay River Basin has been well studied (Bertaco et al., 2016).



The original description of the species was based on a few specimens (one holotype and 15 paratypes), currently in the Museo De La Plata (MLP) and Muséum National d'Histoire Naturelle (MHNG) (vouchers MLP 9584, 9585 e 9586 e MHNG 2623.65) (Azpelicueta et al., 2002). The other records of *A. paris* from scientific collections also consist of few specimens. The Pontificia Universidade Católica do Rio Grande do Sul (MCP) has six specimens collected in the state of Santa Catarina (voucher MCP 40063), two from São Domingos River in the municipality of Cunha Porã (26.8891658783°S, 53.180557251°W) and three from Uruguay River in São Joaquim (26.8891658783°S, 53.180557251°W) (Bertaco et al., 2016). The collection of the Núcleo de Pesquisa em Limnologia Ictiologia e Aquicultura (Nupélia) da Universidade Estadual de Maringá (UEM) has six other specimens from the same state (vouchers NUP 16279 e 16282), all collected in Rio das Contas, municipality of Bom Jardim da Serra (28.4933333°S, 49.7825°W). UEM also has five specimens labeled as '*A. aff. paris*' (voucher NUP 16279) from Ijuí in Rio Grande do Sul (28.3016667°S, 53.8927778°W); however, their identification should be confirmed.

The lack of changes in the feeding behavior of *A. paris* according to the sampling site, despite the marked environmental characteristics in the two streams where it was collected, indicates the species is a probable insectivorous specialist feeder. Insectivorous fish influence both aquatic and terrestrial environments and play an important ecological role in regulating populations of their prey (Knight et al., 2005; Wesner, 2012; Xiang et al., 2016).

This research confirms the hypothesis that *A. paris* presents ontogenetic variation in the diet with specific prey items for each life cycle stage. The variation of food items according to the standard length shows that different age classes play different functional roles in the trophic dynamics of the species habitat. Trophic webs are often studied through a traditional approach wherein species are assigned to guilds or trophic groups, without considering ontogeny (Rudolf et al., 2014). This practice has often been adopted in the existing research on *Astyanax* species (Bennemann et al., 2005; Silva et al., 2014). However, ontogenetic niche shifts are known from 80% of animal taxa (Werner, 1988; Hertz et al., 2016); furthermore, the main source of intraspecific diversity in ecosystems is the variation across ontogenetic stages and size of individuals (Rudolf and Rasmussen, 2013). These aspects may lead to intraspecific functional differences in the role of individuals within ecosystems and affect the structural dynamics of communities (Hertz et al., 2016).

*Astyanax paris* moves from a diet of aquatic to terrestrial insects as it ages. Ontogenetic shifts in the diet are often correlated with ontogenetic shifts in micro-habitat use, or preference for prey of different sizes (Rudolf and Rasmussen, 2013). Small individuals of *A. paris* feed mainly on aquatic Ephemeroptera, which are smaller than terrestrial Hymenoptera, Hemiptera, Coleoptera, and Orthoptera. These four items, in respective order of importance, made up most of the diet in terms of volume of large fish, although only Hymenoptera was

found to be an indicator of this size category. The shifting from soft to hard and larger prey, which are more difficult to catch, was observed in *A. paris*. Mobility and higher competition capacity have often been cited as the aspects of larger fish prey selectivity (Russo et al., 2014). From this perspective, the ontogenetic shifts in the diet of *A. paris* can be viewed as a trophic strategy to reduce intraspecific competition, as seen in other Neotropical freshwater fish (Bonato and Fialho, 2014; Cavalheiro and Fialho, 2016; Dala-Corte et al., 2016).

Species that change their diet during growth and show 'specialist phases' may well appear generalists at species level if size is not taken in account in the study of their diets. Furthermore, these species may behave as sequential specialists as they change their trophic niche during development and are hypersensitive to food resource loss and habitat degradation (Rudolf and Lafferty, 2011). Studies investigating the ontogenetic influences on diet of species inhabiting areas vulnerable to impacts are essential. Ibicuí and Lajeado Grande streams show poorly conserved riparian vegetation. This may affect *A. paris*, which relies on terrestrial food resources.

*Astyanax paris* relies on varied food resources (terrestrial and aquatic) across its life-stages. Protection of its habitats should consider not only the environmental quality of the streams, but also the integrity of adjacent riparian vegetation. The importance of riparian vegetation to fish diet is well recognized and documented for the allochthonous feeder *Astyanax* species (Gomiero and Braga, 2003; Borba et al., 2008; Ferreira et al., 2012; Souza and Lima-Junior, 2013; Silva et al., 2014; Leite et al., 2015). Conserving the streams is also important for those autochthonous feeders (Cavalheiro and Fialho, 2016).

In conclusion, *A. paris* has an insectivorous tendency and plays different roles in the stream trophic web during its life-history. It shows marked ontogenetic shifts in diet, changing its food source from aquatic to terrestrial insects as it grows.

## Acknowledgements

The authors would like to thank Gilmar Nunes Cavalheiro, Maria Ivone Wociechoski Cavalheiro, Amanda A. S. Santos, Dario F. Fuster, José Vanderlei da Silva, Juliano Ferrer, Júnior A. Chuctaya, Laura M. Donin, Leomar B. Medeiros and Rafael Angrizani for help and companionship in fieldwork, and Priscilla C. Silva for help with species identification. The first author received a PhD scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

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## CONCLUSÕES

- A ictiofauna encontrada nos seis riachos amostrados na bacia do rio Ijuí está distribuída em cinco ordens, 13 famílias, 33 gêneros e 55 espécies;

- A riqueza de espécies encontrada segue o padrão dos peixes de água doce da região Neotropical, com as ordens Characiformes e Siluriformes sendo as mais ricas em número de espécies;

- A ordem Siluriforme foi a mais abundante em número de indivíduos coletados seguida de Characiformes, seguindo o padrão Neotropical;

- Nossa hipótese de que a composição da comunidade de peixes não é homogênea ao longo dos riachos amostrados foi confirmada e observamos que a complexidade de espécies aumenta dos riachos localizados mais próximos das áreas de cabeceiras do rio Ijuí em direção aos riachos localizados mais próximos à sua foz (confluência com o rio Uruguai), seguindo o conceito do rio contínuo.

- A espécie *Astyanax paris* tem uma tendência à insetivoria em sua dieta e desempenha diferentes papéis na teia trófica durante sua história de vida. Esta espécie mostra marcadas mudanças ontogenéticas em sua dieta, modificando sua fonte de alimento de insetos aquáticos para terrestres na medida em que cresce, consumindo presas específicas nos diferentes estágios do seu ciclo de vida.

- Indivíduos pequenos de *A. paris* se alimentam principalmente de Ephemeropteras aquáticos, que são presas menores que os himenópteros, hemípteros, coleópteros e ortópteros, que compunham a maior parte da dieta (em termos de volume) dos exemplares grandes desta espécie de peixe.