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JOÃO DANIEL FERRAZ

ECOLOGIA TRÓFICA, SOBREPOSIÇÃO ALIMENTAR E ECOMORFOLOGIA DE PEIXES NATIVOS E INVASORES EM DOIS RESERVATÓRIOS VIZINHOS, BAIXO RIO PARANAPANEMA, BRASIL

Londrina
2024

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“Quando você não consegue encontrar a luz
Que te levou a atravessar os dias nublados
Quando as estrelas não estão brilhando
Você se sente perdido

Quando as luzes de velas do seu lar
Queimam muito distante
Bem, você deve deixar sua alma brilhar
Assim como meu pai costumava dizer

Ele costumava dizer que o brilho da alma
É melhor do que o brilho do sol
É melhor do que o brilho da lua
E, com certeza, é melhor do que a chuva

Mas garoto, não se importe
Todos nós sentimos isso às vezes
Deixe sua alma brilhar
Brilhar até o fim do dia.”

(Soulshine - The Allman Brothers Band)

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FERRAZ, João Daniel. **Ecologia trófica, sobreposição alimentar e ecomorfologia de peixes nativos e invasores em dois reservatórios vizinhos, Baixo Rio Paranapanema, Brasil.** 2024. 128 páginas. Tese (Doutorado em Ciências Biológicas) – Universidade Estadual de Londrina, Londrina, 2024.

RESUMO GERAL

Em rios sob influência de barramentos, a assembleia de peixes sofre drásticas mudanças em composição e estrutura, onde espécies com morfologia e dieta adaptada a ambientes lênticos têm maiores chances de prosperar. Desta forma, o estudo da alimentação e da morfologia é de suma importância para compreender o uso do habitat e dos recursos alimentares em ambientes impactos por reservatórios. O objetivo deste estudo foi avaliar a ecologia alimentar e ecomorfologia da ictiofauna dos reservatórios de Rosana (ROS) e Taquaruçu (TAQ), Baixo Rio Paranapanema, estados de São Paulo e Paraná. Os peixes foram capturados entre setembro de 2018 e setembro de 2020, sendo eutanasiados com eugenol e fixados em formalina. Em laboratório, tiveram o estômago removido e o conteúdo identificado até o menor nível taxonômico possível. Foram analisados 815 indivíduos de 16 espécies, que consumiram 10 categorias de presas. O volume e frequência de ocorrência revelaram que as populações de peixes do reservatório ROS apresentaram maior consumo de recursos alóctones, enquanto as do reservatório TAQ apresentaram maior consumo de recursos autóctones. Os índices de Shannon-Wiener e Pianka demonstraram que as espécies nativas apresentaram menor amplitude de nicho do que as espécies não-nativas, e que a sobreposição de nicho trófico foi maior em TAQ. A PERMANOVA revelou diferenças significativas na composição da dieta da maioria das espécies entre os reservatórios, enquanto a PERMDISP indicou diferenças significativas na amplitude de nicho entre os indivíduos. Duas espécies não-nativas simpátricas foram selecionadas para análises ecomorfológicas (morfologia e dieta), culminando em 84 indivíduos submetidos a 25 medidas morfométricas que foram aplicadas em 23 índices ecomorfológicos. A PERMANOVA revelou diferença significativa entre índices relacionados com as nadadeiras e olhos, além do tamanho da cabeça e da boca. *Auchenipterus osteomystax* consumiu recursos autóctones e apresentou nicho mais restrito, enquanto *Trachelyopterus galeatus* consumiu principalmente recursos alóctones e nicho mais amplo, vindo o índice de Pianka a indicar a baixa sobreposição de nicho alimentar. Após as análises morfológicas constatou-se a presença de deformidades morfológicas em indivíduos de *T. galeatus*, onde radiografias comprovaram as anomalias. Estes resultados nos permitem observar que há uma relação com as alterações ambientais promovidas pelo barramento e o uso e ocupação da área, como alterações fisico-quimicas da água e influxo de poluentes, além da fragmentação populacional que favorece a endogamia resultando em incremento da taxa de anomalias durante a ontogenia dos peixes. Concluímos que, de modo geral, as populações de peixes de ROS tendem ao comportamento alimentar especialista, enquanto as populações de TAQ se comportam como generalistas. A alta sobreposição de nichos alimentares foi impulsionada por espécies não-nativas, pois, todas as espécies mudaram sua dieta entre os reservatórios, porém, espécies não-nativas apresentaram maior flexibilidade. Logo, as populações de ROS apresentam comportamento próximo daquelas em trechos livres de barragem da planície de inundação do Alto Rio Paraná, enquanto as de TAQ corroboraram o padrão alimentar da maioria das populações em reservatórios brasileiros, demonstrando a compartimentalização ambiental. Para a ecomorfologia, conclui-se que as diferenças morfológicas entre os auchinepterídeos pode ser determinante na segregação espacial e divergência alimentar proporcionando a coexistência no ambiente invadido. Em adição, o registro das anomalias é um achado de extrema importância para evidenciar o impacto antrópico nas comunidades aquáticas, uma vez que essas informações podem ser utilizadas nos sistemas de gestão e monitoramento ambiental.

Palavras-chave: Amplitude de Nicho; Anomalia morfológica; Barramento; Dieta; Espécies não-nativas; Índices morfológicos.

FERRAZ, João Daniel. **Trophic ecology, dietary overlap and ecomorphology of native and non-native fish in two neighboring reservoirs, Lower Paranapanema River, Brazil.** 2024. 128 pp. Thesis (Doctorate degree in Biological Sciences) – Universidade Estadual de Londrina, Londrina, 2024.

GENERAL ABSTRACT

In rivers under dam influence, the fish assemblage undergoes drastic changes in composition and structure, where species with morphology and diet adapted to lentic environments have greater chances of sucess. Therefore, the study of food and morphology is extremely important to understand the use of habitat and food resources in environments impacted by reservoirs. The objective of this study was to evaluate the feeding ecology and ecomorphology of the ichthyofauna of the Rosana (ROS) and Taquaruçu (TAQ) reservoirs, Lower Paranapanema River, states of São Paulo and Paraná, Brazil. The fish were captured between September 2018 and September 2020, being euthanized with eugenol and fixed in formalin. In laboratory, the stomach was removed and the contents were identified to the lowest taxonomic level possible. 815 individuals of 16 species were analyzed, which consumed 10 categories of prey. The volume and frequency of occurrence revealed that fish populations in ROS reservoir showed greater consumption of allochthonous resources, while those in the TAQ reservoir showed major consumption of autochthonous resources. The Shannon-Wiener and Pianka indexes demonstrated that native species had a smaller niche breadth than non-native species, and that trophic niche overlap was greater in TAQ. PERMANOVA revealed significant differences in the diet composition of most species between reservoirs, while PERMDISP indicated significant differences in niche breadth between individuals. Two sympatric non-native species were selected for ecomorphology study (morphology and diet), culminating in 84 individuals subjected to 25 morphometric measurements applied to 23 ecomorphological indexes. PERMANOVA revealed a significant difference between indexes related to fins and eyes, in addition to head and mouth size. *Auchenipterus osteomystax* consumed autochthonous resources and had a more restricted niche, while *Trachelyopterus galeatus* consumed mainly allochthonous resources and a broader niche, with the Pianka index indicating low dietary niche overlap. After morphological analysis, was verified the presence of morphological deformities in individuals of *T. galeatus*, where radiographs confirmed the anomalies. These results allow us to observe that there is a relationship with the environmental changes promoted by the damming and the use and occupation of the area, such as physical-chemical changes in the water and the influx of pollutants, in addition to population fragmentation that favors inbreeding, resulting in increase in the rate of anomalies during fish ontogeny. We conclude that, in general, ROS fish populations tend towards specialist feeding, while TAQ populations behave as generalists. The high overlap of food niches was driven by non-native species, as all species changed their diet between reservoirs, however, non-native species showed greater flexibility. Therefore, ROS populations show behavior similar to those in dam-free stretches of the Upper Paraná River floodplain, while TAQ populations corroborate the dietary pattern of most populations in Brazilian reservoirs, demonstrating environmental compartmentalization. For the ecomorphology, it is concluded that the morphological differences between auchinepterids may be crucial in spatial segregation and dietary divergence, providing coexistence in the invaded environment. In addition, recording anomalies is an extremely important finding to highlight the anthropogenic impact on aquatic communities, since this information can be used in environmental management and monitoring systems.

Keywords: Damming; Diet; Morphological anomaly; Morphological indexes; Niche breadth; Non-native species.

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SUMÁRIO

1. APRESENTAÇÃO

Prezados membros da banca avaliadora, o documento está estruturado em formato de artigos científicos. Desta forma, consta abaixo introdução geral para fins de contextualização, seguida pela ordenação dos capítulos. Estes se dispõem como manuscritos para submissão nos respectivos periódicos científicos. A ordenação dos capítulos buscou organizar o estudo partindo de uma ótica ampla para mais restrita, ao apresentar primeiro a extensa descrição de aspectos alimentares da comunidade de peixes e, em segundo plano, a comparação ecomorfológica entre populações de espécies simpátricas não-nativas. Durante a aplicação de metodologia para análise morfológica, foi possível verificar e descrever anormalidades em alguns indivíduos, estudo que compõem a terceira seção. O capítulo um está redigido sob as normas da revista científica Neotropical Ichthyology. O segundo capítulo segue mesma formatação, visto que o periódico ao qual se pretende submetê-lo (Journal of Applied Ichthyology) não exige normatização do manuscrito. O terceiro e último capítulo se encontra com a formatação da revista em que foi submetido (Journal of Fish Biology), tendo sido publicado no ano de 2021 e incluso na tese por ter sido utilizado na qualificação do candidato.

2. INTRODUÇÃO GERAL

A bacia do Alto Rio Paraná é explorada para produção energética através de empreendimentos hidrelétricos (Agostinho *et al.*, 2007). Nesse sentido, especialmente o Rio Paranapanema foi impactado, sendo demasiadamente fragmentado por 11 reservatórios em sequência (Orsi *et al.*, 2016). Em ambientes aquáticos, a construção de barragens modifica o regime natural de fluxo lótico em um artificialmente lêntico sob controle da demanda de produção energética, evento que altera drasticamente as características limnológicas dos rios (Agostinho *et al.*, 2007). Em consequência, ocorre a alteração dos ciclos biogeoquímicos e modificação das funções ecológicas e serviços ecossistêmicos, o que pode levar a degradação do sistema ao longo do tempo (Agostinho *et al.*, 2007; Orsi & Britton, 2014). O estabelecimento de empreendimentos hidrelétricos prejudica as bacias hidrográficas também por facilitar o acesso de espécies, sejam elas plantas, invertebrados ou peixes, para além de sua distribuição original através da eliminação das barreiras naturais e simplificação do habitat (Júlio Júnior *et al.*, 2009; Vitule *et al.*, 2012). Uma vez que essas espécies não-nativas conseguem completar seus ciclos de vida e colonizar o novo ambiente, tornam-se invasoras (Vitule *et al.*, 2012; Orsi & Britton, 2014). Desta forma, as alterações nas assembleias de peixes devido ao barramento e influenciadas pelas invasões biológicas levam a redução da diversidade, onde ao longo do tempo, diversas comunidades aquáticas em diferentes locais tornam-se semelhantes, fenômeno denominado homogeneização biótica (Vitule *et al.*, 2012; Daga *et al.*, 2019).

Os peixes apresentam papel de grande importância dentro das comunidades aquáticas, sendo um deles a participação na ciclagem, transporte de nutrientes e fluxo de energia através da alimentação (Winemiller *et al.*, 2008; Small *et al.*, 2011). A disponibilidade de recursos em ambientes Neotropicais selecionou diversas estratégias alimentares em espécies dulcícolas que habitam essa região (Zatti *et al.*, 2012). Desta forma, algumas espécies apresentam uma grande plasticidade alimentar, a qual obedece a padrões comportamentais e ontogenéticos, além de responder a variações espaço-temporais da disponibilidade de alimento (Abelha *et al.*, 2001). Portanto, em ambientes sob influência de barramentos, a medida que o ambiente é alterado, algumas dietas também podem sofrer modificações (Freitas & Siqueira-Souza, 2009; Zatti *et al.*, 2012).

Em assembleias de peixes que sofrem interferência direta de reservatórios, é importante compreender como os indivíduos exploram os recursos, entre eles o uso de itens alimentares autóctones e alóctones (Vidoto-Magnoni, 2009), e a adoção de estratégias generalistas ou especialistas (Figueiredo *et al.,* 2015). Isto é especialmente relevante porque os peixes respondem às características do ambiente em que vivem (Abelha *et al.,* 2001). Assim, populações de peixes em reservatórios podem explorar recursos autóctones como detritos, algas, plantas aquáticas, invertebrados aquáticos e peixes (Vidotto-Magnoni & Carvalho, 2009; Lima *et al.,* 2018). No entanto, outros reservatórios podem apresentar heterogeneidade ambiental (Casatti *et al.,* 2003) e/ou sofrem grande influência dos entornos (Smith *et al.,* 2018), proporcionando recursos alóctones para os peixes como sementes, frutos e invertebrados terrestres. Estudos sobre a dieta são, portanto, importantes para a compreensão das relações ecológicas entre as espécies e como estas são impulsionadas pelas características dos seus habitats (Lima *et al.*, 2018). Nesse sentido, estes estudos atuam como um potencial indicador da saúde dos ecossistemas (Figueiredo *et al.,* 2015).

Outra ferramenta fundamental para compreender a relação entre as espécies e o meio ambiente é a ecomorfologia (Breda *et al.*, 2005; Oliveira *et al.*, 2010). A partir de análises morfométricas e de alimentação é possível averiguar o nicho ocupado pelas espécies, isto é, a relação entre a distribuição espacial e a dieta (Kirchheim & Goulart, 2010; Freitas *et al.*, 2017), onde é sabido que o primeiro vem a influenciar o segundo em uma correlação robusta (Garcia *et al.*, 2020). Desta maneira, o habitat pode selecionar as melhores características morfológicas para o sucesso da espécie em um determinado local, levando a mudanças em sua dieta (Sampaio *et al.,* 2013). Nesse sentido, esta análise pode ser extremamente útil em ambientes que sofreram simplificação ambiental por ação de barragens, uma vez que a heterogeneidade ambiental é suprimida a partir do estabelecimento do reservatório e regime de fluxo lêntico (AGOSTINHO *et al.,* 2007). Assim, espécies que são relacionadas filogeneticamente e morfologicamente provavelmente terão um forte potencial competitivo (WOOTTON, 1999), uma vez que ocorrem no mesmo habitat e lidam com uma gama de recursos alimentares reduzida. Logo, a ecomorfologia nos ajuda a compreender o uso espacial e o comportamento alimentar das espécies (Neves *et al.,* 2015; Baldasso *et al.,* 2019).

A análise morfológica também nos permite registrar alterações nos padrões da ontogênia e sobrevivência dos peixes, como anomalias e deformidades em individuos. Embora raras, deformidades morfológicas foram descritas para diferentes espécies de peixes ao redor do mundo em ecossistemas marinhos (Gangan *et al.*, 2018; Jawad *et al.*, 2018) e de água doce (Rutkayová *et al.*, 2016; Da Silva & Casas, 2020). O desenvolvimento de anomalias na morfologia dos peixes ocorre durante as primeiras fases da vida, quase sempre associado a condições ambientais (Sfakianakis *et al.,* 2004), endogamia (Tave *et al.*,1983) ou poluição (Browder *et al.,* 2004; Lemly, 2002). Em ambientes barrados, isto é, que sofreram fragmentação ambiental e de suas populações, a restrição do fluxo gênico e aumento da endogamia pode maximar a frequência das deformidades (Browder *et al.*, 1993; Lemly, 2002), bem como a diminuição de predadores favorece a permanência desses indivíduos anômalos nas comunidades aquáticas (Lemly, 2002). Para além dos prejuízos a ictiofauna, o registro de tais anomalias é importante para o uso dos recursos hídricos, uma vez que deformidades em peixes podem denotar a má qualidade da água tornando-a imprópria para uso humano e o consumo do pescado (Mise *et al.*, 2017).

No final do século XX, o baixo rio Paranapanema sofreu sucessivas fragmentações por pequenos empreendimentos hidrelétricos em regime de fio d'água como Canoas I, Canoas II, Taquaruçu e Rosana, instalados como complemento ao grande reservatório de acumulação Capivara (Britto & Carvalho, 2013). A construção da Barragem de Rosana em 1986 criou um trecho temporário de 190 km que continham diversos habitats relevantes para a história de vida dos peixes (Casimiro *et al.*, 2016). Entretanto, este trecho foi novamente fragmentado em 1991 através da construção da barragem de Taquaruçu (Casimiro *et al.*, 2016). Desta forma, ocorreu a separação de habitats críticos para a sobrevivência das espécies, o que pode ter impacto severo nas populações de peixes (Pompeu *et al.*, 2012). Contrariando o conceito de que estes reservatórios são semelhantes, o reservatório de Rosana possui curso sinuoso com diversas lagoas marginais com leitos de macrófitas circundados por florestas (Cassati *et al.*, 2003; Pelicice & Agostinho, 2006) e importantes afluentes (Agostinho *et al.*, 2007), enquanto o reservatório de Taquaruçu apresenta curso retilíneo e ausência de lagoas e margens florestadas, bem como possui poucos afluentes e estes são impactados pela atividade humana (Vidotto-Magnoni *et al.*, 2015; Garcia *et al.*, 2018).

Garcia et al. (2018) observaram que peixes com grande flexibilidade alimentar obtiveram sucesso na manutenção de suas populações no Baixo Rio Paranapanema, sendo boas partes delas espécies não-nativas. No reservatório de Rosana, estudos sobre a alimentação dos peixes foram realizados majoritariamente com as espécies que habitam as lagoas marginais (Cassati *et al.*, 2003; Pelicice & Agostinho, 2006). Em adição, não foram realizadas até o momento investigações amplas sobre o comportamento alimentar dos peixes do reservatório de Taquaruçu. Desta forma, maiores estudos sobre as estratégias alimentares e a dieta das espécies nesses trechos do Rio Paranapanema podem contribuir para uma melhor compreensão da dinâmica na assembleia de peixes impactada pelos reservatórios (Carvalho *et al.*, 2015, 2017; Garcia *et al.*, 2018).

Portanto, o objetivo deste estudo foi descrever a dieta e investigar a ecologia alimentar e ecomorfologia da ictiofauna presentes nos reservatórios de Rosana e Taquaruçu, sendo este relatório importante para atualizações do conhecimento sobre alimentação dos peixes no baixo rio Paranapanema, bem como útil para estudos comparativos no futuro. Consequentemente, estes dois reservatórios fornecem um sistema experimental natural para testar as seguintes previsões: (i) diferentes condições ambientais entre reservatórios fazem com que as suas populações de peixes apresentem padrões alimentares distintos de acordo com recursos autóctones versus alóctones; (ii) diferentes condições ambientais entre reservatórios fazem com que suas populações de peixes apresentem padrões divergentes de amplitude e sobreposição de nicho trófico, variando de especialistas a generalistas; e (iii) diferenças morfológicas influenciam o uso do habitat e a dieta levando a baixa sobreposição de nicho alimentar, o que permite a coexistência de espécies não-nativas simpátricas.

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4. CAPÍTULOS

4.1 CAPÍTULO 1

TROPHIC ECOLOGY OF THE FISH ASSEMBLAGE FROM NEIGHBOURING NEOTROPICAL RESERVOIRS, PARANAPANEMA RIVER BASIN

Capitulo redigido segundo as normas da revista Neotropical Ichthyology. Normas para formatação disponíveis em: https://www.ni.bio.br/

4.1.1 Tittle - Trophic ecology of the fish assemblage from neighbouring Neotropical reservoirs, Paranapanema River Basin

4.1.2 Authors

4.1.3 Authors Addresses

4.1.4 Abstract

Fish can exhibit high plasticity in their diet through their feeding strategies, which can vary depending on environmental conditions. Thus, studies on the diet of fishes in reservoirs are important for understanding the ecological relationships between species and habitat characteristics. The aim of this study was to describe the diet and feeding ecology of the fish community from the two last neighbouring reservoirs in the Paranápapanema River, Taquaruçu and Rosana, states of Paraná and São Paulo, Brazil. So, samples were collected quarterly from September 2018 to September 2020 at seven sites in each reservoir with gillnets, trawls, sieves, and cast nets in the marginal zone and aquatic macrophyte beds. All captured individuals were anesthetized and euthanized, fixed in 10% formaldehyde and preserved in 70% ethanol. In the laboratory, the stomach of individuals was removed and their content was analysed under a stereomicroscope, being the prey items identified and organized by volume between ten categories. The data analyses were conducted in two steps, incorporating descriptive (16 species) and analytical (nine species) study. A total of 815 individuals were analysed, which had consumed 10 prey categories. The Volume and Frequency of Occurrence revealed that Rosana Reservoir populations showed major consumption of allochthonous resources, while those from Taquaruçu Reservoir higher consumption of autochthonous resources. With the Shannon-Wiener and Pianka indexes, we verify native species presented lower niche breadth than non-native species, and the overlap of niche was higher in Taquaruçu Reservoir. The PERMANOVA revealed significant differences in the diet composition of most species between the reservoirs, and PERMDISP indicated significant differences in niche breadth among the analysed individuals. We concluded that Rosana populations tends to specialist diet, while Taquaruçu populations behaves as generalist. The high dietary niche overlap was driven by non-native species, since species changed their diet between reservoirs, however, native species had a lower flexibility than non-native species. So, we conclude that the Rosana Reservoir populations display closer to those of free-of-dam stretches of the Upper Paraná River floodplain, while those from Taquaruçu reservoir behaves as most in the Brazilian reservoirs, corroborating the compartmentalization tendency in the cascade of reservoirs.

Keywords: Damming, Food resources, Food overlap; Niche breadth; Upper Paraná River.

4.1.5 Resumo

Os peixes podem apresentar alta plasticidade em sua dieta através de estratégias alimentares, que podem variar dependendo das condições ambientais. Assim, estudos sobre a dieta de peixes em reservatórios são importantes para a compreensão das relações ecológicas entre as espécies e as características do habitat. O objetivo deste estudo foi descrever a dieta e a ecologia alimentar da comunidade de peixes dos dois últimos reservatórios vizinhos do Rio Paranápapanema, Taquaruçu e Rosana, estados de Paraná e São Paulo, Brasil. Por isso, amostras foram coletadas trimestralmente de setembro de 2018 a setembro de 2020, em sete locais em cada reservatório com redes de emalhar, redes de arrasto, peneiras e tarrafas na zona marginal e leitos de macrófitas aquáticas. Todos os indivíduos capturados foram anestesiados e eutanasiados, fixados em formol 10% e preservados em etanol 70%. Em laboratório, o estômago dos indivíduos foi retirado e seu conteúdo analisado em estereomicroscópio, sendo as presas identificadas e organizadas por volume entre dez categorias. A análise dos dados foi realizada em duas etapas, incorporando métodos descritivos (16 espécies) e analíticos (nove espécies). Foram analisados 815 indivíduos, que consumiram 10 categorias de presas. O Volume e frequência de ocorrência revelaram que as populações do reservatório de Rosana apresentaram maior consumo de recursos alóctones, enquanto as do reservatório de Taquaruçu apresentaram maior consumo de recursos autóctones. Com os índices de Shannon-Wiener e Pianka, verificamos que as espécies nativas apresentaram menor amplitude de nicho do que as espécies não-nativas, e a sobreposição de nicho foi maior no reservatório de Taquaruçu. A PERMANOVA revelou diferenças significativas na composição da dieta da maioria das espécies entre os reservatórios, e a PERMDISP indicou diferenças significativas na amplitude de nicho entre os indivíduos analisados. Concluímos que as populações de Rosana tendem ao comportamento especialista, enquanto as populações de Taquaruçu se comportam como generalistas. A alta sobreposição de nichos alimentares foi impulsionada por espécies não-nativas, uma vez que as espécies mudaram sua dieta entre os reservatórios, porém, as espécies nativas tiveram menor flexibilidade do que as espécies não-nativas. Assim, concluímos que as populações do reservatório de Rosana apresentam-se mais próximas daquelas dos trechos livres de barragem da planície de inundação do Alto Rio Paraná, enquanto as do reservatório de Taquaruçu se comportam como a maioria nos reservatórios brasileiros, corroborando a tendência de compartimentalização na cascata de reservatórios.

Palavras-chave: Alto Rio Paraná; Cadeia alimentar, Presa; Recursos alimentares; Represamento.

4.1.6 Running head - Diet and feeding ecology of fishes from Neotropical reservoirs

4.1.7 Introduction

As human societies seek sustainable energy production, hydropower schemes are often employed due to their potential for delivering reliable sources of electricity (Twardek *et al.* 2022). However, such schemes are considered to constitute one of the most significant threats to freshwater biodiversity (Reid *et al.*, 2019; Twardek *et al.*, 2022), primarily due to the adverse effects of river fragmentation caused by impoundments (Deinet *et al.*, 2020). However, impacts can also arise from the alteration of river flows and flood pulses, modified thermal regimes, and the conversion of lotic to lentic habitats that drives changes in assemblage composition (Twardek *et al.* 2022). In Brazil, hydropower reservoirs have been developed in all major watersheds, particularly in the southeast and south regions (Agostinho *et al.*, 2007) where, in some cases, dams have been constructed in a cascade formation, creating sequences of reservoirs (Garcia *et al.*, 2018a). These reservoirs all support fish assemblages based on the original, pre-impoundment assemblage, but that have undergone taxonomic and functional simplification over time through the loss of riverine specialist species and the introduction of non-native fishes (Daga *et al.*, 2019).

The extent of the modification of the fish assemblages between reservoirs can, however, be context-dependent, as this modification is driven by local intrinsic and extrinsic factors that can result in marked differences between neighbouring reservoirs (Ganasin *et al.*, 2021). For example, differences in the extent of incoming river flow and water retention time (Nogueira *et al.*, 2012, Ferrareze *et al.*, 2014), human activities in the surrounding areas (Benneman *et al.*, 2011; Koushlesh *et al.*, 2023), the composition of the original fish assemblage, and the propagule pressure of non-native fishes into the newly formed reservoir can strongly influence how the fish assemblage responds to the switch from being in a lotic to lentic habitat (Daga *et al.*, 2019; Ganasin *et al.*, 2021).

In addition to the changes in species richness and assemblage composition following reservoir construction, it is also important to understand how the fish species present in the reservoir exploit the prey resources present, including understanding the extent of diet generalism versus specialism, and the exploitation of autochthonous versus allochthonous resources. For example, in Neotropical hydropower reservoirs, fish populations can exploit autochthonous resources, including detritus, phytoplankton, benthic meiofauna and macroinvertebrates, and fish (Vidotto-Magnoni & Carvalho, 2009; Lima *et al.*, 2018).

However, some reservoirs have relatively high habitat heterogeneity (albeit lower than pre-impoundment) through the presence of marginal lagoons (Casatti *et al.*, 2003), extensive macrophyte beds (Pelicice & Agostinho, 2006), and incoming river tributaries (Smith *et al.*, 2018), which can provide access to rich allochthonous prey resources, including seeds, fruits and terrestrial invertebrates (Agostinho *et al.*, 2007).

Fish can exhibit high plasticity in their diet composition through their expression of feeding strategies at the individual and population level, which can vary depending on environmental conditions (Oliveira *et al.*, 2020; Restrepo-Santamaría *et al.*, 2022; Garcia *et al.*, 2023). In periods of high prey abundance, populations within fish communities often specialise in exploiting specific prey items, resulting in patterns of trophic niche partitioning between species that reduces competitive interactions (Merona & Rankin-de-Merona, 2004; Hakami *et al.*, 2013; Cardoza-Martinez, 2021). In periods of prey resource scarcity, however, populations might broaden their trophic niche by being more generalist in their diet, resulting in patterns of inter-specific niche convergence and dietary overlaps (Liu *et al.*, 2019; Hossain *et al.*, 2017), especially in the presence of non-native species (Schmitt *et al.*, 2018; Glassic *et al.*, 2023). However, the patterns of species dietary niche amplitude and overlap are variable and, in some cases, random (Neves *et al.*, 2017). So, inter-specific trophic niche partitioning can also occur under conditions of prey scarcity, where populations become more specialised in their resource use, facilitating their co-existence (Figueiredo *et al.,* 2015).

Studies on the diet of fishes in reservoirs are important for understanding the ecological relationships between species and how these are driven by differences in their habitat characteristics (Lima *et al.*, 2018; Smith *et al.*, 2018). These studies can provide indications on prey resource presence and availability (Vidoto-Magnoni, 2009), potentially acting as an indicator of ecosystem health (Figueiredo *et al.*, 2015). Understanding how fish exploit the available prey resources can consider the entire dietary spectrum that can be described by both descriptive and comparative analyses (Amundsen & Sánchez-Hernández, 2019). Thus, methods based on the frequency and abundance of food items can be applied (e.g. frequency of occurrence (FO) (Hamidan *et al.*, 2015) and volumetric proportion (%) (Hellawell & Abel, 1971)). Additionally, indexes measuring the dietary niche breadth of populations can help assess inter-specific dietary overlap (Grossman, 1986) and the feeding strategies used, with multivariate analyses then providing quantitative comparisons between population samples, enabling spatial-temporal evaluations (Anderson *et al.*, 2004; 2008).

The Upper Paraná River remains one of the most important watersheds in Brazil due to its significant ichthyofaunal and hydrological characteristics, despite being impacted by hydropower development (Agostinho *et al.*, 2007). The Paranápapanema River, a major tributary of the Upper Paraná River (Sampaio, 1944), has undergone extensive fragmentation in the last 60 years through the construction of a cascade of 11 reservoirs (Garcia *et al.*, 2018a), which have divided the river into three main sections: Upper, Middle, and Lower (Sampaio, 1944). The Lower Paranapanema River begins downstream of the Salto Grande Falls, which is currently submerged by the Salto Grande Reservoir. The river encompasses a series of reservoirs from upstream to downstream, including Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu, and Rosana (Duke Energy, 2008).

The aim of this study was to describe the diet and feeding ecology of the fish community from the two last neighbouring reservoirs in the Paranápapanema River: The Taquaruçu and Rosana reservoirs. Despite being in close proximity, there are substantial physical differences between the reservoirs: Rosana Reservoir have several marginal lagoons with macrophytes beds surrounding by forests (Cassati *et al.*, 2003; Pelicice & Agostinho, 2006), plus large tributaries that flow into its main channel, which can increase the availability of food resources from external of the aquatic environment (Agostinho *et al.*, 2007). In other hand, Taquaruçu Reservoir lacks marginal lagoons, forested surroundings, and has only a few tributaries impacted by human activity (Vidotto-Magnoni *et al.*, 2015; Garcia *et al.*, 2018b), which may restrict food resources to only items of aquatic origin. Consequently, these two reservoirs provide a natural experimental system for testing the following hypotheses: (i) different environmental conditions between reservoirs result in fish populations with distinct food exploitation. This way, the prediction is that fish from Rosana Reservoir will explore more allochthonous, whereas those from Taquaruçu Reservoir will use more autochthonous resources; and (ii) different environmental conditions between reservoirs result in their fish populations showing divergent patterns of dietary niche breadth and overlap. Thus, the prediction is that fish from Rosana Reservoir will display specialist feeding ecology and low overlap, while those from Taquaruçu Reservoir will behaves major as generalists increasing the overlap.

4.1.8 Material and methods

4.1.9 *Study Area*

The Paranapanema River originates in the "Serra de Paranápiacaba", located in the Atlantic Plateau of the municipality of Capão Bonito (Sâo Paulo State), in the south-eastern region of Brazil (Sampaio, 1944). It flows for 930 km until it joins the left bank of the Upper Paraná River, with approximately 330 km of its main channel forming the border between the southeastern region of the Sâo Paulo State (SP) and the northern region of the Paraná State (PR) (Maack, 1981). Due to its slopes, the Paranapanema River has been extensively used for hydropower since 1950, resulting in the transformation of its main channel into a cascade of 11 reservoirs (Garcia *et al.*, 2018a). The study areas are located within the influence zones of the last two dams, Rosana and Taquaruçu (Figure 1).

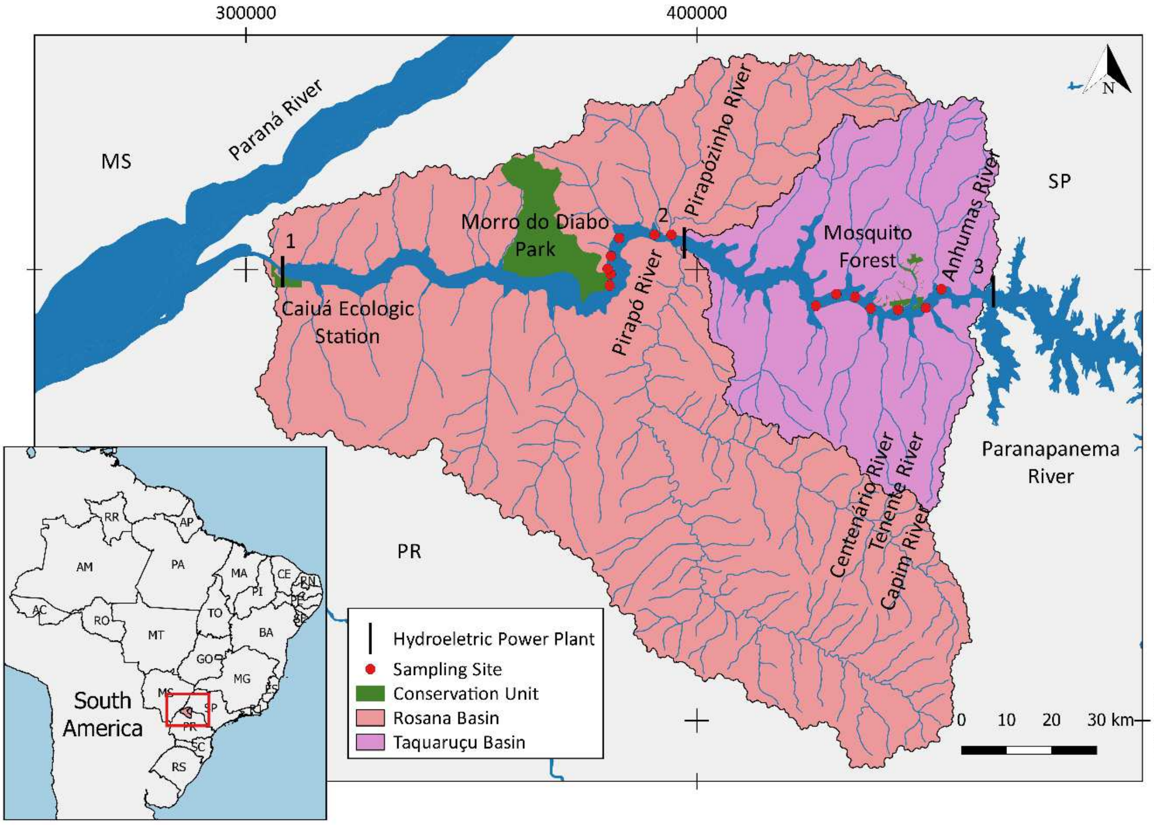

Figure 1. Samplings sites in the Rosana and Taquaruçu reservoirs, lower Paranapanema River. Hydroelectric power Terrestrial Plants: 1 = Rosana; 2 = Taquaruçu; 3 = Capivara. MS = Mato Grosso do Sul State; PR = Paraná State; SP = São Paulo State.

The Rosana Dam was constructed in 1980 and began operating in 1986. It is located between the municipalities of Diamante do Norte (PR) and Primavera (SP). The reservoir formed by the dam has a run-of-river flow, stretches over a length of 110 km, has a maximum depth of 26 m, and covers an area of 220 km^2 (Ferrareze *et al.*, 2014). The main channel of the reservoir follows a sinuous course, allowing the formation of marginal lagoons resembling the original Upper Paraná River Floodplain (Agostinho *et al.*, 2007). These lagoons are characterized by dense macrophytes coverage (Casatti *et al.*, 2003; Ferrareze *et al.*, 2015) (Figure S2, Supplementary material). The reservoir encompass conservation units (UCs) and important tributaries: The Morro do Diabo Park (UC), the Pirapozinho River (second largest tributary in the basin) and the Iancã, Cuiabá and Bonito streams on right bank (SP), and the Caiuá Ecologic Station (UC) and the Pirapó River (largest tributary in the basin) on the left bank (PR) (Figure 1). As a result of nutrients and organic matter influx from the surrounding areas, the reservoir presents a mesotrophic profile (Ferrareze *et al.*, 2014). However, a significant portion reservoir's vicinity is occupied by pastures, while the tributaries are affected by human activities such as deforestation in the surrounding areas and the discharge of effluents from industrial and agriculte (Rodrigues *et al.*, 2019). Although the Paranapanema River basin has high number of species (> 220), the lower region that presents the greatest richness is major influenced by non-native species (> 140 native; > 50 non-native species) (Jarduli *et al.*, 2019). In this sense, the Rosana Reservoir has the highest record of non-native species in the entire basin, which resulting from fish stocking, fish farm escapes, aquarium dumping and introductions for sport fishing (Garcia *et al.*, 2018a).

The Taquaruçu Dam was built in 1989 and commenced operation in 1991. It is situated between the municipalities of Itaguaje (PR) and Sandovalina (SP). The reservoir has a run-of-river flow, a length of 80 km, maximum depth of 18 m, and flooded area of 105.5 km^2 (Britto, Carvalho, 2006), less than the half of the Rosana Reservoir flooded area. The reservoir follows a straight course, with few meanders, resulting in a surrounding area that differs from the original Upper Paraná River Floodplain. Consequently, the vicinity of the reservoir features scattered marginal lagoons with low density macrophytes (Vidotto-Magnoni *et al.*, 2015) (Figure S3, Supplementary material). Additionally, the reservoir has fewer tributaries compared to Rosana Reservoir. The most significant tributaries are the Capim, Centenário, and Tenente rivers on the lefkt bank (PR), and the Anhumas River (largest tributary in the basin) on the right bank (SP) (Figure 1). Notably, only these tributaries have undergone reforestation efforts (Mosquito Forest) (Leme *et al.*, 2015). As a result, the reservoir is associated with an oligotrophic profile (Nogueira *et al.*, 2012). Nevertheless, these tributaries are subject to various anthropogenic impacts, including deforestation in surroundings, land use (agriculture and pasture), urbanization, and the discharge of domestic and industrial effluents (Vidotto-Magnoni *et al.*, 2015). About the ichthyofauna, it follows the same patterns as the lower region of the Paranapanema River (Jarduli *et al.*, 2019). Thus, it has the second highest rate of biological invasion in the entire basin, species coming from the same introduction vectors of the Rosana Reservoir (Garcial *et al.*, 2018a).

4.1.10 *Sampling*

Fish samples were collected quarterly from September 2018 to September 2020 at seven sites within both reservoirs (Figure 1). The samplings covered both the pelagic zone and the marginal zone using gillnets with mesh sizes ranging from 20 to 120 mm between opposed knots. The gillnets were set for a 24-h period and checked every 12 h. Additionally, trawls, sieves, and cast nets were employed to capture fish in the marginal zone and along aquatic macrophyte beds whenever present. In these sampling sites, a standardized effort of two hours was exerted, covering a distance of 100 m to effectively explore the environments. All captured individuals were anesthetized and euthanized (overdoes of Eugenol at a concentration of 1 g mL^{-1}). Subsequently, they were fixed in 10% formaldehyde for 48 hours and preserved in 70% ethanol. All samplings were authorized by The Animal Ethics Committee of the Universidade Estadual de Londrina (CEUA-UEL N° 24310.2017.78). Species identification was carried out using specific literature (Ota *et al.*, 2018). Further, a collection of voucher specimens was deposited at MZUEL.

4.1.11 *Dietary analyses*

In the laboratory, the stomach of captured individuals was removed, and their content was analysed under a stereomicroscope. The prey items found in the stomachs were identified to the lowest taxonomic level possible using specific literature as a reference (Thomaz et al., 2002; Mugnai et al, 2010; Biolo & Rodrigues, 2011). The volume (V) of each stomach content was determined by its compression it in a petri dish and the volume was recorded in mm^3 before converting to mL, following the methodology outlined by Hellawell & Abel (1971). Identified prey items were categorized into 10 groups and represented as percentages (%), according to Table 1.

Table 1. Prey categories and prey items used to organize the diet of fish from Rosana and Taquaruçu reservoirs.

Prey Category	Prey Item
Algae	Filamentous Algae
Aquatic Insects	Aquatic Insect Fragment, Coleoptera Larvae, Coleoptera Pupe, Diptera Larvae, Diptera Pupe, Ephemeroptera Nymph, Odonata Nymph And Trichoptera Nymph
Detritus	Inorganic Detritus, Organic Detritus
Fish	Fish, Fish Scale
Macrocrustacean	Crab, Shrimp
Microcrustacean	Cladocera, Copepoda, Microcrustacean Fragment, Ostracoda
Mollusc	Bivalvia, Gastropoda
Other	Microplastic
Plant	Fruit, Leaf, Stick, Seed
Terrestrial Invertebrates	Terrestrial Acari, Aranae, Blattodea (Isoptera), Blattodea Adult, Coleoptera Adult, Diplopoda, Diptera Adult, Ephemeroptera Adult, Hemiptera Adult, Hymenoptera Adult, Lepidoptera Adult, Terrestrial Insect Fragment And Thysanoptera Adult

The dietary data analyses were then conducted in two stages, incorporating descriptive and analytical criteria. Initially, stomach content analysis was performed on all captured individuals to determine the diet composition of a maximum number of species from the studied reservoirs. However, due to the limited sample size for some samples a subset of the most abundant species (minimum of twenty individuals) and constant in the samples was selected for further analysis. From the initial set of species, 16 were chosen for the description of their feeding ecology. Subsequently, this number was further reduced to nine species based on their abundance and frequency in both reservoirs. This subset of species was utilised for subsequent data analysis, focusing on their feeding patterns and ecological interactions.

To initially analyse the diet and feeding ecology of the 16 species, the prey categories were represented as 'frequency of occurrence' (FO) following the methodology described by Hamidan *et al.* (2015) with adaptations. The frequency of occurrence is defined as the percentage of stomachs in which a particular prey category occurred and was calculated using the formula: $\%Fi = (ni/ n) \times 100$, where %FI represents the frequency of occurrence of prey category I, *ni* is the number of stomachs containing prey category, and *n* is the total number of stomachs analysed. However, to assess the amplitude and dietary niche overlap of the species, we used the prey category volume (%) data matrix. The Shannon-Wiener index

(Shannon, 1948) measured the niche width of species: $H' = -\Sigma\, pk$ x $\ln pk$, where H' = Shannon-Wiener niche width measure, pk = proportion of individuals collected using the k resource, and ln = the neperian logarithm of the pk value. Dietary niche overlap between species was calculated using the Pianka index, according to: $Ojk = ({}^{n}\sum_{i=j}|P_{ij} - P_{ik}|) / {}^{n}\sum_{i=j} P_{ij}^{2}.$ ${}^{n}\sum_{i=j} P_{ik}^{2}$, where Ojk = Pianka dietary niche overlap between species j and species k; pij = proportion of prey category i = total number of prey categories used by species j; pik = proportion of prey category i in the total of prey categories used by species k, and n = total number of prey categories. Niche overlap was considered low as values <0.40, intermediate at values of 0.40-0.60, and high at values > 0.60 (Grossman, 1986). It should be noted that both analyzes may be biased due to the organization of prey into categories, as well as variation in the prey identification (some prey at order level, others at class level, and so on).

4.1.12 *Statistical analyses*

The permutational variation analysis (PERMANOVA) (Anderson *et al.*, 2008), was used to verify differences in the fish diet by reservoirs based on a Bray-Curtis similarity matrix of volume data (log transformed, x + 1), where the pseudo-F statistic resulting from this analysis was tested by the Monte Carlo method using 999 randomizations. When the PERMANOVA result was significant, we used the permutational analysis of multivariate dispersions (PERMDISP) to verify differences in niche breadth of species between reservoirs (Anderson, 2004), with the pairwise comparisons to determine which species differed significantly, being the pseudo-F statistic results tested by the Monte Carlo method using 999 randomizations. After, we used a principal coordinate analysis (PCoA) to visualized fish diet by reservoirs (individuals of Rosana Reservoir versus individuals of Taquaruçu Reservoir) and the population's niche breadth of same species between reservoirs, both based on a Bray-Curtis dissimilarity matrix (Bray & Curtis, 1957). All the analyses were carried out using the R Programming software version 3.5.3 (R Development Core Team, 2023), using the “vegan” package (Oksanen *et al.*, 2018), and the “ggplot2” package (Wickham, 2016).

4.1.13 Results

4.1.14 *Sample size and prey categories*

A total of 1028 individual fish from 27 species in the Rosana Reservoir and 34 species in the Taquaruçu Reservoir were analysed, covering a total of 41 fish species across both (Supplementary Material - Table S1, S2). There were 815 individuals analysed in the 16 fishes selected to further analysis (Rosana reservoir = 328 individuals; Taquaruçu Reservoir

= 487 individuals), which had consumed 10 prey categories (Supplementary Material - Table S3; Table S4). In the Rosana Reservoir, we observed major consumption of terrestrial invertebrates (allochthonous resources), and in the Taquaruçu Reservoir higher consumption of aquatic insects, microcrustacean and fish (autochthonous resources).

4.1.15 ***Frequency of occurrence and dietary overlap***

The FO analyses of the 16 species indicated differences in fish diet between the reservoirs, with a high occurrence of terrestrial invertebrates and terrestrial plants (allochthonous resources) in the diets of the Rosana Reservoir fishes, but with diets in Taquaruçu Reservoir having higher occurrences of aquatic insects and microcrustaceans (autochthonous resources) (Table 2,3). The smallest niche breadth in the Rosana Reservoir was in the native species *H. marginatus* (H’ = 0.79) and the largest was in the non-native *H. eques* (H’ =1.51), while in Taquaruçu Reservoir, the smallest niche was in the non-native *A. osteomystax* (H’ = 0.93), and the largest was in the native *M. intermedia* (H’ =1.52) (Table 4, 5). There was a high dietary overlap between species in both reservoirs, where it was mainly between the smaller bodied fishes in the Rosana Reservoir (*e.g.*, non-natives *A. dentatus* and *H. eques* versus the native *A. lacustris*), but for the Taquaruçu Reservoir, the overlap was across all species, but with higher levels among the small-bodied fishes (*e.g.,* non-native *A. dentatus*, *H. eques*, *M. lippincotianus*, *R. descalvadensis*, and the natives *A. lacustris*, *H. marginatus*, and *M. intermedia*) (Table 4,5).

4.1.16 ***Differences in diet composition and niche breadth between the reservoirs***

The PERMANOVA of the nine species revealed some significant differences in the diet composition of most fishes between the reservoirs, except for *A. dentatus* and *H. marginatus* (Table 6), and the PERMDISP indicated that there were significant differences in diet among the analysed individuals in five of the nine species between the reservoirs (Table 6). The first two axes of the PCoA of individual by reservoir were significant, explaining 95.35% of the differences (Figure 2), and the PCoA by species between reservoirs revealing the differences in the population's niche breadth (Figure 3,4).

Tabel 2. Rosana Reservoir Frequency of Occurrence of Prey Category (%). * = Non-native species to the Upper Paraná River Basin.

Prey category	**Species**										
	_A. dentatus_*	_A. lacustris_	_H. eques_	_H. marginatus_	_I. labrosus_	_L. platymetopon_*	_P. maculatus_	_P . squamossisimus_*	_S. nasutus_	_S. notomelas_	_T. galeatus_*
	n	n	n	n	n	n	n	n	n	n	n
	20	29	54	30	27	26	26	28	17	32	39
	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO
Aquatic Insect	50.00	27.59	22.22	20.00	100	2.17	73.08	50.00	-	37.50	17.95
Terrestrial invertebrates	100	82.76	57.41	83.33	22.22	-	46.15	3.57	-	46.88	100
Microcrustacean	50.00	13.79	27.78	16.67	3.70	2.17	3.85	-	-	9.38	2.56
Macrocustacean	-	-	-	-	-	-	15.38	85.71	-	-	15.38
Mollusc	-	1.72	3.70	-	100	8.70	100	3.57	5.88	-	-
Fish	-	-	-	-	-	-	7.69	32.14	-	15.63	-
Algae	-	10.34	3.70	3.33	3.70	-	7.69	-	52.94	25.00	-
Terrestrial Plant	15.00	100	35.19	33.33	85.19	19.57	80.77	-	76.47	31.25	38.46
Detritus	-	6.90	37.04	6.67	100	100	34.62	-	82.35	90.63	-
Other	-	3.45	5.56	-	7.41	-	7.69	-	-	-	-

Table 3. Taquaruçu Reservoir Frequency of Occurrence of Prey Category (%). * = Non-native species to the Upper Paraná River Basin.

Prey category	**Species**													
	*A. dentatus**	*A. osteomystax**	*A. lacustris*	*H. eques*	*H. marginatus*	*L. platymetopon**	*M. intermedia*	*M. lippincotianus**	*O. niloticus**	*P. maculatus*	*P . squamosissimus**	*R. descalvadensis**	*S. notomelas*	*T. galeatus**
	n	n	n	n	n	n	n	n	n	n	n	n	n	n
	40	17	46	42	27	41	34	23	24	23	81	36	25	15
	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO	FO
Aquatic Insect	42.50	58.82	100	42.86	59.26	2.44	44.12	39.13	33.33	100	43.18	19.44	44.00	92.00
Terrestrial invertebrates	70.00	100	100	47.62	85.19	-	79.41	47.83	12.50	13.04	-	58.33	44.00	100
Microcrustacean	35.00	23.53	4.35	100	25.93	21.95	52.94	17.39	12.50	13.04	-	2.78	76.00	-
Macrocustacean	2.50	-	6.52	7.14	-	2.44	-	-	-	4.35	75.31	-	4.00	76.00
Mollusc	-	-	13.04	-	-	9.76	-	17.39	-	78.26	3.70	8.33	8.00	15.38
Fish	-	-	-	4.76	-	-	2.94	8.70	8.33	17.39	29.63	44.44	8.00	15.38
Algae	-	-	-	7.14	3.70	-	26.47	69.57	20.83	13.04	-	-	-	15.38
Terrestrial Plant	40.00	-	56.52	11.90	29.63	7.32	23.53	8.70	54.17	47.83	6.17	22.22	24.00	30.76
Detritus	5.00	-	19.57	9.52	-	97.56	14.71	13.04	95.83	60.87	1.23	-	32.00	15.38
Other	2.50	-	2.17	7.14	3.70	-	2.94	8.70	4.17	-	-	2.78	8.00	-

Table 4. Niche breadth (H’) and dietary niche overlap by Pianka Index (Ojk) of species from Rosana Reservoir. Values above 0.60 are considered significant (high overlap) and are marked in bold. *=Non-native species to the Upper Paraná River Basin.

	Dietary niche overlap (Ojk)										
Species	*A. dentatus**	*A. lacustris*	*H. eques**	*H. marginatus*	*I. labrosus*	*L. platymetopon**	*P . maculatus*	*P . squamossisimus**	*S. nasutus*	*S. notomelas*	*T. galeatus**
*A. dentatus** (H’= 1.22)	-	**0.87**	**0.94**	**0.85**	**0.74**	0.63	**0.90**	**0.70**	**0.74**	**0.78**	**0.89**
A. lacustris (H’ = 1.37)	-	-	**0.94**	0.65	**0.80**	0.67	**0.90**	**0.72**	**0.90**	**0.81**	**0.82**
*H. eques** (H’ = 1.51)	-	-	-	**0.72**	**0.87**	**0.80**	**0.92**	**0.75**	**0.88**	**0.91**	**0.87**
H. marginatus (H’ = 0.79)	-	-	-	-	0.62	0.53	0.63	0.59	0.63	0.64	0.54
I. labrosus (H’ = 1.29)	-	-	-	-	-	**0.90**	**0.77**	**0.71**	**0.88**	**0.93**	0.64
*L. platymetopon** (H’ =0.88)	-	-	-	-	-	-	0.65	0.61	**0.84**	**0.97**	0.54
P. maculatus (H’ = 1.33)	-	-	-	-	-	-	-	**0.80**	**0.78**	**0.79**	**0.92**
*P. squamossisimus** (H’ = 1.09)	-	-	-	-	-	-	-	-	0.71	0.71	0.60
S. nasutus (H’ = 1.28)	-	-	-	-	-	-	-	-	-	**0.91**	0.63
S. notomelas (H’ = 1.38)	-	-	-	-	-	-	-	-	-	-	0.69
*T. galeatus** (H’ = 0.81)	-	-	-	-	-	-	-	-	-	-	-

Table 5. Niche breadth (H') and dietary niche overlap by Pianka Index (Ojk) of species from Taquaruçu Reservoir. Values above 0.60 are considered significant (high overlap) and are marked in bold. *=Non-native species to the Upper Paraná River Basin.

Species	**Dietary niche overlap (Ojk)**													
	*A. dentatus**	*A. lacustris*	*A. osteomystax**	*H. eques**	*H. marginatus*	*L. platymetopon**	*M. intermedia*	*M. lippincotianus**	*O. niloticus**	*P. maculatus*	*P. squamossisimus**	*R. descalvadensis**	*S. notomelas*	*T. galeatus**
*A. dentatus** (H' =1.33)	-	**0.86**	**0.79**	**0.95**	**1.00**	**0.72**	**0.91**	**0.80**	**0.78**	**0.82**	**0.73**	**0.89**	**0.89**	**0.96**
A. lacustris (H' = 1.18)	-	-	**0.98**	**0.85**	**0.88**	0.66	**0.83**	**0.75**	**0.72**	**0.89**	**0.71**	**0.86**	**0.76**	**0.93**
*A. osteomystax** (H' = 0.93)	-	-	-	**0.81**	**0.81**	0.60	**0.77**	0.69	0.66	**0.82**	0.66	**0.81**	**0.72**	**0.87**
*H. eques** (H' = 1.48)	-	-	-	-	**0.94**	**0.78**	**0.92**	**0.80**	**0.79**	**0.85**	**0.78**	**0.86**	**0.97**	**0.87**
H. marginatus (H' = 1.31)	-	-	-	-	-	**0.71**	**0.91**	**0.79**	**0.77**	**0.83**	**0.73**	**0.90**	**0.87**	**0.97**
*L. platymetopon** (H' = 1.08)	-	-	-	-	-	-	**0.75**	**0.75**	**0.94**	**0.85**	0.67	0.69	**0.87**	0.65
M. intermedia (H' = 1.52)	-	-	-	-	-	-	-	**0.83**	**0.82**	**0.84**	**0.87**	**0.98**	**0.88**	**0.86**
*M. lippincotianus** (H' = 1.39)	-	-	-	-	-	-	-	-	**0.86**	**0.82**	**0.72**	**0.78**	**0.78**	**0.76**
*O. niloticus** (H' = 1.33)	-	-	-	-	-	-	-	-	-	**0.89**	**0.74**	**0.79**	**0.84**	**0.72**
P. maculatus (H' = 1.43)	-	-	-	-	-	-	-	-	-	-	**0.76**	**0.83**	**0.85**	**0.81**
*P. squamossisimus** (H' =1.17)	-	-	-	-	-	-	-	-	-	-	-	**0.86**	**0.73**	**0.70**
*R. descalvadensis** (H' = 1.34)	-	-	-	-	-	-	-	-	-	-	-	-	**0.79**	**0.90**
S. notomelas (H' = 1.37)	-	-	-	-	-	-	-	-	-	-	-	-	-	0.76
*T. galeatus** (H' = 1.10)	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 6. Results of permutational multivariate analysis of variance (PERMANOVA) and permutational analysis of multivariate dispersions (PERMDISP) of species diet between reservoirs. ROS = Rosana Reservoir; TAQ = Taquaruçu Reservoir. Values in bold denote significant variance ($p \leq 0.05$). *= Non-native species to the Upper Paraná River Basin.

Species	PERMANOVA	Centroid (D)		PERMDISP
		ROS	TAQ	
_A. dentatus_*	$F_{(0.57)} = 1.70$; $p = 0.117$	0.47	0.59	$F_{(0.18)} = 11.97$**; $p = 0.001$**
A. lacustris	$F_{(2.03)} = 6.74$; **$p = 0.001$**	0.50	0.54	$F_{(0.02)} = 1.31$; $p = 0.25$
_H. eques_*	$F_{(3.53)} = 11.46$; **$p = 0.001$**	0.55	0.50	$F_{(0.04)} = 1.92$; $p = 0.16$
H. marginatus	$F_{(0.27)} = 0.85$; $p = 0.052$	0.49	0.56	$F_{(0.08)} = 2.11$; $p = 0.15$
_L. platymetopon_*	$F_{(0.85)} = 6.89$; **$p = 0.001$**	0.15	0.39	$F_{(1.38)} = 2.73$; **$p = 0.001$**
P. maculatus	$F_{(1.67)} = 5.34$; **$p = 0.001$**	0.54	0.51	$F_{(0.01)} = 4.74$; $p = 0.49$
_P. squamossisimus_*	$F_{(1.96)} = 6.18$; **$p = 0.001$**	0.43	0.54	$F_{(0.26)} = 4.11$; **$p = 0.004$**
S. notomelas	$F_{(2.84)} = 10.09$; **$p = 0.001$**	0.43	0.55	$F_{(0.19)} = 5.09$; **$p = 0.002$**
_T. galeatus_*	$F_{(1.16)} = 4.97$; **$p = 0.002$**	0.41	0.55	$F_{(0.18)} = 6.42$; **$p = 0.002$**

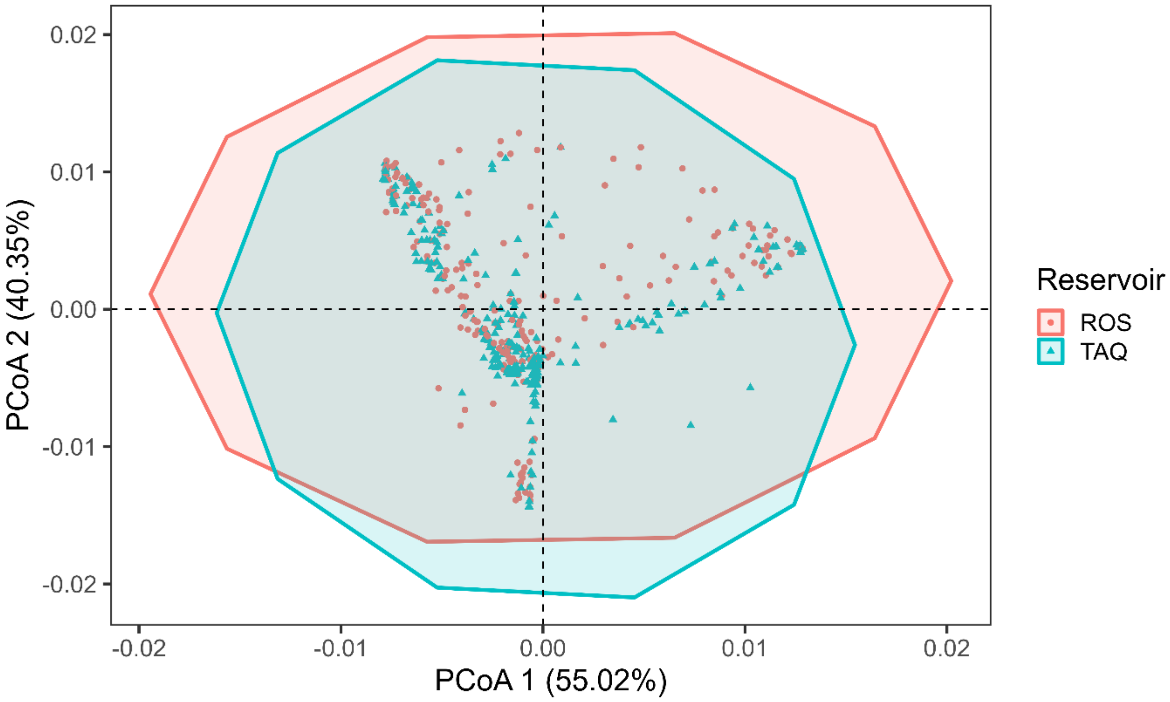

Figure 2. Ordering of the first two PCoA axes for the fish diet from Rosana and Taquaruçu reservoirs.

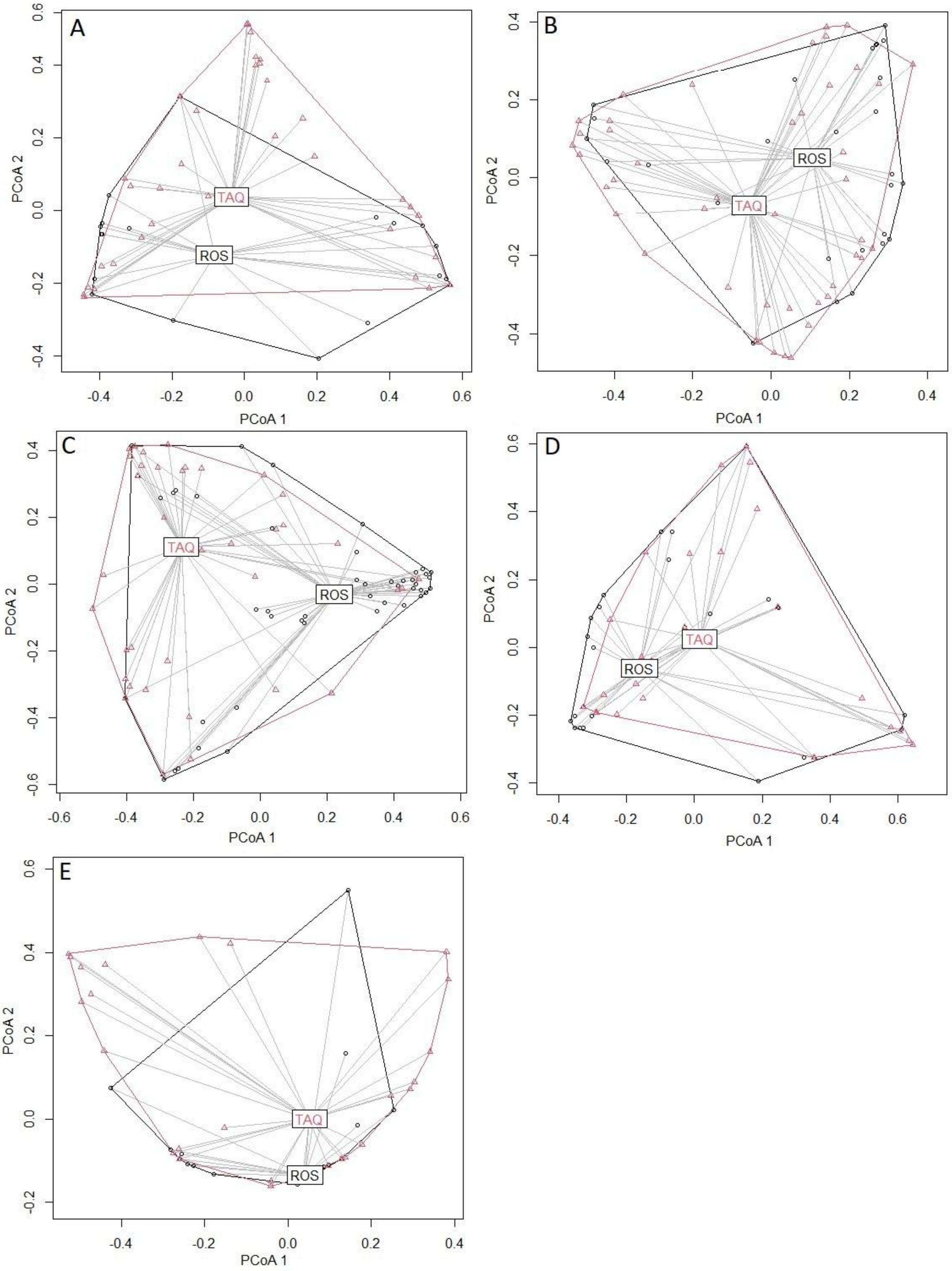

Figure 3. Ordination of population's niche breadth by reservoir using the first two axes of PCoA: A= *A. dentatus* (PCoA explanation = 42%); B = *A. lacustris* (PCoA explanation = 50.4%); C= *H. eques* (PCoA explanation = 78%); D = *H. marginatus* (PCoA explanation = 44.3%); E = *L. platymetopon* (PCoA explanation = 49.8%). ROS = Rosana Reservoir; TAQ = Taquaruçu Reservoir.

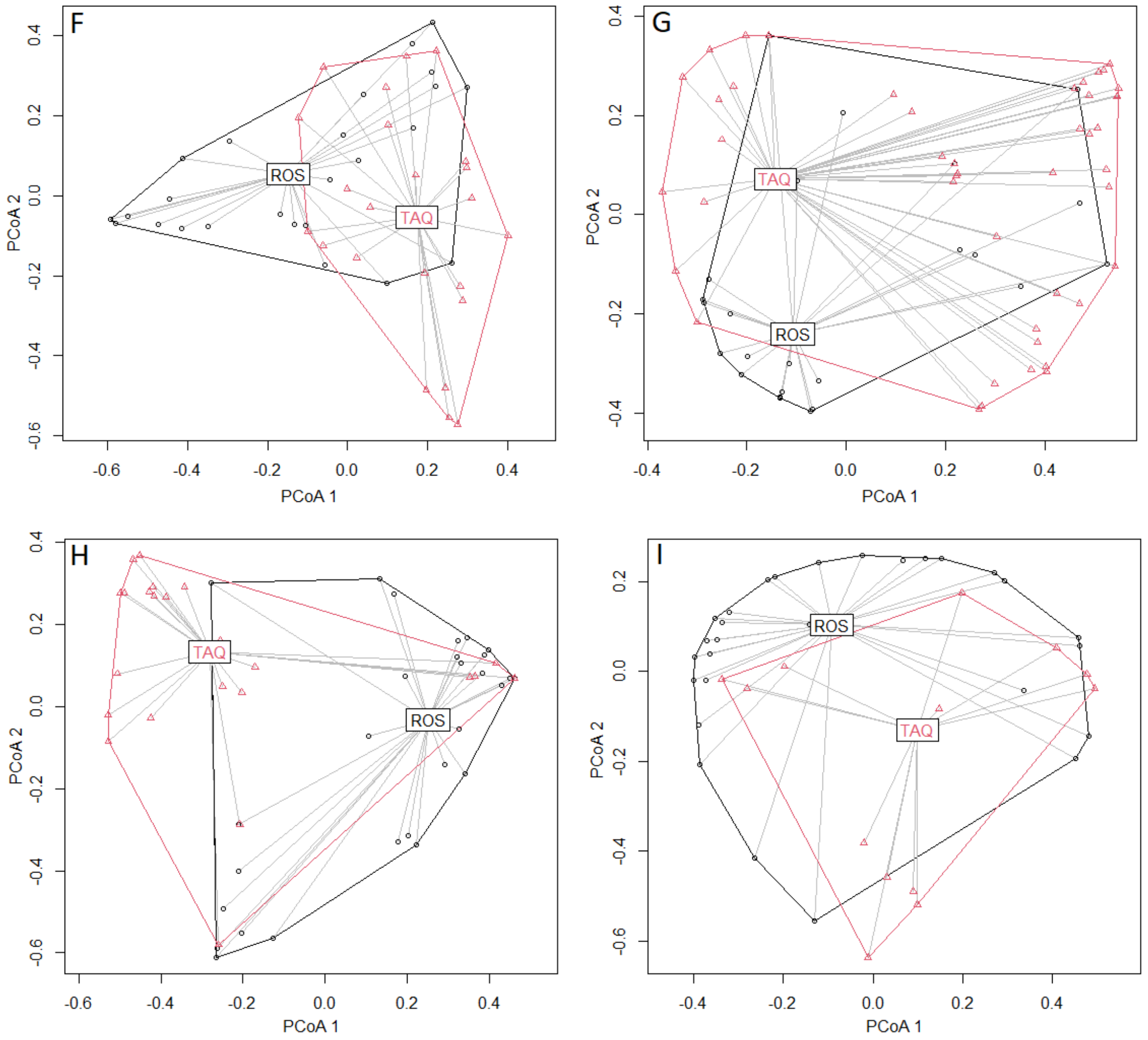

Figure 4. Ordination of population's niche breadth by reservoir using the first two axes of PCoA: F = *P. maculatus* (PCoA explanation = 64%); G = *P. squamossisimus* (PCoA explanation = 72%); H = *S. notomelas* (PCoA explanation = 48%); I = *T. galeatus* (PCoA explanation = 55.7%). ROS = Rosana Reservoir; TAQ = Taquaruçu Reservoir.

4.1.17 Discussion

Across the two reservoirs, dietary analyses were completed on 54 populations belonging to 41 fish species, but with a focus on 16 of these populations where sample sizes enabled robust diet quantification and subsequent analyses. Across these 16 populations and between the two reservoirs, there were significant differences in the diet, resource use, niche breadth, dietary overlap, and intra-individual variation. These results align with the concept of compartmentalization between habitats influenced by the damming, as observed by Nobile *et al.* (2019) in fish communities. While it might have been expected that fishes in neighbouring environments within the same flow type and reservoir cascade would exhibit similar dietary responses in the reservoirs (Santos *et al.*, 2017; Ganassin *et al.*, 2021), the fragmentation of the sites during the 1990s (Casimiro *et al.*, 2017) created two distinct environments. These differences were driven by both intrinsic factors (*e.g.,* differences in water retention times and habitat heterogeneity (Pompeu *et al.*, 2012; Ganassin *et al.*, 2021) and extrinsic ones (*e.g.,* differences in anthropogenic activities in the surroundings, presence of riparian forest, and species introductions (Koushlesh *et al.*, 2023). Within these factors, the introductions of new species into the reservoirs are key, as these alter the fish functional traits present via their adaptive responses (Schmitt *et al.*, 2018; Glassic *et al.*, 2023**)**, even in locations within the same eco-region (Daga *et al.*, 2019). In this way, the Paranapanema River has a long history of biological invasion (Garcia *et al.*, 2018a) where the species interactions in each reservoir could have culminated in the divergent results (Ganassin *et al.*, 2021).

The dominance of allochthonous resources (particularly terrestrial invertebrates), in the diet of fish populations in the Rosana Reservoir is consistent with the findings in Colombia. In this study, was compared the diet of fish from two neighbouring reservoirs of small size and similar flow, but with divergent surroundings and human activities, which culminated in differences in the feeding of populations of the same species (Restrepo-Santamaría *et al.*, 2022). So, the heavily presence of terrestrial invertebrates in the non-native species diet such *A. dentatus*, *H. eques,* and *T. galeatus*, in addition to the native P. *maculatus,* may have influenced the dietary patterns observed in the Rosana Reservoir. Thus, the characteristics of the Rosana Reservoir, including the presence of habitats that facilitate exchange with the terrestrial zone such as larger tributaries, its winding course through forested margins of conservation units, and marginal lagoons were also likely contribute to a high availability of allochthonous resources (Nogueira *et al.*, 2012; Smith *et al.*, 2018). However, the water turbidity of the reservoir is also relatively low, being related with the sedimentation and increase of transparency in part due to it being the last reservoir in the cascade (Santos *et al.*, 2017; Smith *et al.*, 2018), which favours primary production and consequently the abundance of zooplankton that can be utilized by fish (Agostinho *et al.*, 2007). In this way, previous studies conducted in this reservoir have indeed demonstrated a greater reliance on aquatic insects and microcrustaceans in fish diets, particularly in relation to the focus on marginal lagoons and macrophyte beds (Casatti *et al.*, 2003; Pelicice & Agostinho, 2006; Ferrareze *et al.*, 2015). Nonetheless, our study also explored the main channel of the reservoir, providing a more comprehensive understanding of the dietary dynamics in the study area. Run-of-river reservoirs like Rosana Reservoir are more influenced by tributaries, leading to increased water turbidity and availability of allochthonous resources (Nogueira *et al.*, 2012). This reinforces the mesotrophic profile of the reservoir (Ferrareze *et al.*, 2014) and can explain the divergent results observed in comparison to studies focused on marginal lagoons. Consequently, the heterogeneity of habitats and fish community responses in the Rosana Reservoir resemble those of the free-of-dam stretches of the Upper Paraná River floodplain (Agostinho *et al.*, 2007), and our findings contribute to the growing knowledge of the feeding ecology in this environment.

In the Taquaruçu Reservoir, there was a relatively high dietary contribution of autochthonous resources, such as aquatic insects, microcrustaceans and fish by both native and non-native fishes, including *A. lacustris, A. osteomystax*, *H. eques*, *M. intermedia*, *R. descalvadensis*. Additionally, there were notable changes in the diets of *T. galeatus* and *P. maculatus* in comparison to the populations of Rosana Reservoir, which the one increased its consumption of aquatic insects and the second had a larger stomach volume occupied by molluscs. These findings confirm the plasticity of fish species in exploiting food resources in reservoirs (Oliveira *et al.*, 2020; Restrepo-Santamaría *et al.*, 2022; Garcia *et al.*, 2023), which can be influenced by the food availability in the environment (Benneman *et al.*, 2011; Lima *et al.*, 2018). The Taquaruçu Reservoir, with its small watershed, straight-line channel, lack of surrounding forests, and absence of marginal lagoons, as well as sparse and short tributaries, likely experiences limited influx of allochthonous resources (Nogueira *et al.*, 2012). This oligotrophic pattern, characterized by a reliance on autochthonous resources, is common in reservoirs lacking habitat heterogeneity (Ferrareze *et al.*, 2014). So, similar patterns have been observed in other impoundments with major use of detritus, aquatic insects, crustaceans and fish in the diet of fishes from Paranapanema River (Benneman *et al.*, 2011; Lima *et al.*, 2018), and aquatic insects and aquatic plants in the diet of fishes from

Tietê River (Vidotto-Magnoni & Carvalho, 2009; Smith *et al.*, 2018). Thus, these findings highlight the influence of environmental factors on resource availability and subsequent dietary preferences of fish populations in different reservoirs.

The Frequency of Occurrence (FO) analyses partially supported the divergences of the population's diet from the species between reservoirs. High FO levels can indicate large environmental availability of food (Hamidan *et al.*, 2015; Cardoza-Martinez, 2021), as well as the importance of certain preys for some species (Amundsen & Sánchez-Hernández, 2019). In this way, the results observed in the Rosana Reservoir denotes the high availability of terrestrial invertebrates as food resources to the fishes. However, it is important to note that the FO of terrestrial invertebrates in Taquaruçu Reservoir was also high. According to Amundsen & Sánchez-Hernández (2019) the FO index may overestimate the importance of preys ingested accidentally or sporadically, especially in species with a generalist diet. Therefore, a reconciliation of frequency and abundance methods is often a more reliable approach. In the case of the Taquaruçu Reservoir, although the FO of terrestrial invertebrates was high, it was not supported by volumetric data. This discrepancy suggests that these resources may not be highly available in the environment (Hakami *et al.*, 2013; Cardoza-Martinez, 2021). Consequently, it can be assumed that the populations in the Rosana Reservoir exhibit more specialized feeding habits (as supported by the correlation between frequency of occurrence and stomach volume), while the populations in the Taquaruçu Reservoir display more generalist strategies. These differences in feeding strategies can have implications for niche breadth and overlap among populations (Hamidan *et al.*, 2015). In this study, lower dietary overlap was observed in the Rosana Reservoir compared to the Taquaruçu Reservoir. In environments with high food availability, species can display preferences and trophic segregation in their prey resource exploitation (Sánchez-Hernández *et al.*, 2017), as previously observed in the Lower Paranapanema River (Casatti *et al.*, 2003; Pelicice & Agostinho, 2006), Upper Paraná River (Quirino *et al.*, 2015), Iguacu River (Pini *et al.*, 2019), Uruguay River (Neves *et al.*, 2018); and Amazon (Merona & Rankin-de-Merona, 2004). Therefore, these findings highlight the importance of food availability and resource partitioning in shaping the feeding ecology and niche dynamics of fish populations in different river systems.

The high dietary overlap observed in small fish in the Rosana reservoir differs from previous studies in the same environment. It should be noted that this studies where conduced in the Rosana Dam early years, and until then had recorded low overlap between small bodied species, even for those with a similar dietary niche (Casatti *et al.*, 2003; Pelicice &

Agostinho, 2006). By this, our results (based on data of the end of the 20s) can indicate a change in the fish trophic structure overtime, which could have been influenced by the aging of the reservoir with consequent depletion of food resources (Lima *et al.*, 2018). It is noteworthy that the native species, such as *H. marginatus*, displayed a narrower niche compared to non-native species with larger niches that directly overlap with their diet, such as *A. dentatus* and *H. eques*. This suggests that the non-native species are exploiting similar resources as the native ones, potentially leading to competition for food resources. In the Taquaruçu Reservoir, the situation is concerning as all species showed dietary overlap, indicating a potential food restriction in this environment. When the food availability is not ideal, species tend to display more generalist behaviour and share resources. (Sánchez-Hernández *et al.*, 2017). This situation can be further aggravated by the presence of non-native species due to them often being superior competitors (Schmitt *et al.*, 2018; Glassic *et al.*, 2023). However, it is worth noting that studies have shown species coexisting with high dietary overlap by partitioning resources to avoid direct competition, as observed in North-eastern Brazil (Figueiredo *et al.*, 2015), Central China (Liu *et al.*, 2019), and South Australia (Hossain *et al.*, 2017). Therefore, further research is needed to understand the mechanisms of coexistence and resource partitioning in the Taquaruçu Reservoir to better assess the potential impacts of dietary overlap on the fish community.

The significant results obtained from the PERMANOVA analysis, indicating differences in the use of resources between populations in the reservoirs, further support the findings of our study. This confirms the feeding plasticity exhibited by fish in reservoirs, which is dependent on food availability (Delariva *et al.*, 2013; Oliveira *et al.*, 2020; Restrepo-Santamaría *et al.*, 2022; Garcia *et al.*, 2023). The flexibility in diet observed in species such as *A. lacustris*, *P. maculatus*, and *P. squamossisimus*, which are widely distributed in Brazilian reservoirs, align with previous studies on their behaviour (Agostinho *et al.*, 2007; Vidotto-Magnoni, 2009; Benneman *et al.*, 2011). However, it is worth noting that certain small-bodied fishes do not exhibit significant changes in their population's diet between reservoirs, which can be considered as a dynamic characteristic of these species. *Aphyocharax dentatus*, for example, displays a generalist/opportunist feeding behaviour with a broad niche breadth, which may contribute to the lack of significant differences observed between their populations in the two reservoirs. This behaviour is likely influenced by the seasonal dynamics of its native habitat in the Brazilian Pantanal (Novakowski *et al.*, 2008). On the other hand, *H. marginatus* tends to specialize as an insectivore (Fragoso-Moura *et al.*, 2017), but it can exhibit omnivorous behaviour when the preferred resources are not available in the environment, as we observed in our study. Therefore, *A. dentatus* and *H. marginatus* could potentially have a competitive relationship, as indicated by the high dietary overlap between these species in both reservoirs, particularly considering that *H. marginatus* displayed a smaller niche breadth in the Rosana Reservoir.

The results of the PERMDISP analysis, which examined intra-population variations between reservoirs, revealed that non-native species such as *A. dentatus*, *L. platymetopon*, *P. squamossisimus* and *T. galeatus* showed high levels of intra-variation, indicating their adaptative capacity in exploiting food resources (Vidotto-Magnoni, 2009; Benneman *et al.*, 2011). This could be attributed to their ability to randomly consume a variety of food items, including aquatic insects, detritus, microcrustaceans, macrocrustaceans, molluscs, and terrestrial plants in the Taquaruçu Reservoir. Non-native species often have a broader niche breadth, allowing them to better exploit available food resources (Novakowski *et al.*, 2008) and they tend to exhibit opportunistic behaviour in response to the changing availability of prey resources (Garcia *et al.*, 2018b). In contrast, native species, such as *A. lacustris* and *P. maculatus*, which are known to display generalist/opportunistic feeding behaviour in Brazilian reservoirs (Vidotto-Magnoni, 2009; Benneman *et al.*, 2011; Smith *et al.*, 2018), demonstrated low intra-population variation in the Taquaruçu Reservoir and exhibited a tendency to rely more on autochthonous food items (Vidotto-Magnoni & Carvalho, 2009; Lima *et al.*, 2018; Restrepo-Santamaría *et al.*, 2022). These results suggest that native species may have a limit to their dietary plasticity, while non-native species appear to have a wider range of food resource exploitation (Schmitt *et al.*, 2018; Glassic *et al.*, 2023).

In summary, we describe the diet and feeding strategies of fish from two neighbour reservoirs and found divergences, with could be related with environmental heterogeneity. In this way, the fish community of the Rosana Reservoir exploits more allochthonous resources and display behaviour which tends to specialist, while Taquaruçu Reservoir populations is restricted to the use of autochthonous resources and behaves as generalist. We also found a high dietary niche overlap driven by non-native species, especially in the Taquaruçu Reservoir. Species changed their diet patterns between reservoirs demonstrating feeding plasticity, however, native species had a lower range of flexibility than non-native species, reinforcing the adaptive capacity of the latter to colonize new environments. So, we conclude that the Rosana Reservoir populations response closer to those of free-of-dam stretches of the Upper Paraná River floodplain, while those from Taquaruçu reservoir behaves as most in the Brazilian reservoirs, corroborating the compartmentalization tendency in the cascade of reservoirs.

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4.1.21 Supplementary files

4.1.22 Material and Methods

4.1.23 *Study Area*

The Paranapanema River rises in the “Serra de Paranápiacaba”, the Atlantic Plateau of the municipality of Capão Bonito (Sâo Paulo State), Southeast Brazil (Sampaio, 1944). One of the main tributaries on the left bank of the Upper Paraná River, the river runs through 930 km, where about 330 km from its main channel define the borders between the Southeast of the Sâo Paulo State (SP) and North of the Paraná State (PR) (Maack, 1981). Due to your hydrographic of slopes, the Paranapanema River has been exploited for hydropower, where the main channel was transformed into a cascade of eleven reservoirs (Duke Energy, 2008). Its course is divided into three main sections: Upper, Middle, and Lower Paranapanema (Sampaio 1944) (Figure S1). The Lower Paranapanema River begins after Salto Grande Falls (currently flooded by the Salto Grande Reservoir), covering from upstream to downstream the reservoirs of Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu, and Rosana (Duke Energy, 2008). The stretches studied belongs to the areas of influence of the last two dams, Rosana and Taquaruçu (Figure S1 to S3).

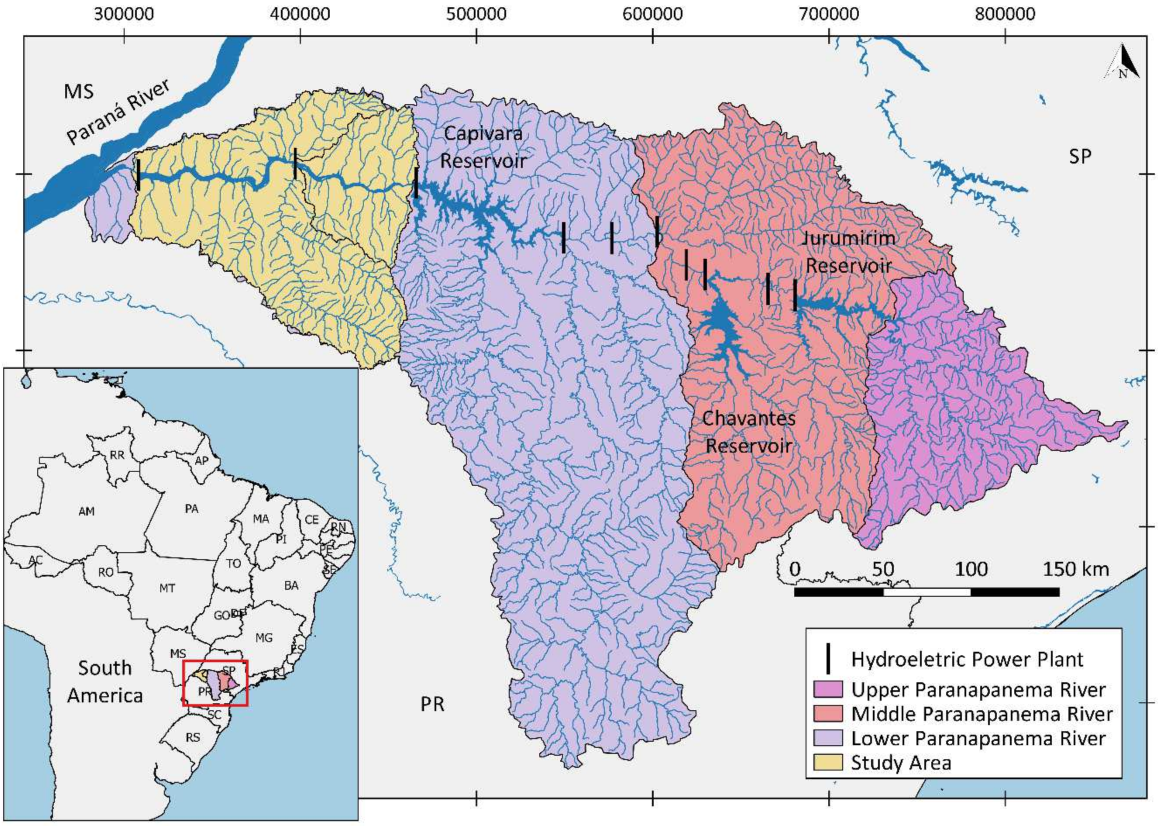

Figure 5 (S1). The Paranapanema River Basin with the three main sections and the study area in the Lower Paranapanema River. MS = Mato Grosso do Sul State; PR = Paraná State; SP = São Paulo State.

4.1.24 *Samplings*

Our samplings were performed quarterly from September 2018 to September 2020: Rosana Reservoir – site 1 (22.601220 S, 52.165324 W), site 2 (22.601569, 52.160614), site 3 (22.600590, 52.160098), site 4 (22.636232, 52.161589), site 5 (22.612902, 52.162611), site 6 (22.636299, 52.158774), and site 7 (22.599940, 52.159673). Taquaruçu Reservoir - site 1 (22°39’15.0”S 51°40’42.0”W); site 2 (22°39’37.0”S 51°37’53.8”W); site 3 (22°41’24.7”S 51°34’50.5”W); site 4 (22°41’10.8”S 51°32’20.9”W), site 5 (22.676369 S, 51.714037 W), site 6 (22.667733 S, 51.683496 W), and site 7 (22.657963 S, 51.658144 W).

4.1.25 *Diet analysis*

In laboratory, individuals had their stomachs removed and the content was analysed under a stereomicroscope, being the preys identified at the lowest taxonomic level with help of specific literature (Mugnai et al, 2010). The volume (V) of each stomach content was obtained by compression in a millimeter Petri dish, with a volume given in mm^3 and later transformed into mL (Hellawell & Abel, 1971). The prey items was grouped into 10 categories and represented in percentage (%), as follow: Algae (Filamentous Algae); Aquatic Insects (Aquatic Insect Fragment, Coleoptera Larvae, Coleoptera Pupe, Diptera Larvae, Diptera Pupe, Ephemeroptera Nymph, Odonata Nymph and Trichoptera Nymph); Detritus (Inorganic Detritus, Organic Detritus); Fish (Fish, Fish Scale); Macrocrustacean (Crab, Shrimp); Microcrustacean (Cladocera, Copepoda, Microcrustacean Fragment, Ostracoda); Mollusc (Bivalvia, Gastropoda); Other (Microplastic); Terrestrial Plant (Fruit, Leaf, Stick, Seed), and Terrestrial Invertebrates [Terrestria Acari, Aranae, Blattodea (Isoptera), Blattodea Adult, Coleoptera Adult, Diplopoda, Diptera Adult, Ephemeroptera Adult, Hemiptera Adult, Hymenoptera Adult, Lepidoptera Adult, Terrestrial Insect Fragment and Thysanoptera Adult]. After, the prey category was organized into food resources, based on the origin of prey categories: Autochthonous (Aquatic Insect; Microcrustacean; Macrocrustacean; Mollusc; Fish, Algae and Detritus), and allochthonous (Terrestrial invertebrates; Terrestrial Plants; and Others).

The trophic guild was investigated by the percentage of the volume of each prey category from the species, where an adapted step by step procedure was performed according to Delariva et al., 2013. Step 1: 50% or more of detritus/sediment in the stomachs: detritivore; Step 2: 50% of more of algae in the stomach: algivores; Step 3: 50% or more of plant material (supplemented with algae) in the stomachs: herbivores; Step 4: 50% or more of plankton in the stomachs: planktivores; Step 5: 50% or more of aquatic insects in the stomachs: aquatic insectivores; Step 6: 50% or more of terrestrial insects in the stomachs: terrestrial insectivores; Step 7: 50% or more of decapods in the stomachs: carcinophages; Step 8: 50% or more of various invertebrates in the stomachs: invertivores; Step 9: 50% or more of fish (including scales) in the stomachs: piscivores; Step 10: none of the above statements and adding items of plant and animal origins: omnivores.

To investigate the feeding strategy of the species, the prey categories were represented as ‘frequency of occurrence’ (FO) and the ‘relative abundance of prey’ (RAP) according to Hamidan et al., 2015, with adaptations. To calculate the frequency of occurrence (defined as the percentage of stomachs in which that prey occurred) was used: $\%Fi = (ni/ n) \times 100$, where: ni = number of stomachs containing prey category, and n = total number on stomachs analysed. To the relative abundance of prey (defined as the percentage of total volume of prey in all stomachs analysed), was used: $\%RAP = (\Sigma Si/\Sigma St) \times 100$, where Si = the stomach contents (volume) composed of investigated prey, and St = the total stomach contents (volume) of all stomachs analysed. Then, feeding strategy diagrams were constructed following Costello’s (1990) method with the modifications suggested by Amundsen et al.

(1996). By the observation of the points distribution in the diagram, it is possible to extract information about the feeding strategy and the importance of prey for the species: the feeding strategy is represented in the vertical axis from the bottom (generalization) to the top (specialization), and the prey importance is represented in the horizontal axis from the diagonal of the lower left (rare prey) to upper right (dominant prey) (Amundsen et al., 1996).

4.1.26 Results

A total of 1028 individuals were analysed into 27 populations from Rosana Reservoir and 34 populations from Taquaruçu Reservoir, concerning 41 species of the Lower Paranapanema River in a total of 38 prey items (Table S1 and Table S2). There were 815 individuals analysed in the 16 fishes selected to further analysis (Rosana reservoir = 328 individuals; Taquaruçu Reservoir = 487 individuals), which had consumed 10 prey categories (Supplementary Material - Table S3; Table S4). Of all prey items observed, 20 had autochthonous origin and 18 allochthonous origin, where fish varied the use of these resources between reservoirs (Figure S4, Figure S5). The Frequency of Occurrence (FO) and the Relative Abundance of Prey (RAP) demonstrated the difference in the use of food resources, providing the construction of 24 feeding strategy diagrams (Figure S6 to Figure S9), were most of the species showed a generalist feeding strategy, except to *A. osteomystax, L. platymetopon* and *T. galeatus* (Table S5, Figure S6 to Figure S9). Of this, was possible to defined eight trophic guilds: Algivore (one species); Aquatic insectivore (two species); Carcinophage (one species); Detritivore (three species); Herbivore (one specie, considering the sum between algae and plant volume); Invertivore (two species); Omnivore (eight species), and Terrestrial invertivore (two species) (Table 5). Four species presented variations in trophic guild by reservoir, *A. lacustris*, *H. marginatus, P. maculatus* and *S. notomelas* (Table S5).

Table 7 (S1). Total volume of food (prey item) identified in stomach contents of fishes from the Rosana Reservoir, Lower Paranapanema River. * = Non-native species to the Upper Paraná River.

	Prey item	**Rosana Reservoir Prey Itens (Volumetric)**																											
		Species																											
		A. affinis	*A. dentatus**	*A. lacustris*	*C. britskii*	*E. trilineata*	*H. eques**	*H. malabaricus*	*H. marginatus*	*I. labrosus*	*L. friderici*	*L. platymetopon**	*L. similima*	*M. lippincotianus**	*M. Paranánus*	*P. maculatus*	*P. squamossisimus**	*P. stramineus*	*R. descalvadensis**	*R. vulpinus**	*Rhinelоricaria sp.*	*S. brevipinna**	*S. intermedius*	*S. marginatus**	*S. nasutus*	*S. notomelas*	*S. papaterra**	*T. galeatus**	**Total volume of prey**
		n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
		5	20	29	6	3	54	8	30	27	4	26	3	2	4	26	28	8	6	4	3	10	5	3	17	32	12	39	414
Arachnid	Terrestrial Acari	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0.075	0	0	0	0	0	0	0	0	0.002	0	0.002	0.08
	Araneae	0	0.011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.03	0.041
Insect	Aquatic Insect Fragment	0	0	0.025	0	0	0.031	0	0.033	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.067	0	0	0.156
	Blattodea Adult	0	0	0	0.021	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.021
	Coleoptera Adult	0	0	0.025	0	0	0	0	0	0	0	0	0	0	0	4.11	0	0.02	0	0	0	0	0	0	0	0	0	20.01	24.167
	Coleoptera Larvae	0	0	0.02	0	0	0	0	0	0.002	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0.875	0.907
	Diptera Adult	0	0.019	0	0	0	0	0	0.014	0.005	0	0	0	0	0	0.005	0	0.04	0	0	0	0	0	0	0	0	0	0	0.083
	Diptera Larvae/Pupe	0	0.017	0.059	0	0.001	0	0	0	0.025	0	0.005	0	0	0	0.052	0	0.001	0	0	0	0	0	0	0	0	0	0.002	0.162
	Ephemeroptera Nymph	0	0.03	0.01	0.01	0	0.029	0	0.005	0.049	0	0	0	0	0	0.01	0	0.04	0	0	0	0	0	0.01	0	0	0.006	0.025	0.224
	Hemiptera Adult	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0.012	0	0	0	0	0	0	0	0	0	0	0	0.412	0.434
	Hymenoptera Adult	0	0.143	0.333	0	0	0	0	0.022	0.02	0.05	0	0	0	0	4.13	0	0.085	0	0	0	0	0	0	0	0	0.001	18.32	23.108
	Lepidoptera Adult	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0.015	0	0	0	0	0	0	0	0	0	0.025	0.041
	Odonata Nymph	0	0.002	0.202	0.092	0	0.023	0	0	0	0	0	0	0	0	0.052	0.895	0.01	0	0	0	0	0	0	0	0	0.005	0.042	1.324
	Terrestrial Insect Fragment	0.001	0.044	0.209	0.027	0.085	0.133	0	0.232	0.007	0.221	0	0	0	0	0.001	0	0.2	0.028	0	0	0	0	0.015	0	0.084	0.006	0	1.293
	Trichoptera Nymph	0	0	0.01	0	0	0	0	0	0.009	0	0	0	0	0	0.144	0	0	0.003	0	0.005	0	0	0	0	0	0.001	0	0.172
ac	Cladocera	0	0.005	0.03	0	0	0.017	0	0	0.001	0	0.005	0	0	0	0.005	0	0	0	0	0	0	0	0	0	0	0.001	0	0.064

		Rosana Reservoir Prey Itens (Volumetric)																											
		Species																											
	Prey item	_A. affinis_	_A. dentatus_*	_A. lacustris_	_C. britskii_	_E. trilineata_	_H. eques_*	_H. malabaricus_	_H. marginatus_	_I. labrosus_	_L. friderici_	_L. platymetopon_*	_L. similima_	_M. lippincottianus_*	_M. Paranánus_	_P. maculatus_	_P. squamossissimus_*	_P. stramineus_	_R. descalvadensis_*	_R. vulpinus_*	_Rhineloricaria sp._	_S. brevipinna_*	_S. intermedius_	_S. marginatus_*	_S. nasutus_	_S. notomelas_	_S. papaterra_*	_T. galeatus_*	**Total volume of prey**
		n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
		5	20	29	6	3	54	8	30	27	4	26	3	2	4	26	28	8	6	4	3	10	5	3	17	32	12	39	414
	Copepoda	0	0.187	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.188
	Decapoda (Crab)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.38	0	0	0	0	0.38
	Decapoda (Shrimp)	0	0	0	0	0	0	0.25	0	0	0	0	0	0	0	0.24	19.44	0	0	0.02	0	0	0	0	0	0	0	0.244	20.194
	Microcrustacean Fragment	0	0	0.025	0	0	0	0	0.095	0	0	0	0	0	0	0	0	0	0.057	0	0	0	0	0	0	0.025	0	0	0.202
	Ostracoda	0	0	0.001	0	0.001	0.022	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0	0	0.025
Mollusc	Bivalvia	0	0	0.002	0.001	0	0.003	0	0	0.524	0.355	0.031	0.03	0	135	0.357	0	0	0	0	0.07	0	0.765	0.02	0.1	0	0.022	0	137.28
	Gastropoda	0	0	0.047	0	0	0	0	0	0.037	0.01	0	0.035	0	0	0.368	0.005	0	0	0	0	0	0.01	0.002	0	0	0.045	0	0.5595
Fish	Fish	0	0	0	0	0	0	6.875	0	0	0	0	0	0	0	0.05	15.22	0	0	20	0	0	0	0	0	0	0	0	42.145
	Fish Scale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0	0	0	0	0	0.025	0	0	0.03
Algae	Filamentous Algae	0	0	0.03	0	0	0.006	0.05	0.01	0.001	0	0	0	0.137	0	0.006	0	0	0	0	0	0	0.28	0	1.075	0.054	0	0	1.648
Terrestrial Plant	Plant Fragment (Fruit)	0	0	0.036	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.425	0.461
	Plant Fragment (Leaf And Stick)	0.005	0.012	0.39	0.015	0.072	0.048	0.05	0.06	0.105	0.137	0.083	0.001	0	0	1.52	0	0	0.001	0	0	0.05	0.959	0.001	1.707	0.043	0.03	0.325	5.614
	Plant Fragment (Seed)	0	0	0.435	0	0	0	0	0	0.01	0	0	0	0	0	0.351	0	0	0	0	0	0	0.025	0	0	0.001	0	0.025	0.847
Detritus	Inorganic Detritus	0	0	0.015	0	0	0.012	0	0.005	0.038	0	0.064	0	0	0	0.03	0	0	0	0	0	0	0	0	0.205	0.038	0.015	0	0.4221

	Prey item	**Rosana Reservoir Prey Itens (Volumetric)**																											
		Species																											
		A. affinis	_A. dentatus_*	_A. lacustris_	_C. britskii_	_E. trilineata_	_H. eques_*	_H. malabaricus_	_H. marginatus_	_I. labrosus_	_L. friderici_	_L. platymetopon_*	_L. similima_	_M. lippincottianus_*	_M. Paranánus_	_P. maculatus_	_P. squamossisimus_*	_P. stramineus_	_R. descalvadensis_*	_R. vulpinus_*	_Rhineloricaria sp._	_S. brevipinna_*	_S. intermedius_	_S. marginatus_*	_S. nasutus_	_S. notomelas_	_S. papaterra_*	_T. galeatus_*	**Total volume of prey**
		n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
		5	20	29	6	3	54	8	30	27	4	26	3	2	4	26	28	8	6	4	3	10	5	3	17	32	12	39	414
	Organic Detritus	0.06	0	0.015	0	0.05	0.067	0	0.003	0.615	0.3	1.226	0.01	0	16	0.155	0	0	0.001	0	0	0.177	0.12	0	1.16	0.401	0.326	0	20.686
Other	Microplastic	0	0	0.001	0.001	0	0.001	0	0	0.001	0	0	0	0	0	0.002	0	0	0	0	0	0	0	0.002	0	0	0	0	0.006
Total Volume Of Specie		0.066	0.48	1.92	0.167	0.209	0.391	7.225	0.479	1.448	1.139	1.414	0.076	0.137	151	11.60	35.635	0.421	0.096	25.25	0.075	0.227	2.159	0.43	4.247	0.74	0.458	40.77	288.265

Table 8 (S2). Total volume of food (prey item) identified in stomach contents of fishes from the Taquaruçu Reservoir, Lower Paranapanema River. * = Non-native species to the Upper Paraná River Basin.

		Taquaruçu Reservoir Prey Itens (Volumetric)																																		
		Species																																		
	Prey item	*A. affinis*	*A. anisitsi*	*A. dentatus**	*A. osteomystax**	*Ac. lacustris*	*A. lacustris*	*C. britskii*	*C. kelberi**	*E. trilineata*	*G. inaequilabiatus**	*H. ancistroides*	*H. eques**	*H. malabaricus*	*H. marginatus*	*I. labrosus*	*L. araguaiae**	*L. platymetopon**	*M. intermedia*	*M. lippincotianus**	*O. eigenmanni**	*O. niloticus**	*P. maculatus*	*P. platana**	*P. squamosissimus**	*R. descalvadensis**	*Rineloricaria sp.*	*S. brevipinna**	*S. insculpta*	*S. maculatus*	*S. marginatus**	*S. nasutus*	*S. notomelas*	*T. galeatus**	*T. paraguaiensis**	**Total volume of prey**
		n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
		13	10	40	17	6	46	10	6	3	4	12	42	8	27	10	3	41	34	23	4	24	23	4	81	36	3	7	8	5	10	11	25	13	5	614
Arachnid	Terrestrial Acari	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0.001	0	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.007
	Araneae	0	0	0	0.08	0	0.0341	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1241
Insect	Aquatic Insect Fragment	0	0.005	0.022	0	0	0.0002	0	0	0	0	0	0.015	0	0.0025	0	0.002	0	0.01	0	0	0.00225	0	0.1	0	0.003	0	0	0	0	0	0	0.02	0.05	0	0.231
	Blattodea (Isoptera)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
	Coleoptera Adult	0	0.008	0	0.1526	0	0.6424	0	0	0	0	0	0	0.05	0.022	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.59	0	8.475
	Coleoptera Larvae	0	0	0.056	0	0	0.023	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0.032	0	0	0	0	0	0	0	0.001	0.028	0	0.15
	Coleoptera Pupe	0	0	0.006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.006
	Collembola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.006	0	0	0.006
	Diptera Adult	0	0	0.002	0.0046	0	0.139	0	0	0.0001	0	0	0.001	0	0.002	0.01	0	0	0.02	0	0.001	0	0.002	0	0	0	0	0	0	0	0	0	0.002	0.02	0	0.203
	Diptera Larvae/Pupe	0.003	0	0.004	0	0	0.0091	0	0	0.43	0	0	0.0005	0	0.006	0.298	0	0.01	0	0.001	0	0.0051	0.139	0	0	0.005	0	0	0	0	0.001	0	0.00075	0	0.051	0.963
	Ephemeroptera Adult	0	0	0.001	0	0	0.03	0	0	0	0	0	0.012	0	0	0	0	0	0	0	0	0	0	0	0	0.006	0	0	0	0	0	0	0	0	0	0.049
	Ephemeroptera Nymph	0.001	0.021	0.0619	1.45	0	0.134	0.03994	0.075	0.321	0	0	0.043	0	0.074	0.012	0.002	0	0.172	0.1494	0.002	0.008	0.0852	0	0	0.068	0	0	0	0.106	0.0645	1.002	0.03	0	0.003	3.923
	Hemiptera Adult	0	0	0	0.2106	0	0.016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0.018	0.008	0	0.272
	Hymenoptera Adult	0	0	0.019	0.0024	0	0.6648	0	0	0	0	0	0	0	0.119	0	0	0	0.308	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0025	0.75	0	1.8657

Taquaruçu Reservoir Prey Itens (Volumetric)

Species

	Prey item	*A. affinis*	*A. anisitsi*	*A. dentatus**	*A. osteomystax**	*Ac. lacustris*	*A. lacustris*	*C. britskii*	*C. kelberi**	*E. trilineata*	*G. inaequilabiatus**	*H. ancistroides*	*H. eques**	*H. malabaricus*	*H. marginatus*	*I. labrosus*	*L. araguaiae**	*L. platymetopon**	*M. intermedia*	*M. lippincotianus**	*O. eigenmanni**	*O. niloticus**	*P. maculatus*	*P. platana**	*P. squamosissimus**	*R. descalvadensis**	*Rineloricaria sp.*	*S. brevipinna**	*S. insculpta*	*S. maculatus*	*S. marginatus**	*S. nasutus*	*S. notomelas*	*T. galeatus**	*T. paraguaiensis**	**Total volume of prey**
		n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
		13	10	40	17	6	46	10	6	3	4	12	42	8	27	10	3	41	34	23	4	24	23	4	81	36	3	7	8	5	10	11	25	13	5	614
	Lepidoptera Adult	0	0	0.003	0	0	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	0	0	0	0	0	0	0	0	0	0.003	0	0	0	0.012
	Lepidoptera Pupe	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
	Odonata Nymph	0	0.03	0.002	2.99	0	5.558	0.00925	0	0.3	0.001	0	0.004	0	0.02	0	0	0	0.051	0.002	0.007	0	1.0811	0	4.1974	0	0	0	0	2	0.241	0	0	6.552	0.008	23.05
	Terrestrial Insect Fragment	0	0.041	0.3689	0	0	0.0916	0	0	0	0.02	0	0.0391	0	0.097	0	0.015	0	0.072	0.218	0	0.011	0.002	0	0	0.0661	0	0	0	0	0	0	0.015	0	0	1.056
	Trichoptera Nymph	0	0	0.001	0.0004	0	0.004	0	0	0.3	0	0	0.00025	0	0	0.02	0	0	0.028	0	0	0	0.381	0	0.005	0	0	0	0	0	0	0	0	0	0.015	0.754
	Thysanoptera Adult	0	0	0	0.0018	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001
Myriapoda	Diplopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0.5
Crustacean	Cladocera	**0**	0	0.013	0.042	0	0.001	0	0	0	0	0	0.1101	0	0	0	0	0.02	0.026	0.001	0	0	0.001	0	0	0	0	0	0	0	0	0	0.02955	0	0	0.243
	Copepoda	0	0	0.0525	0.2	0	0.001	0	0	0	0	0	0.0158	0	0.0001	0	0	0.06	0	0	0	0.0042	0.05	0	0	0.001	0	0	0	0	0	0	0	0	0	0.384
	Ostracoda	**0**	0	0	0	0	0	0	0	0.0001	0	0	0.006	0	0	0.36	0	0.352	0	0.016	0	0	0.1	0	0	0	0	0	0	0	0	0	0.0125	0	0.3385	1.185
	Microcrustacean Fragment	0	0.007	0.139	0	0	0	0	0	0	0	0	0.002	0	0.098	0	0	0	0.375	0	0	0	0	0	0	0	0	0	0	0	0	0	0.268	0	0	0.889
	Decapoda (Shrimp)	0	0	0.001	0	0	0.036	0	0.0012	0	0	0	0.019	1.35	0	0	0	0.05	0	0	0	0.002	0.05	0	37.7669	0	0	0	0	0	0.15	0	0.002	0.05	0	39.48

		Taquaruçu Reservoir Prey Itens (Volumetric)																																		
		Species																																		
	Prey item	*A. affinis*	*A. anisitsi*	*A. dentatus**	*A. osteomystax**	*Ac. lacustris*	*A. lacustris*	*C. britskii*	*C. kelberi**	*E. trilineata*	*G. inaequilabiatus**	*H. ancistroides*	*H. eques**	*H. malabaricus*	*H. marginatus*	*I. labrosus*	*L. araguaiae**	*L. platymetopon**	*M. intermedia*	*M. lippincotianus**	*O. eigenmanni**	*O. niloticus**	*P. maculatus*	*P. platana**	*P. squamosissimus**	*R. descalvadensis**	*Rineloricaria sp.*	*S. brevipinna**	*S. insculpta*	*S. maculatus*	*S. marginatus**	*S. nasutus*	*S. notomelas*	*T. galeatus**	*T. paraguaiensis**	**Total volume of prey**
		n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
		13	10	40	17	6	46	10	6	3	4	12	42	8	27	10	3	41	34	23	4	24	23	4	81	36	3	7	8	5	10	11	25	13	5	614
Mollusc	Bivalvia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.303	0	0.0395	0	0	0.03	0	0.06	0	0.6	0.0025	0.015	0	0	0	0	0	0	0	0.011	1.061
	Gastropoda	0	0	0	0	0	1.095	0	0	0.0001	0	0	0	0	0	0.081	0	0.025	0	0.0866	0.02	0	2.165	0	0.0001	0	0	0	0	0	0.4	0.0828	0.002	0.0083	0.043	4.008
Fish	Fish	0	0	0	0	11.3015	0	0	5.35	0	0.8	0	0	39.052	0	0	0	0	0	0	0	0.112	0.001	0	28.3006	0	0	0	0	3	0.2	0	0	0	0	88.11
	Fish Scale	0	0	0	0	0	0	0	0	0	0	0	0.00035	0.05	0	0	0	0	0.008	0.0011	0	0	0.013	0	0.02	0.139	0	0	0	0	0	0	0.006	0.024	0	0.261
Algae	Filamentous Algae	0	0	0	0	0	0	0	0	0	0.0001	0.01	0.005	0	0.0001	0.001	0	0	0.148	1.2793	0	0.2253	0.045	0	0	0	0	0	0	0	0	2.1091	0	0.07	0	3.892
Terrestrial Plant	Plant Fragment (Leaf And Stick)	0.0012	0.01	0.083	0	0	0.1596	0	0	0	0.004	0.01	0.009	0	0.047	0.01	0.01	0.021	0.121	0.2012	0	0.404	0.2462	0	0.493	0.016	0	0.015	0	0	0.101	9.38	0.031	0.17	0.005	11.54
	Plant Fragment (Seed)	0	0	0	0	0	0.025	0	0	0	0	0	0.002	0	0	0	0	0	0.001	0	0	0	0.4205	0	0	0	0	0	0	0	0	0.0004	0.005	0.01	0	0.463
Detritus	Inorganic Detritus	0.011	0	0	0	0	0.013	0	0	0	0	0.08	0.007	0	0	0.001	0	0.055	0.016	0.005	0.01	0.0736	0	0.064	0.025	0	0.015	0	0	0	0	0	0.02	0	0	0.395
	Organic Detritus	0.3393	0	0.006	0	0	0.023	0.005	0	0.02	0.2005	0.263	0.003	0	0	0.503	0	1.6652	0.006	0.294	0.11	0.7455	1.6752	0	0	0	0	0.23	0.33	0	0	0.3565	0.115	0.07	0.604	7.564
Other	Microplastic	0	0	0.001	0	0	0.0001	0	0	0	0	0	0.0003	0	0.0001	0	0	0	0.0001	0.0002	0	0.0001	0	0	0	0.0001	0	0	0	0	0	0	0.0002	0	0	0.002

Prey item	Taquaruçu Reservoir Prey Itens (Volumetric)																																		
	Species																																	
	A. affinis	_A. anisitsi_	_A. dentatus*_	_A. osteomystax*_	_Ac. lacustris_	_A. lacustris_	_C. britskii_	_C. kelberi*_	_E. trilineata_	_G. inaequilabiatus*_	_H. ancistroides_	_H. eques*_	_H. malabaricus_	_H. marginatus_	_I. labrosus_	_L. araguaiae*_	_L. platymetopon*_	_M. intermedia_	_M. lippincotianus*_	_O. eigenmanni*_	_O. niloticus*_	_P. maculatus_	_P. platana*_	_P. squamosissimus*_	_R. descalvadensis*_	_Rineloricaria sp._	_S. brevipinna*_	_S. insculpta_	_S. maculatus_	_S. marginatus*_	_S. nasutus_	_S. notomelas_	_T. galeatus*_	_T. paraguaiensis*_	**Total volume of prey**
	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n total
	13	10	40	17	6	46	10	6	3	4	12	42	8	27	10	3	41	34	23	4	24	23	4	81	36	3	7	8	5	10	11	25	13	5	614
Total Volume Of Specie	0.355	0.122	0.852	5.134	11.301	8.701	0.054	5.426	1.371	1.025	0.363	0.299	40.502	0.509	1.599	0.029	2.297	1.373	2.254	0.181	1.597	6.517	0.164	145.69	0.326	0.03	0.245	0.33	5.106	1.157	13.092	0.586	15.9	1.078	275.573

Table 9 (S3). Rosana Reservoir Prey Category in percentage (%). * = Non-native species to the Upper Paraná River Basin

Prey Category	Prey Volume (%)										
	Species										
	*A. dentatus**	*A. lacustris*	*H. eques**	*H. marginatus*	*I. labrosus*	*L. platymetopon**	*P. maculatus*	*P. squamossisimus**	*S. nasutus*	*S. notomelas*	*T. galeatus**
	n	n	n	n	n	n	n	n	n	n	n
	20	29	54	30	27	26	26	28	17	32	39
Aquatic Insect	10.21	16.98	21.07	0.38	5.86	0.35	1.56	2.51	-	9.05	2.32
Terrestrial invertebrates	47.29	29.53	33.76	2.72	2.28	-	49.89	0.21	-	11.62	95.18
Microcrustacean	40.00	2.92	9.90	96.11	0.07	0.35	0.03	-	-	3.38	-
Macrocrustacean	-	-	-	-	-	-	1.45	54.55	-	-	0.60
Mollusc	-	2.55	0.76	-	38.69	2.19	4.39	0.01	2.35	-	-
Fish	-	-	-	-	-	-	30.21	42.71	-	3.38	-
Algae	-	1.56	1.52	0.10	-	-	0.04	-	25.31	7.30	-
Terrestrial Plant	2.50	44.84	12.18	0.61	7.93	5.94	11.30	-	40.19	5.95	1.90
Detritus	-	1.56	20.05	0.08	45.03	91.17	1.12	-	32.14	59.32	-
Other	-	0.05	0.76	-	0.14	-	0.01	-	-	-	-
Sum	100	100	100	100	100	100	100	100	100	100	100

Table 10 (S4). Taquaruçu Reservoir Prey Category in percentage (%). * = Non-native species to the Upper Paraná River Basin.

Prey Category	**Prey Volume (%)**													
	Species													
	_A. dentatus_*	_A. osteomystax_*	_A. lacustris_	_H. eques_*	_H. marginatus_	_L. platymetopon_*	_M. intermedia_	_M. lippincotianus_*	_O. niloticus_*	_P. maculatus_	_P. squamosissimus_*	_R. descalvadensis_*	_S. notomelas_	_T. galeatus_
	n 40	n 30	n 46	n 42	n 27	n 41	n 34	n 23	n 24	n 23	n 81	n 36	n 25	n 15
Aquatic Insect	17.96	86.48	65.83	20.59	22.06	0.44	12.05	6.76	0.96	25.87	5.93	23.17	8.82	41.69
Terrestrial invertebrates	47.31	8.80	18.62	18.95	49.42	-	18.98	9.67	1.26	0.06	-	28.05	7.42	55.64
Microcrustacean	24.06	4.71	0.02	43.79	19.24	18.80	18.51	0.75	0.26	2.32	-	0.30	52.86	-
Macrocustacean	0.12	-	0.41	6.21	-	2.18	-	-	-	0.77	52.87	-	0.34	0.31
Mollusc	-	-	12.58	-	-	2.81	-	3.84	-	34.14	0.84	0.91	0.34	0.05
Fish	-	-	-	1.31	-	-	36.93	0.05	7.01	0.21	39.64	42.38	1.02	-
Algae	-	-	-	1.63	0.02	-	6.83	56.74	14.11	0.69	-	-	-	0.44
Terrestrial Plant	9.74	-	2.12	3.59	9.22	0.91	5.63	8.92	25.30	10.23	0.69	4.88	6.14	1.13
Detritus	0.70	-	0.41	3.27	-	74.87	1.02	13.26	51.29	25.70	0.03	-	23.02	0.44
Other	0.12	-	0.01	0.98	0.20	-	0.05	0.09	0.06	-	-	0.30	0.34	-
Sum	100	100	100	100	100	100	100	100	100	100	100	100	100	100

Figure 6 (S2). Rosana Reservoir habitats. A = marginal lagoon entrance on the left bank; B = marginal lagoon in the right bank close to the UC Morro do Diabo Park; C = detailing of the macrophyte vegetation from a marginal lagoon inside the UC Morro do Diabo Park, covered by *Eichhornia* spp., *Elodea* sp., *Sagittaria* sp., and *Salvinia* sp. D = Pirapozinho River and its riparian forest; E = detailing of the Cuiaba Stream and its surroundings.

Figure 7 (S3). Taquaruçu Reservoir habitats. A = left bank without marginal lagoons; B = right bank without marginal lagoons; C = detailing of the right bank without marginal lagoons, suppression of the riparian forest and presence of pasture grass. D = Anhumas River with its reforested banks. E = detailing of the Tenente River under silting impact.

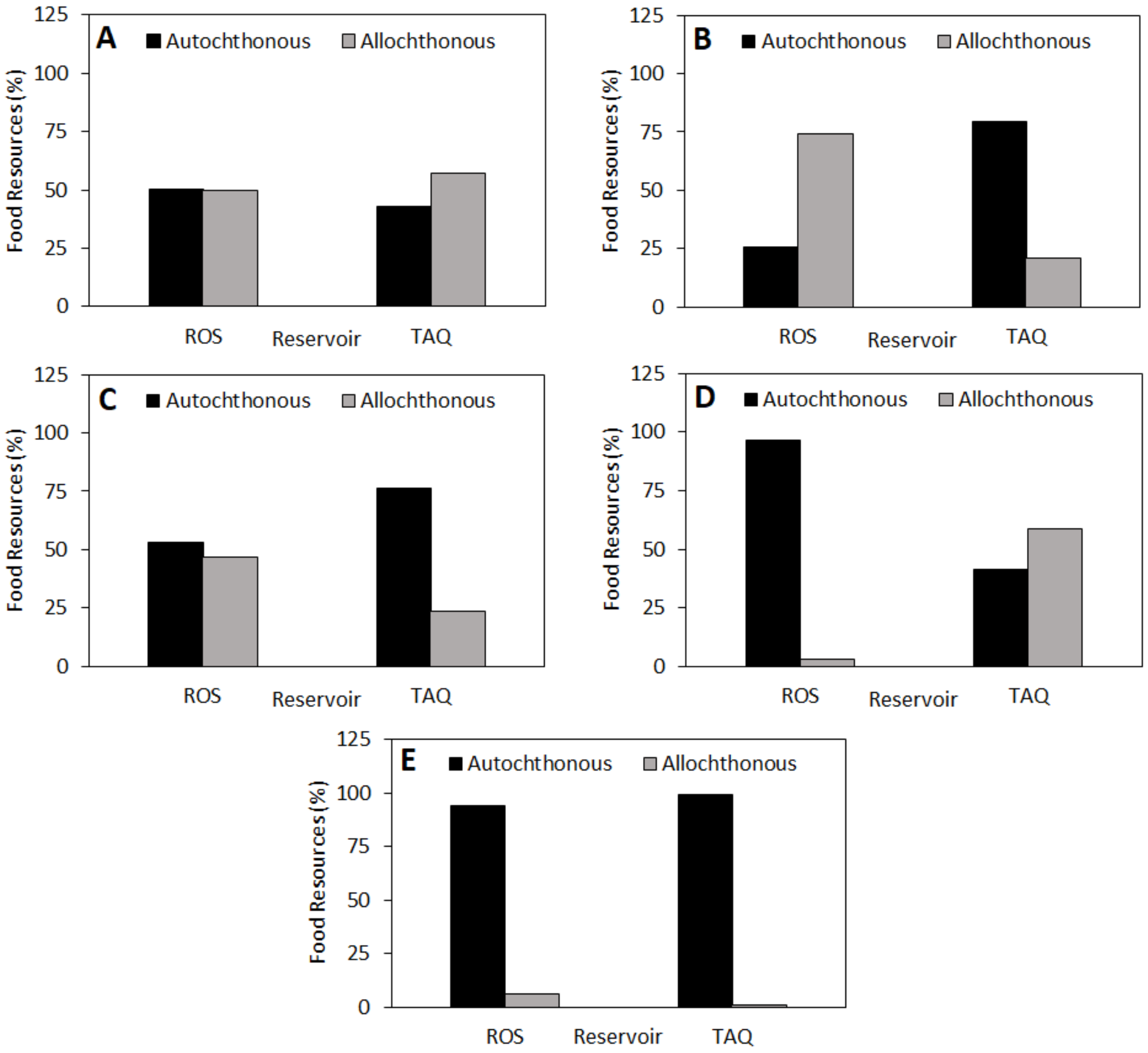

Figure 8 (S4). Food resources exploitation between reservoirs. A= *A. dentatus*; B = *A. lacustris*; C = *H. eques*; D = *H. marginatus*; E = *L. platymetopon*. ROS = Rosana; TAQ = Taquaruçu.

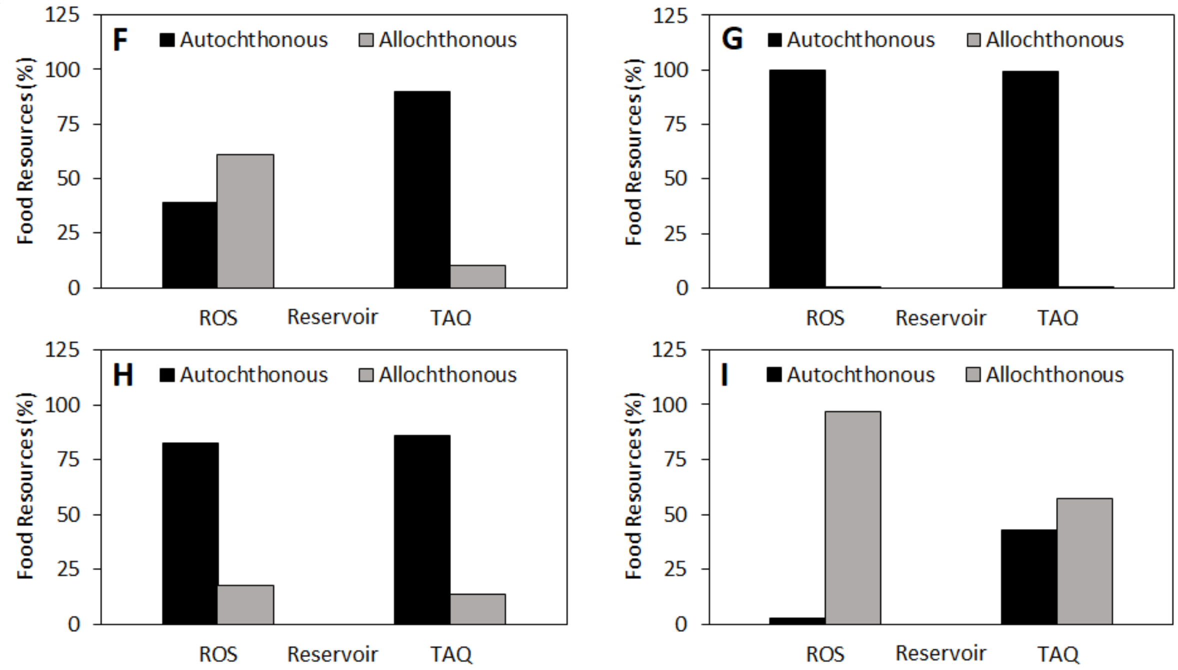

Figure 9 (S5). Food resources exploitation between reservoirs. F = *P. maculatus*; G = *P. squamossisimus*; H = *S. notomelas*; I = *T. galeatus*. ROS = Rosana; TAQ = Taquaruçu.

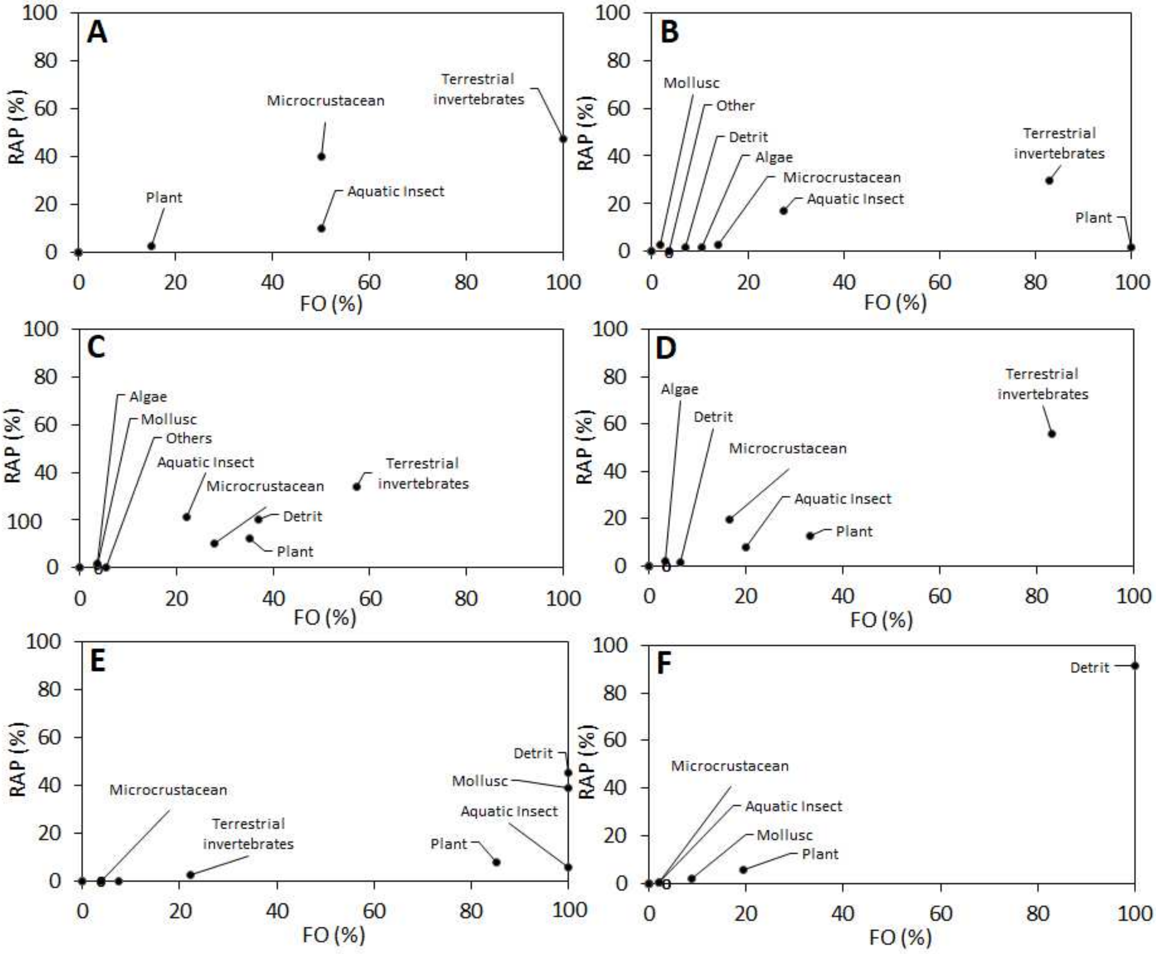

Figure 10 (S6). Feeding strategy of species from Rosana Reservoir (Costello's 1990 method with modifications by Amundsen et al., 1996). A = *A. dentatus*; B = *A. lacustris*; C = *H. eques*; D = *H. marginatus*; E= *I. labrosus*; F = *L. platymetopon*. FO = Frequency of occurrence of prey category; RAP = Relative abundance of prey category.

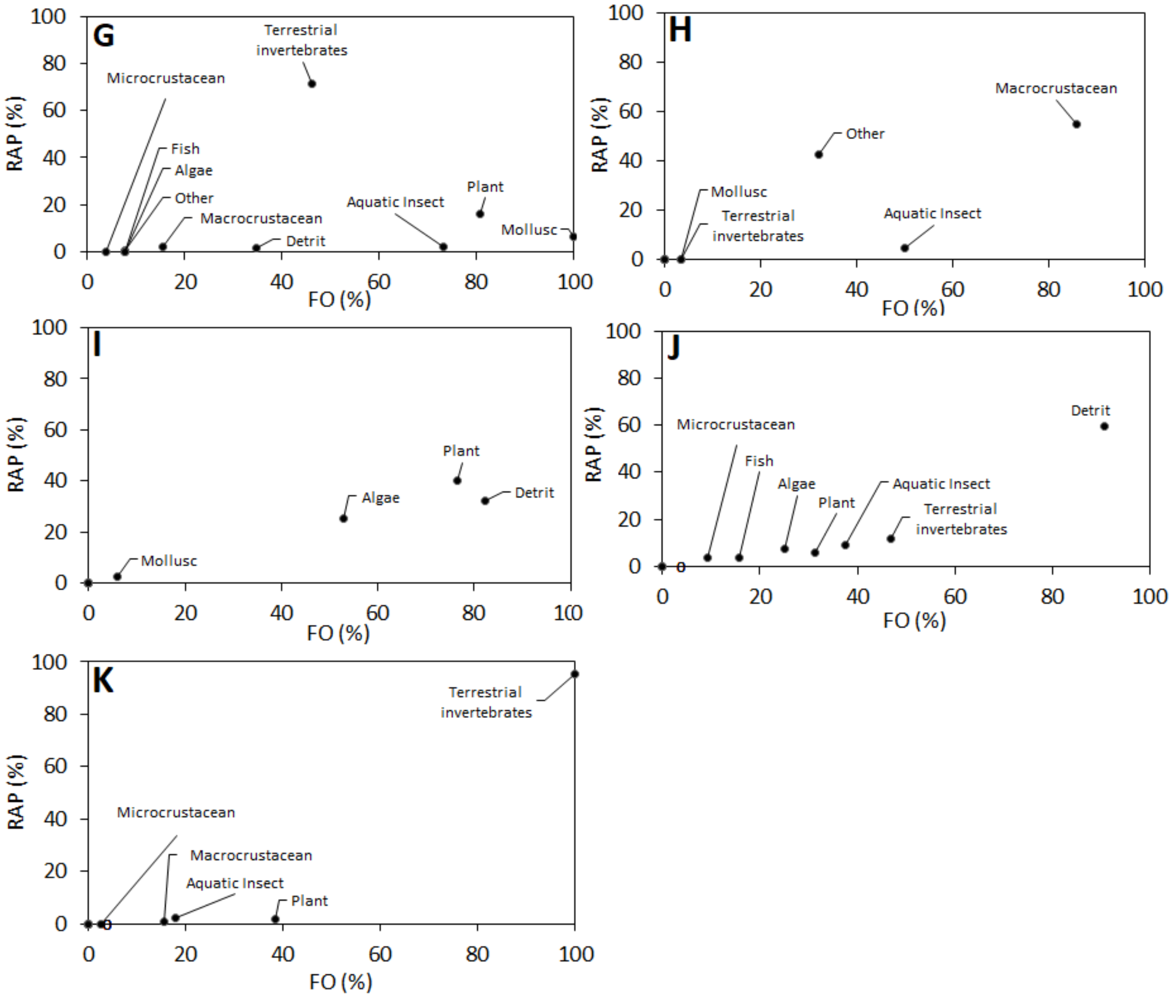

Figure 11 (S7). Feeding strategy of species from Rosana Reservoir (Costello's 1990 method with modifications by Amundsen et al., 1996). G= *P. maculatus*; H = *P. squamossisimus*; I =*S. nasutus*; J = *S. notomelas*; K = *T. galeatus*. FO = Frequency of occurrence of prey category; RAP = Relative abundance of prey category.

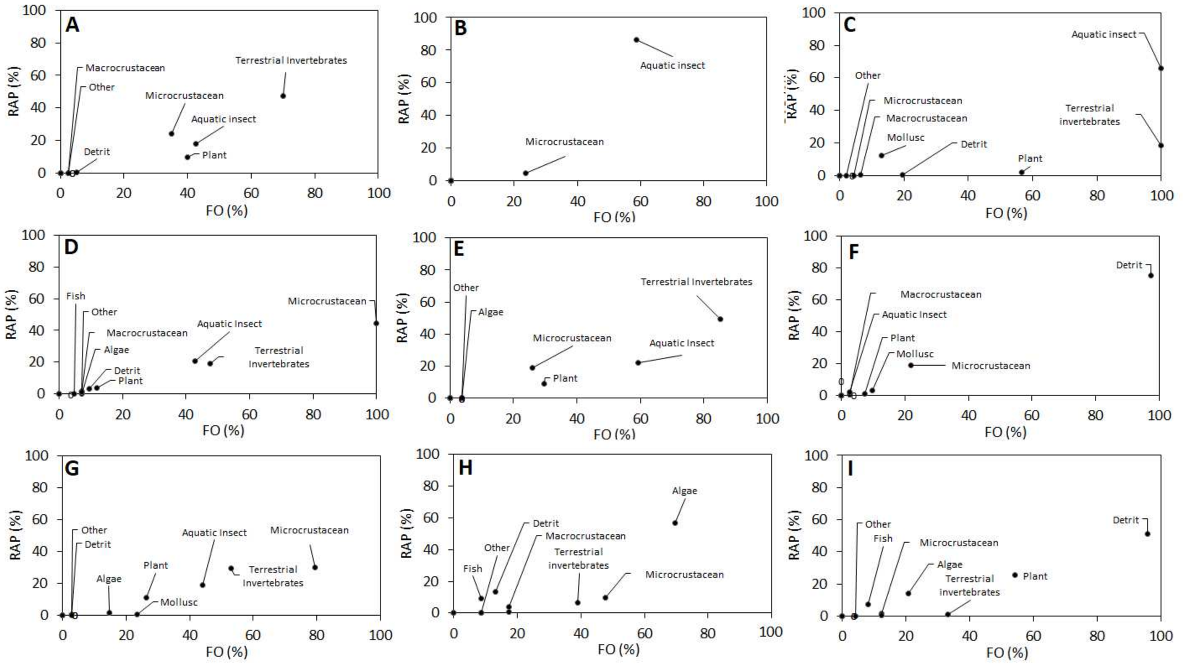

Figure 12 (S8). Feeding strategy of species from Taquaruçu Reservoir (Costello's 1990 method with modifications by Amundsen et al., 1996). A= *A. dentatus*; B = *A. osteomystax*; C = *A. lacustris*; D = *H. eques*; E = *H. marginatus*; F = *L. platymetopon*; G = *M. intermedia*; H = *M. lippincotianus*; O = *O. niloticus*. FO = Frequency of occurrence of prey category; RAP = Relative abundance of prey category.

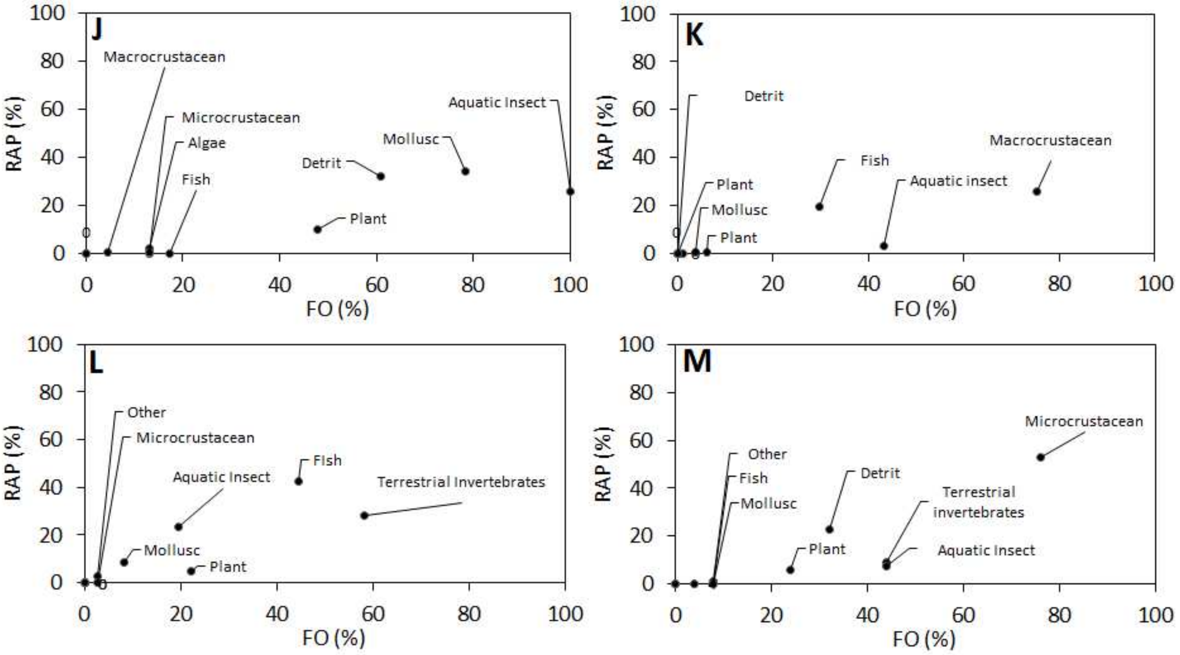

Figure 13 (S9). Feeding strategy of species from Taquaruçu Reservoir (Costello's 1990 method with modifications by Amundsen et al., 1996). J = *P. maculatus*; K = *P. squamossissimus*; L = *R. descalvadensis*; M = *S. notomelas*. FO = Frequency of occurrence of prey category; RAP = Relative abundance of prey category.

Table 11 (S5). Trophic Guild and Feeding Strategy of fish from Rosana and Taquaruçu reservoirs. * = Non-native species to the Upper Paraná River Basin. Values in bold denote changes in trophic guild and feendig strategy by reservoir.

Species	**Trophic Guild**		**Feeding Strategy**		**Voucher**
	Rosana	**Taquaruçu**	**Rosana**	**Taquaruçu**	
Aphyocharax dentatus Eigenmann & Kennedy, 1903*	Invertivore	Invertivore	Generalist	Generalist	MZUEL 20735
Auchenipterus osteomystax (Miranda Ribeiro, 1918)*	-	Aquatic Insectivore	-	Specialist	MZUEL 20739
Astyanax lacustris (Lütken, 1875)	**Omnivore**	**Aquatic Insectivore**	Generalist	Generalist	MZUEL 20753
Hyphessobrycon eques (Steindachner, 1882)*	Omnivore	Omnivore	Generalist	Generalist	MZUEL 20732
Hemigrammus marginatus Ellis, 1911	**Invertivore**	**Omnivore**	**Specialist**	**Generalist**	MZUEL 20773
Iheringichthys labrosus (Lütken, 1874)	Omnivore	-	Generalist	-	MZUEL 20747
Loricariichthys platymetopon Isbrücker & Nijssen, 1979*	Detritivore	Detritivore	Specialist	Specialist	MZUEL 20738
Metynnis lippincottianus (Cope, 1870)*	-	Algivore	-	Generalist	MZUEL 20737
Moenkhausia intermedia Eigenmann, 1908	-	Omnivore	-	Generalist	MZUEL 20790
Oreochromis niloticus (Linnaeus, 1758)*	-	Detritivore	-	Generalist	MZUEL 20757
Pimelodus maculatus Lacepède, 1803	**Terrestrial invertebrates**	**Omnivore**	Generalist	Generalist	MZUEL 20768
Plagioscion squamosissimus (Heckel, 1840)*	Carcinophage	Carcinophage	Generalist	Generalist	MZUEL 20742
Roeboides descalvadensis Fowler, 1932*	-	Omnivore	-	Generalist	MZUEL 20772
Schizodon nasutus Kner, 1858*	Herbivore	-	Generalist	-	MZUEL 20758
Serrapinnus notomelas (Eigenmann, 1915)	**Detritivore**	**Invertivore**	Generalist	Generalist	MZUEL 20736
Trachelyopterus galeatus (Linnaeus, 1766)*	Terrestrial Invertivore	Terrestrial Invertivore	**Specialist**	**Generalist**	MZUEL 20755

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4.2 CAPÍTULO 2

WHY THEY COEXIST? ECOMORPHOLOGY AND DIET REVEALS NICHE SEGREGATION OF TWO SYMPATRIC NON-NATIVE CATFISHES (AUCHENIPTERIDAE) IN THE PARANAPANEMA RIVER, BRAZIL

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4.2.1 TITLE - Why they coexist? Ecomorphology and diet reveals niche segregation of two sympatric non-native catfishes (Auchenipteridae) in the Paranapanema River, Brazil

4.2.2 Authors

4.2.3 Affiliation

4.2.4 Abstract

Sympatric species are those that coexist in the same environment, being able to share the resources offered by the habitat. Thus, an interesting question in the field of biological invasion is the interaction between native and non-native sympatric species. However, an even more intriguing question is how non-native species behave in the presence of similar species in environments where both are non-native, which can force competition for survival. Therefore, the objective of this study was to investigate the morphology and diet of two sympatric catfish (Auchenipteridae) in the Lower Paranapanema River, where both are non-native. Fishes were captured in Rosana and Taquaruçu reservoirs between September 2018 and September 2020 with gill nets, being euthanized in Eugenol and fixed in formalin. A total of 84 individuals (54 of *T. galeatus* and 30 of *A. osteomyxtax*) were evaluated by twenty-five linear measures and had the stomach content analyzed. The PERMANOVA revealed significant difference in the twenty-three morphological indexes applied between species, where results related with the fins areas, eyes, head and mouth size segregated individuals in the Principal Component Analysis (PCA). We identified 25 food items, where *A. osteomystax* consumed mostly autochthonous resources (aquatic invertebrates), while *T. galeatus* consumed mostly allochthones resources (terrestrial invertebrates and terrestrial plants). The trophic niche breadth showed narrower niche to *A. osteomystax* in relation to the *T. galeatus*, and the Pianka's index showed a low dietary niche overlap. In conclusion, our results revealed morphological differences between the sympatric auchinepterids which can be determinant in the spatial segregation and dietary divergence, as well as low niche overlap. These factors seem to be essential to the coexisting of the non-native species in the invaded environment, avoiding competitive exclusion.

4.2.5 Introduction

Brazil has reservoirs for hydropower in its main watersheds, especially in the southeast and south (Agostinho *et al.*, 2007), placing dams in sequence as cascades of reservoirs in some cases (Garcia *et al.*, 2018a). In this way, many reservoirs demonstrate taxonomic and functional simplification of the fish communities over time, leading to biotic homogenization (Daga *et al.*, 2019). This trend is strongly influenced by the presence of non-native species (Daga *et al.*, 2019), being the study of these species essential for the understanding of the biological invasion process (Garcia *et al.*, 2018b). Since non-native species have the adaptive capacity to establish themselves in new environments (Alvez *et al.*, 2017; Barilli *et al.*, 2012; Tonella *et al.* 2018), non-native species that coexist could present spatial or feeding divergences, probably to avoid exclusive competition (Capra & Bennemann, 2009; Nieto *et al.*, 2023), the same behaviour that native species display in their natural distribution (Hardin, 1960; Schoener, 1974; Mise *et al.*, 2013; Carniatto *et al.*, 2017).

The ecomorphology is an important tool to understand the relationship between species and the environment (Breda *et al.*, 2005; Oliveira *et al.*, 2010). Thus, the morphology analysis allows the investigation of the dietary niche of species, which is resulting from relations with spatial distribution and feeding (Kirchheim & Goulart, 2010; Freitas *et al.* 2017). Also, it is known that the first influences the second (Garcia *et al.*, 2020). This correlation is quite strong, where each habitat can select the best morphological traits for species success, leading to dietary changes (Sampaio *et al.*, 2013; Freitas *et al.*, 2017). In this sense, species that are phylogenetically and morphologically related probably have a strong competitive potential (Wootton, 1999), since they will inhabit the same habitats and have close diet (Garcia *et al.*, 2020). Therefore, analysis of body morphology combined with diet helps us to understand the spatial use and the feeding behaviour of species, since the partitioning of resources and the trophic segregation is the key to the coexisting (Neves *et al.*, 2015; Pease *et al.*, 2018; Baldasso *et al.*, 2019).

The Auchenipteridae family is widely distributed in South America, popularly known as manduví, zamora, docella, and novia (spanish language), cangati, cachorrinho, anujá, palmito, padre, manduvi (Brazil), and driftwood catfish or slope-head catfish in English (Birindelli, 2014). They are mostly small to medium size fish easily distinguished among catfishes due to their shape, adipose drop-shaped fin, sinusoidal lateral line, barbels that move vertically, and anal fin modified in males for insemination (Birindelli, 2014). Species of the family are distributed in similar habitats, hiding during the day among plants, rocks, leaves, and driftwood, and feeding at night (Ferraris Jr., 2003; De Souza *et al.*, 2016), which requires similar morphology and behaviour (Freitas *et al.*, 2017). In this way, some species tend to be insectivore or frugivore, being closely related to allochthonous resources (Souza *et al.*, 2017; Garcia *et al.*, 2020b; Bianchi-Costa *et al.*, 2023). For the Upper Paraná River (Brazil), most of the species of the family are non-native (Ota *et al.*, 2018; Garcia *et al.*, 2018a), becoming established in the region after the transposition of the Sete Quedas Falls by the construction of the Itaipu Dam (Tonella *et al.* al., 2018).

Auchenipterus osteomystax (Miranda-Ribeiro, 1918) presents body elongated, snout contained, mouth terminal, body darkened in the dorsal region and whitish ventrally, dorsal fins, pelvic and anal clear, and pectoral and caudal with dark margins (Ota *et al.*, 2018). Previous studies in the Upper Paraná River suggesting the specialist feeding of aquatic insects (Barrili *et al.*, 2012; Tonella *et al.*, 2018), but opportunistic behavior was also reported (Garcia *et al.*, 2018b). *Trachelyopterus galeatus* (Linnaeus, 1766) has a short and tall body, a short snout, a terminal mouth, and dark brown body with several irregular black spots that extend to the fins, where the pectoral and dorsal fins have serrated spine (Ota *et al.*, 2018). The specie presented generalist feeding in different environments (Santos, 2005; Peretti & Andrian, 2008; Ximenes *et al.*, 2011; Freitas *et al.*, 2017; Souza *et al.*, 2017), when in the Upper Paraná River behaves as opportunistic behaviour (Garcia *et al.*, 2018b; 2020; Bianchi-Costa *et al.*, 2023). Both species are non-native in the Lower Paranapanema River, one of the main tributaries on the right bank of the Upper Paraná River, where they are often found in abundance and sympatry in reservoirs (Garcia *et al.*, 2018a, b).

Since the species are phylogenetically and morphology related (Birindelli *et al.*, 2014), and shares feeding ecology (Freitas *et al.*, 2017; Garcia *et al.*, 2018b), the aim of this study was to investigate morphological and diet characteristics for elucidate the spatial distribution and the use of food resources, as well as possibility of interspecific competition. Thus, our hypothesis is that *A. osteomystax* and *T. galeatus* have morphological differences which influence the habitat use and diet leading to low niche overlap, which allow the coexistence of these sympatric non-native species. In this sense, our prediction is that: (i) the morphology of *A. osteomystax* provides distribution in flow habitats, superior position in the water column and capture of smaller prey, and (ii) the morphology of *T. galeatus* makes him a bottom species, but with possibility of capture of larger and more diverse prey.

4.2.6 Material and Methods

4.2.7 *Study Area*

The Paranapanema River rises in the Atlantic Plateau of the municipality of Capão Bonito, Sâo Paulo State (SP) (Sampaio, 1944). Being one of the main tributaries on the left bank of the Upper Paraná River Basin, the river runs through 930 km where 330 km from its main channel define the borders between the Southeast of the SP and North of the Paraná State (PR) (Maack, 1981). Due to your slopes hydrographic, the Paranapanema River has been exploited for hydropower, where the main channel was transformed into a cascade of eleven reservoirs (Duke Energy, 2008). Its course is divided into three sections: Upper, Middle, and Lower (Sampaio 1944). The Lower Paranapanema River begins after Salto Grande Falls (currently flooded by the Salto Grande Reservoir), covering from upstream to downstream the reservoirs of Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu, and Rosana (Duke Energy, 2008), the last two our study area (Figure 1).

The hydroelectric power plant of Rosana (Rosana Dam) is located between the municipalities of Diamante do Norte (PR) and Primavera (SP). The reservoir has a run-of-river flow, a length of 110 km, maximum depth of 26 m, and flooded area of 220 km^2. There are two conservation units (UC's) on its surroundings: The Morro do Diabo Park (SP), on the right, and the Caiuá Ecologic Station on the left (PR). As tributaries, there are Pirapó River (left bank), Pirapózinho River (right bank), and three main streams (all on its right bank), the Iancã, Cuiabá and Bonito (Figure 1). The hydroelectric power plant "Escola Politécnica" (Taquaruçu Dam) is located between the municipalities of Itaguajé (PR) and Sandovalina (SP). The reservoir has a run-of-river flow, a length of 80 km, maximum depth of 18 m, and flooded area of 105.5 km^2 (Britto, Carvalho, 2006). About the tributaries, the most important are in the left bank (Capim, Centenário, and Tenente rivers), and one in the right bank, the Anhumas River which is the only that has passed by a reforestation process (Mosquito Forest) (Leme *et al.*, 2015) (Figure 1).

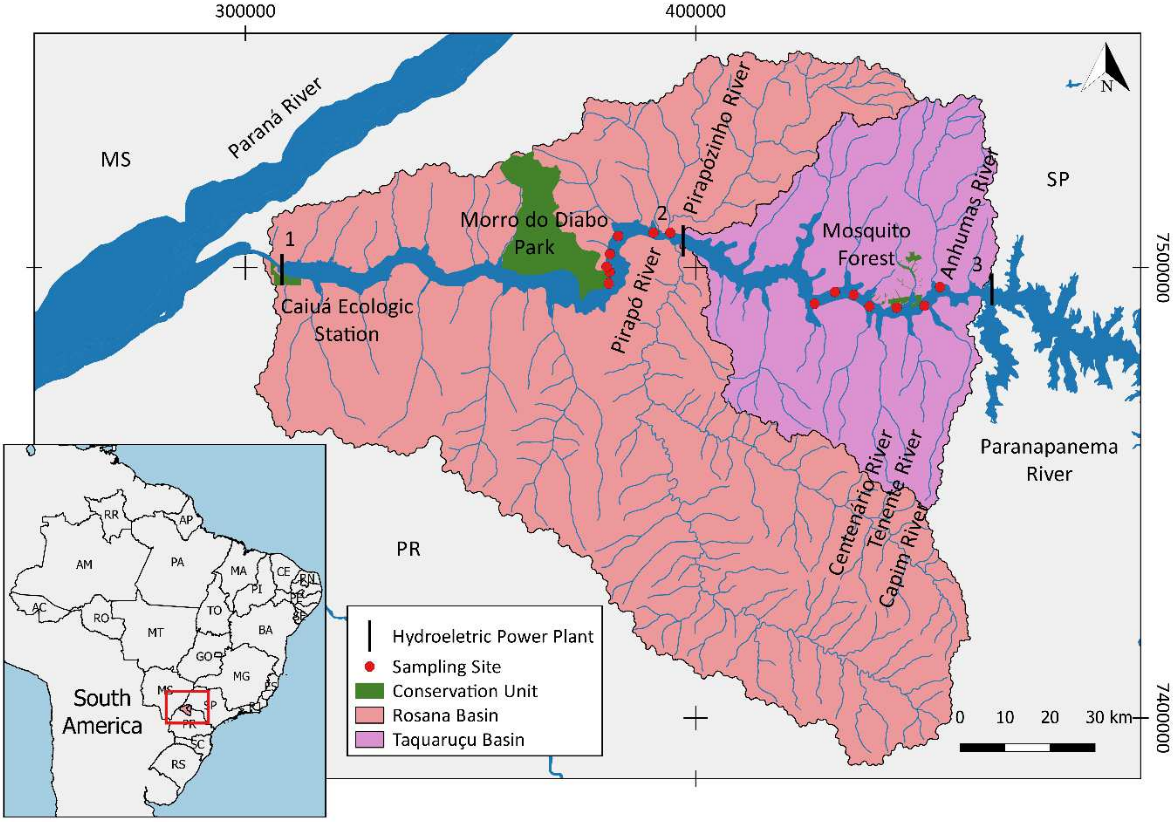

Figure 14 (1). Samplings sites in the Rosana and Taquaruçu reservoirs, Lower Paranapanema River; Paraná and São Paulo states. Hydroelectric power plants: 1 = Rosana; 2 = Taquaruçu; 3 = Capivara. MS = Mato Grosso do Sul State; PR = Paraná State; SP = São Paulo State.

4.2.8 *Samplings*

Samplings were performed quarterly from September 2018 to September 2020 at seven sites in the both reservoirs. Samplings were carried out in the pelagic and marginal zone using gillnets (20 to 120 mm between opposed knots), seated for 24 h and checked every 12 h. We also used trawls, sieves and cast nets to catch fishes under the vegetation in the marginal zone and along aquatic macrophyte beds, when present. In each of these sites we employed two hours of effort, covering an extension of 100 m to explore the microhabitats within the environments. All the captured individuals were anesthetized and euthanized by overexposure to Eugenol 1 g mL-1, fixed in 10% formaldehyde for 48 hours and further stored in 70% alcohol. All samplings were authorized by The Animal Ethics Committee (CEUA-UEL N° 24310.2017.78), and individuals were deposited at the Museu de Zoologia da Universidade Estadual de Londrina (MZUEL) under voucher MZUEL 20739 (*A. osteomystax*) and MZUEL 20755 (*T. galeatus*).

4.2.9 *Morphological analysis*

The morphological measurements were taken on the left side of each adult individual, using a digital caliper with accuracy of 0.01 mm. Twenty-five measurements were performed related to the body, fins, head, barbell and mouth of each captured individual, morphological measures related to the feeding behaviour and exploration of the habitat (Gatz Jr., 1979; Watson & Balon, 1984; Wikramanayake, 1990; Oliveira *et al.*, 2010). In addition, six measurements of fins and eye areas were obtained from the outline of the structures in pictures of each individual, which were later obtained using know scales in the software ImageJ (Rueden *et al.*, 2017) (Table 1). Thus, 23 indexes were calculated to determine the ecomorphological attributes (Table 2) (Breda *et al.*, 2005; Oliveira *et al.*, 2010; Prado *et al.*, 2016).

Table 12 (1). The 25 linear morphological measures and six areas obtained from *A. osteomystax* and *T. galeatus* in the Lower Paranapanema River, Paraná and São Paulo states. Modified from Freitas *et al.* (2017). Min = minimum standard length (mm); Max = maximum standard length (mm); ME = median; SD = standard deviation.

Linear Measures	**Acronym**	**Description**	***A. osteomystax* (n=30)**				***T. galeatus* (n=54)**			
			Min	**Max**	**ME**	**SD**	**Min**	**Max**	**ME**	**SD**
Standard length	SL	Distance from tip of snout to end of caudal peduncle	166	255	225	0.27	100	152.7	128.6	1.02
Maximum body height	MBH	Largest dorso ventral distance perpendicular to largest body axis	34.3	69.1	55.7	0.91	24.9	43.7	34.7	0.35
Body midline height	BMH	Largest ventral to midline distance perpendicular to largest body axis	20.0	47.3	35.3	0.63	18.0	31.6	26.8	0.28
Maximum body width	MBW	Largest body width	20.4	35.8	28.9	0.39	21.0	32.8	27.0	0.23
Caudal peduncle length	CPdL	Distance from end of anal fin to beginning of caudal fin	27.3	48.0	39.2	0.57	18.3	31.7	25.6	0.28
Caudal peduncle height	CPdH	Height of peduncle at its mid-point	16.2	26.0	22.1	0.28	10.7	20.1	16.8	1.78
Caudal peduncle width	CPdW	Width of peduncle at its mid-point	5.59	14.4	11.8	0.22	6.17	10.6	7.97	10.5
Head length	HdL	Distance from tip of snout to end of operculum	33.1	49.5	43.0	0.51	25.6	39.1	33.9	0.27
Head height	HdH	Distance from ventral part and dorsal part of head in the region of the eyes	13.2	26.5	19.3	0.37	8.42	20.6	17.3	0.22
Head width	HdW	Largest distance from opercule to opercule	11.4	38	33.0	0.62	25.3	37.8	32.6	0.25
Length of snout	LS	Distance from tip of snout to beginning of the eye	12.4	20.3	17.7	0.20	9.78	14.6	12.2	1.09
Eye height	EH	Distance from centre of eye to lower jaw	13.1	24.4	20.9	0.28	6.28	13.2	9.16	1.57
Mouth height	MH	Distance between lips of open mouth without distention of muscles	3.3	7.1	4.50	0.87	3.08	7.03	4.1	0.82
Mouth width	MW	Distance between lateral parts of totally open mouth without distention of muscles	11.12	17.1	13.5	1.51	11.8	18.8	15.2	1.59
Dorsal fin length	DL	Distance between the base of the fin and its extremity	24.4	37.1	33.1	0.37	18.5	30.3	24.0	0.24
Dorsal fin height	DH	Largest width of fin on axis perpendicular to the axis of the length of the fin when totally open	15.9	34.5	22.8	0.39	16.7	27.7	22.1	0.27
Caudal fin length	CL	Distance between the base of the fin and its extremity	30.8	51.9	46.9	0.63	16.4	32.9	23.7	0.39
Caudal fin height	CH	Largest width of fin on axis perpendicular to the axis of the length of the fin when totally open	41.1	68.6	54.3	0.89	18.5	40.7	31.3	0.57
Anal fin length	AL	Distance between the base of the fin and its extremity	60.0	89.9	84.0	0.87	27.5	40.6	33.6	0.31
Anal fin height	AH	Largest width of fin on axis perpendicular to the axis of the length of the	6.89	15.4	12.0	0.23	6.26	15.9	10.4	0.2

Linear Measures	**Acronym**	**Description**	***A. osteomystax* (n=30)**				***T. galeatus* (n=54)**			
			Min	**Max**	**ME**	**SD**	**Min**	**Max**	**ME**	**SD**
		fin when totally open								
Pectoral fin length	PtL	Distance between the base of the fin and its extremity	20.0	38.9	33.3	0.50	20.5	37.7	29.8	0.33
Pectoral fin height	PtH	Largest width of fin on axis perpendicular to the axis of the length of the fin when totally open	11.9	26.3	16.7	0.42	8.04	19.8	12.0	0.27
Pelvic fin length	PvL	Distance between the base of the fin and its extremity	30.5	49.8	37.7	0.40	13.4	30.2	17.6	0.26
Pelvic fin height	PvH	Largest width of fin on axis perpendicular to the axis of the length of the fin when totally open	15.0	40.7	23.0	0.64	7.02	17.5	11.2	1.03
Maxillary barbel length	MbL	Distance between the base of the barbel and its extremity when totally distended	43.9	72.2	59.4	0.76	24.4	51.9	37.0	0.6
Eye area	EA	Area of eye	29.4	55.8	37.7	0.85	13.6	62.3	33.4	0.83
Dorsal fin area	DA	Area of dorsal fin when totally distended	12.3	53	39.4	1.03	18.4	80.8	69.7	0.79
Pectoral fin area	PtA	Area of pectoral fin when totally distended	21.8	45.0	29.2	0.61	22.5	89.3	59.8	1.2
Pelvic fin area	PvA	Area of pelvic fin when totally distended	48.7	74.5	42.5	1.59	12.3	45.1	23.0	0.3
Anal fin area	AA	Area of anal fin when totally distended	14.4	38.5	25.2	0.69	13.6	75.6	32.6	0.92
Caudal fin area	CA	Area of caudal fin when totally distended	28.9	55.3	45.4	0.94	14.8	62.6	35.9	0.67

Table 13 (2). The 23 ecomorphological indexes obtained from *A. osteomystax* and *T. galeatus* in the Lower Paranapanema River, Paraná and São Paulo states. Modified from Garcia *et al.* (2020).

Morphologic Indexes	**Equation**	**Description**
Body Compression index	CI = MBH/MBW	High values indicate species with lateral compression of body, expected in fish that occupy lentic habitats (Gatz Jr., 1979; Watson & Balon, 1984).
Body Depression index	DI = BHM/MBH	Low values indicate species with depression of body, expected in fish that explore habitats closer to the bottom (Oliveira *et al.*, 2010; Winemiller, 1991; Watson & Balon, 1984).
Relative body height	RBH = MBH/Sl	Index inversely related to the water velocity and directly related to the ability of maneuverability (Winemiller, 1991; Watson & Ballon, 1984; Gatz Jr., 1979).
Relative lenght of caudal peduncule	RLPd = CPdL/SL	Fish with long caudal peduncles are good swimmers. However, fish adapted to rapid water flows, but not necessarily nectonics, also present long caudal peduncles (Watson & Balon, 1984)
Relative height of caudal peduncule	RHPd = CPdH/MBH	Low values indicate high maneuverability (Winemiller, 1991; Willis *et al.*, 2005).
Relative width of caudal peduncule	RWPd = CPdW/MBW	High values indicate continuous swimmers (Winemiller, 1991; Willis *et al.*, 2005).
Relative lenght of head	RLHd = HdL/SL	Higher values are found in fish that feed on larger prey, thus higher rates are expected for piscivorous species (Watson & Balon, 1984; Winemiller 1991; Willis *et al.*, 2005).
Relative height of head	RHHd = HdH/MBH	Higher values are found in fish that feed on larger prey, thus higher rates are expected for piscivorous species (Winemiller, 1991; Willis *et al.*, 2005).
Relative width of head	RWHd = HdW/MBW	Higher values are found in fish that feed on larger prey, thus higher rates are expected for piscivorous species (Winemiller, 1991; Willis *et al.*, 2005).
Relative height of mouth	RHM = MH/MBH	Higher values are found in fish that feed on larger prey, inferring about the relative size of the prey (Gatz Jr., 1979).
Relative width of mouth	RWM = MW/MBW	Higher values suggesting relatively large prey (Gatz Jr., 1979, Winemiller, 1991).
Eye position	EP = EH/HdH	Index associated with the specie's foraging position in the water column. High values indicate benthic fish (dorsally eyes), while low values indicate nectonic fish (lateral eyes) (Gatz Jr., 1979)
Relative area of eye	RAE = $EA/(SL)^2$	Index related to food detection and visual acuity of the species. It can indicate the position of the species in the water column, as species that inhabit deeper areas have smaller eyes (Gatz Jr., 1979).
Relative area of of dorsal fin	RAD = $DA/(SL)^2$	Higher values present greater stabilization capacity in yaws (Breda *et al.*, 2005)

Morphologic Indexes	**Equation**	**Description**
Relative area of caudal fin	$RAC = CA/(SL)^2$	Higher values are important for acceleration (Oliveira *et al.*, 2010).
Aspect ratio of caudal fin	$ARC = (CH)^2/CA$	Higher values are related with more active and continuous swimmers in which there is a tendency to bifurcate of caudal and reduce their area (Gatz Jr., 1979)
Relative area of anal fin	$RAA = AA/(SL)^2$	Higher values imply greater maneuverability and stabilization during movements (Breda *et al.*, 2005)
Aspect ratio of anal fin	$ARA = (AL)^2/AA$	Higher values imply a greater ability to perform faster progressive and retrograde movements (Breda *et al.*, 2005)
Relative area of pectoral fin	$RAPt = PtA/(SL)^2$	Higher values are found in slow-swimming species, which use it for maneuverability (some Characidae) and may also be high among fishes that inhabit high flow habitats, such as Siluriformes. Smaller areas are found in pelagic fish (Watson & Balon, 1984).
Aspect ratio of pectoral fin	$ARPt = (PtL)^2/PtA$	Higher values indicates long and narrow pectoral fin, which is expected in species that swim continuously and reach high speed in pelagic habitats (Oliveira *et al.*, 2010).
Relative area of pelvic fin	$RAPv = PvA/(SL)^2$	Higher values are found in benthic species and smaller areas in pelagic species (Breda *et al.*, 2005)
Aspect ratio of pelvic fin	$ARPv = (PvL)/Pva$	Higher values are found in pelagic species and are related to the ability to balance. Thus, lowest values are associated with species that prefer rocky bottoms to support the body to the substrate (Gatz Jr., 1979).
Relative length of maxillary barbel	$RLMb = MBL/SL$	Higher values are found in species that feed on the substrate. Long barbels are related to the Siluriformes that inhabit the bottom (Gatz Jr., 1979).

Figure 15 (2). Adult individual of *A. osteomystax* from the Lower Paranapanema River, Paraná and São Paulo states.Standard length = 150 mm. Source: Authors, 2019.

Figure 15 (3). Adult individual of *T. galeatus* from the Lower Paranapanema River, Paraná and São Paulo states. Standard length = 130 mm. Source: Authors, 2019.

4.2.10 *Diet analysis*

Individuals had their stomachs removed and the content was analysed under a stereomicroscope, where the preys were identified at the lowest taxonomic level (Mugnai *et al.*, 2010). Thus, food items were quantified by the frequency of occurrence and volume, which was obtained by the compression of food in a millimeter Petri dish, with a volume given in mm^3 and later transformed into mL (Hellawell & Abel, 1971). So, the prey items was grouped into 10 categories and represented in percentage (%), as follow: Algae (Filamentous Algae); Aquatic Insects (Aquatic Insect Fragment, Coleoptera Larvae, Coleoptera Pupe, Diptera Larvae, Diptera Pupe, Ephemeroptera Nymph, Odonata Nymph and Trichoptera Nymph); Detritus (Inorganic Detritus, Organic Detritus); Fish (Fish, Fish Scale); Macrocrustacean (Crab, Shrimp); Microcrustacean (Cladocera, Copepoda, Microcrustacean

Fragment, Ostracoda); Mollusc (Bivalvia, Gastropoda); Other (Microplastic); Terrestrial Plant (Fruit, Leaf, Stick, Seed), and Terrestrial Invertebrates (Terrestrial Acari, Aranae, Blattodea - Isoptera, Blattodea Adult, Coleoptera Adult, Diplopoda, Diptera Adult, Ephemeroptera Adult, Hemiptera Adult, Hymenoptera Adult, Lepidoptera Adult, Terrestrial Insect Fragment and Thysanoptera Adult). After, the prey category was organized into food resources, based on the origin of prey categories: Autochthonous (Aquatic Insect; Microcrustacean; Macrocrustacean; Mollusc; Fish, Algae and Detritus), and allochthonous (Terrestrial invertebrates; Terrestrial Plant; and Others).

After, we calculated the niche breadth and dietary niche overlap of the species with the prey category matrix of volume data (%). We used the Shannon-Wiener index (1948) in the niche amplitude of species: $H' = -\Sigma\ pk$ x $\ln pk$, where H' means the Shannon-Wiener niche width measure, pk is the proportion of individuals collected using the k resource, and ln is the neperian logarithm of the pk value. Dietary niche overlap between species was calculated using the Pianka index: $Ojk = ({}^{n}\sum_{i=j}|P_{ij} - P_{ik}|) / {}^{n}\sum_{i=j} P_{ij}^{2}.\ {}^{n}\sum_{i=j} P_{ik}^{2}$, where Ojk = measure of Pianka dietary niche overlap between species j and species k; pij = proportion of prey category i in the total of prey categories used by species j; pik = proportion of prey category i in the total of prey categories used by species k, n = total number of prey categories. Thus, the results of Ojk were considered: low (<0.4), intermediate (0.4-0.6), or high (> 0.6) (Grossman, 1986). It should be noted that both analyzes may be biased due to the organization of prey into categories, as well as variation in the prey identification (some prey at order level, others at class level, and so on).

4.2.11 *Data analysis*

The Permutational Variation Analysis (PERMANOVA) was used to verify difference in the ecomorphology species indexes, based on a Bray-Curtis similarity matrix of measures data, log transformed (x + 1) (Anderson *et al.*, 2008). The pseudo-F statistic resulting from this analysis was tested by the Monte Carlo method using 999 randomizations. After, a Principal Component Analysis (PCA) was used to order the species according to their morphological characteristics, since this analysis indicates the grouping pattern of individuals with similar traits. The axes were selected according to the Broken-Stick criterion, in which those with eigenvalues greater than the axes generated by the model were used for interpretation (McCune & Mefford, 1999), adopting the criteria of loadings higher than 0.9 for explanations.

To verify difference in diet, we also used PERMANOVA, with the pseudo-F statistic resulting from this analysis tested by the Monte Carlo method using 999 randomizations. Thus, a Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity matrix (Bray & Curtis, 1957) was used to visualize the ordination of species according to the diet composition. All the analyses were carried out using the R Programming software version 3.5.3 (R Development Core Team, 2020), using the "vegan" package (Oksanen *et al.*, 2018), and the "ggplot2" package (Wickham, 2016).

4.2.12 Results

4.2.13 Morphologic results

A total of 84 individuals were measured and had the stomach content analysed, 54 of *T. galeatus* and 30 of *A. osteomyxtax.* The PERMANOVA revealed significant difference in the morphological indexes between the species (pseudo-$F_{(0.830)}$: 11.23; $p > 0.001$), and the PCA showed the significance of the first two axes according to the Broken-Stick. When together, axis 1 and axis 2 explained 68.61% of the variance of data (Table 3), being used to describe the morphological divergence between *A. osteomyxtax* and *T. galeatus* (Figure 4). When analysing the first axis of PCA, it is observed that *A. osteomysxtax* is located on the negative side presenting lower values for Compression index (CI), Aspect ratio of pectoral fin (ARPt), Aspect ratio of anal fin (ARA), Aspect ratio of pelvic fin (ARPv) and Relative length of head (RLHd), the most influencing variables in the axis 1. On the other hand, *T. galeatus* is located on the positive side of axis 1 having high values of the variables mentioned above, however, the individuals are scattered on both sides of axis 2, showing a greater variance of Relative area of eye (RAE), Relative area of dorsal fin (RAD), Relative area of caudal fin (RAC), Relative area of anal fin (RAA), Relative area of pectoral fin (RAPt), and Relative area of pelvic fin (RAPv), the most influencing variables in the axis 2 (Figure 4).

Tabel 14 (3). Means, standard deviations values, eigenvalues and percentage of variation for each axis as well as the index's loadings of PCA for the 23 morphological indexes obtained from *A. osteomystax* and *T. galeatus* in the Lower Paranapanema River, Paraná and São Paulo states. The indexes that were more important for interpretation are marked in bold. ME = median; SD = standard deviation.

Morphologic Indexes	*A. osteomystax*		*T. galeatus*		Acronym	Axis 1	Axis 2
	MED	SD	MED	SD			
Compression index	1,88	0,01	1,283	0,106	CI	**0.934**	0.169
Aspect ratio of pectoral fin	1,30	1,20	1,517	1,023	ARPt	**0.922**	0.153
Aspect ratio of anal fin	2,60	1,10	1,576	0,630	ARA	**0.912**	0.14
Aspect ratio of pelvic fin	2,03	0,78	3,300	2,160	ARPv	**0.909**	0.147
Relative length of head	0,19	0,02	0,260	0,013	RLHd	**-0.907**	-0.118
Relative area of eye	0,19	0,04	1,820	1,200	RAE	-0.25	**0.967**
Relative area of dorsal fin	0,18	0,06	1,190	2,400	RAD	-0.251	**0.963**
Relative area of caudal fin	2,70	2,30	1,400	3,300	RAC	-0.25	**0.959**
Relative area of anal fin	1,22	0,37	1,920	1,360	RAA	-0.251	**0.915**
Relative area of pectoral fin	0,15	0,04	1,820	1,590	RAPt	-0.255	**0.911**
Relative area of pelvic fin	0,34	0,10	3,300	2,160	RAPv	-0.257	**0.901**
Aspect ratio of caudal fin	2,05	0,53	0,652	0,295	ARC	0.89	0.131
Eye position	1,03	0,12	0,539	0,120	EP	0.845	0.179
Relative width of caudal peduncule	0,41	0,05	0,302	0,040	RWPd	0.795	0.022
Relative height of head	0,37	0,03	0,499	0,073	RHHd	-0.766	-0.139
Relative height of mouth	0,09	0,02	0,127	0,024	RHM	0.741	0.109
Relative height of caudal peduncule	0,41	0,03	0,488	0,057	RHPd	-0.701	-0.113
Depression index	0,67	0,05	0,764	0,051	DI	-0.685	-0.101
Relative width of mouth	0,49	0,05	0,561	0,047	RWM	-0.612	-0.226
Relative length of caudal peduncule	0,18	0,01	0,200	0,021	RLPd	-0.475	-0.181
Relative width of head	1,11	0,19	1,206	0,067	RWHd	-0.397	-0.027
Relative length of maxillary barbel	0,27	0,03	0,291	0,036	RLMb	-0.367	0.197
Relative body height	0,24	0,02	0,271	0,028	RHB	-0.365	-0.037
Eigenvalues						9.842	4.279
Eigenvalues predicted by Broken-Stick						4.3	2.49
Proportion of the variances (%)						42.79	25.82

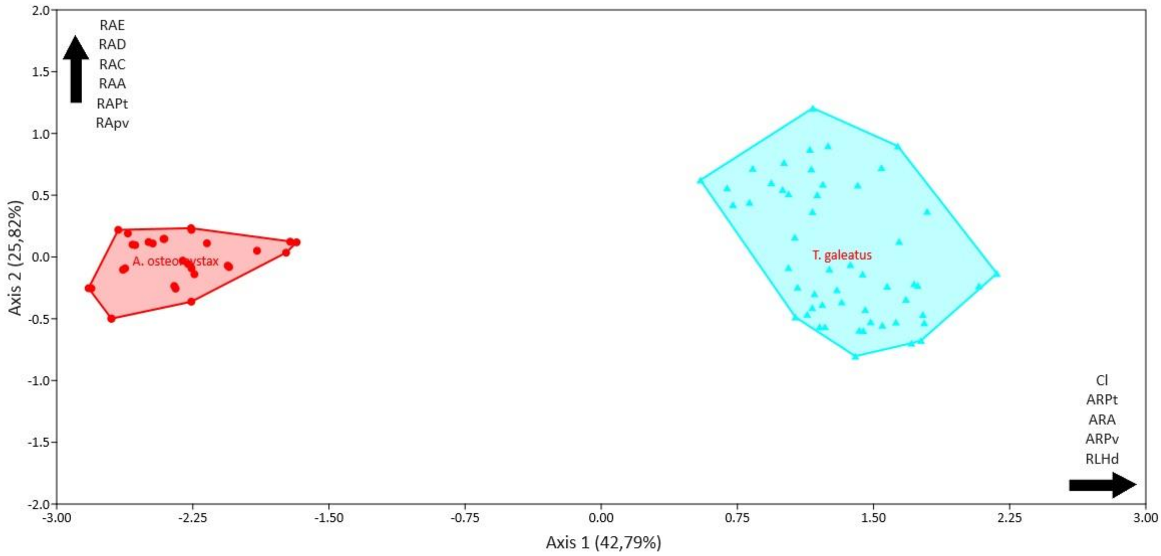

Figure 16 (4). Ordination diagram of the first two PCA axes for the 23 morphological attributes of *A. osteomystax* (●) and *T. galeatus* (Δ). Some points may overlap due to the values. CI = Compression index; ARPt = Aspect ratio of pectoral fin; ARA = Aspect ratio of anal fin; ARPv = Aspect ratio of pelvic fin; RLHd = Relative length of head; RAE = Relative area of eye; RAD = Relative area of dorsal fin; RAC = Relative area of caudal fin; RAA = Relative area of anal fin; RAPt = Relative area of pectoral fin; RAPv = Relative area of pelvic fin. Total variation explained by axis 1 and axis 2 = 68.61%.

4.2.14 Diet results

We identified 25 different food items, such as Arachnids, Insects, Myriapods, Crustaceans, Molluscs, Fish, Algae, Terrestrial Plant and Detritus, which was organized separately (Figure 4, Supplementary material – Table 1). By the observance of the prey categories of *A. osteomystax* and *T. galeatus*, it was possible to notice the difference in the food resources use, since the first species consumed mostly autochthonous resources (Odonata Nymph and Ephemeroptera Nymph as Aquatic insects and a little proportion of Copepoda as Microcrustacean), while the second consumed mostly allochthones resources (Coleoptera Adult, and Hymenoptera Adult as Terrestrial invertebrates, as well as fruits and seeds as Terrestrial Plants) (Table 4, Figure 5). However, it should be noted that the species shared a small portion of the allochthonous resources, since *A. osteomystax* consumed terrestrial invertebrates in low representation (Table 4, Figure 6). The niche breadth showed a narrower niche breadth of *A. osteomystax* (H’ = 0.93) related to *T. galeatus* (H’= 1.10), and the Pianka’s index showed a low dietary niche overlap between species (Ojk = 0.12).

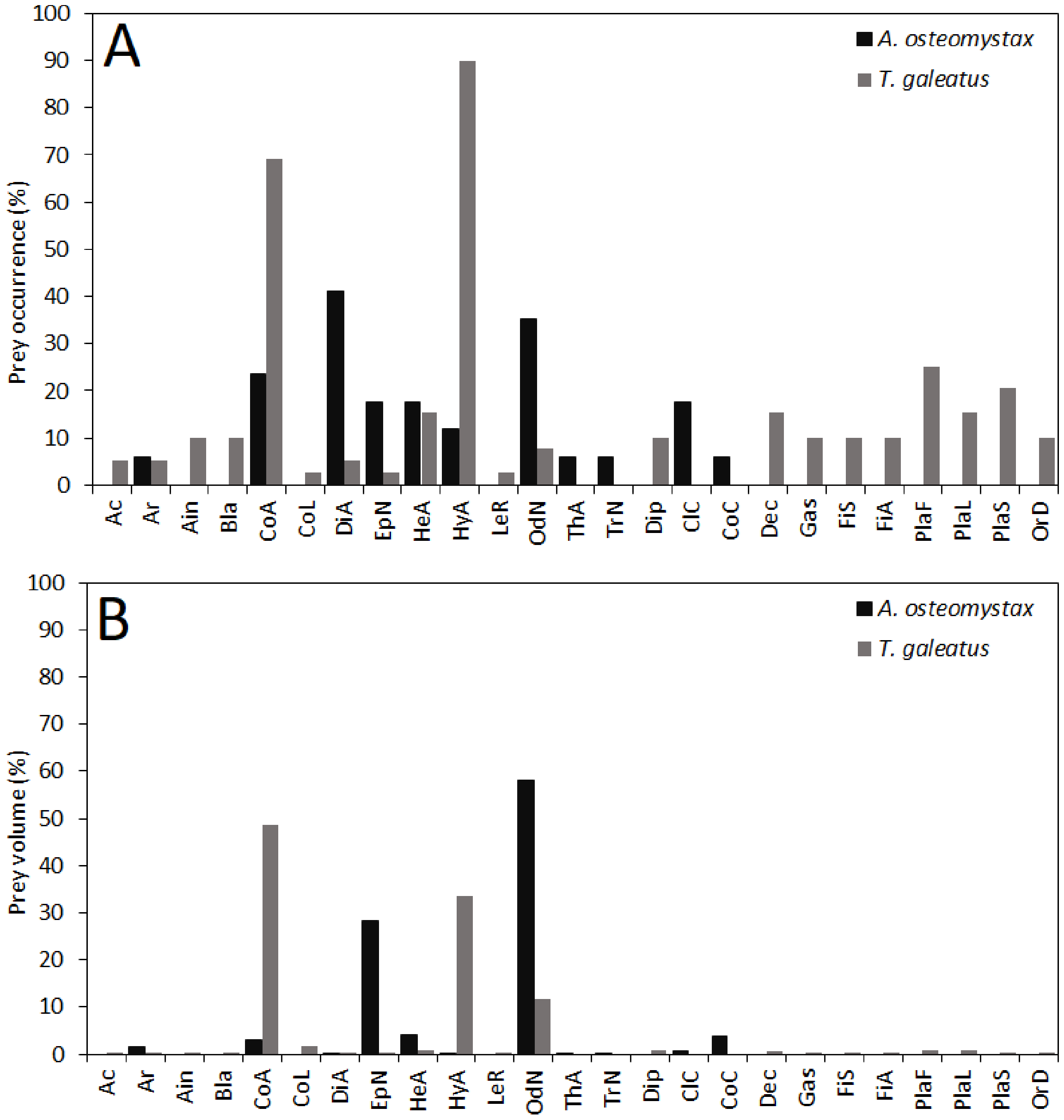

Figure 17 (5). Frequency of occurrence (A) and volume (B) of the prey items in the stomach content of *A. osteomystax* and *T. galeatus*. Prey items with frequency of occurrence equal to zero was excluded to the representation. Ac= Terrestrial Acari; Ar= Aranae; Ain= Aquatic insect fragment; Bla=Blattodea adult; CoA = Coleoptera adult; CoL=Coleoptera larvae; Dia= Diptera adult; EpN = Ephemeroptera nymph; HeA= Hemiptera adult; HyA= Hymenoptera adult; Ler= Lepidoptera adult; OdN = Odonata nymph; ThA= Thysanoptera adult; TrN= Trichoptera nymph; Dip = Diplopoda; ClC= Cladocera; Coc= Copepoda; Dec = Decapoda(Shrimp); Gas= Gastropoda; FiS= Fish scale; FiA = Filamentous algae; PlaF= Plant fragment (fruit); PlaL= Plant fragment (leaf and stick); PlaS= Plant fragment (seed); Ord = Organic detritus.

Tabel 15 (4). Diet composition (%) of *A. osteomystax* and *T. galeatus* in the Lower Paranapanema River, Paraná and São Paulo states.

Prey category	**Species**	
	A. osteomystax **n** 30	*T. galeatus* **n** 54
	Volume (%)	Volume (%)
Aquatic Insect	86.48	2.32
Terrestrial invertebrates	8.80	95.18
Microcrustacean	4.71	0.01
Macrocustacean	0.00	0.60
Mollusc	0.00	0.00
Fish	0.00	0.00
Algae	0.00	0.00
Terrestrial Plant	0.00	1.90
Detritus	0.00	0.00
Other	0.00	0.00
Sum	100.00	100.00

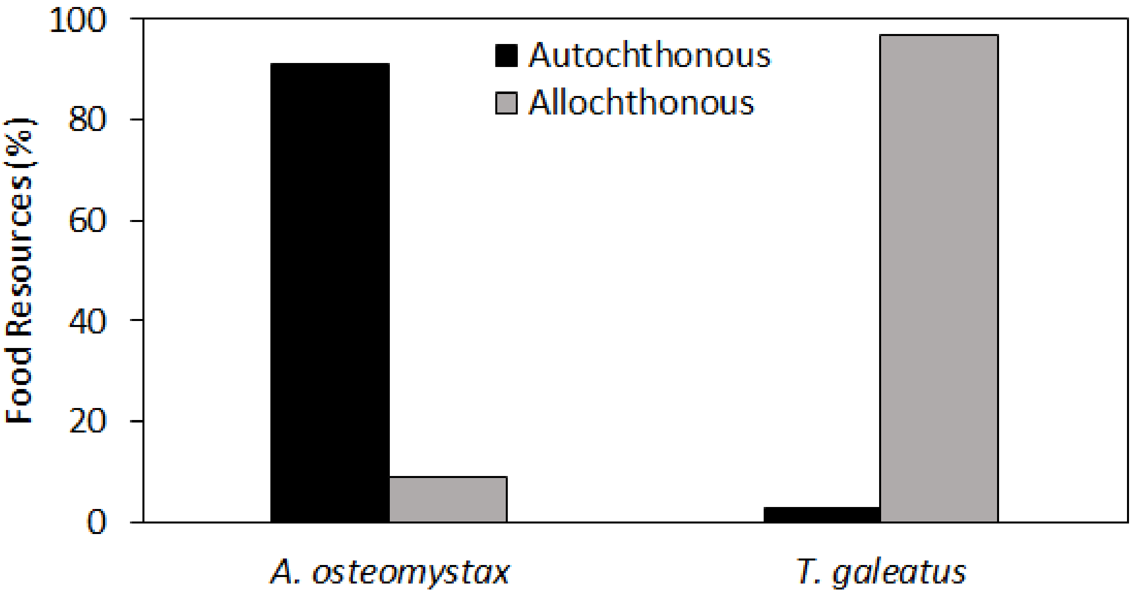

Figure 18 (6). Food resourches (Volume=%) used for *A. osteomystax* and *T. galeatus* in the Lower Paranapanema River, Paraná and São Paulo states.

The PERMANOVA again showed significant difference in diet composition between the species (pseudo-$F_{(0.163)}$: 13.06; p = 0.001), and the PCOA evidenced separation. When together, axis 1 and axis 2 explained 57.61% of the variance of data (Figure 7). Thus, *A. osteomystax* is located in a restrict portion of the positive side of the second axis, while *T.*

galeatus is scattered mostly in the positive side of the first axis, as well in both sides of the second one (Figure 7).

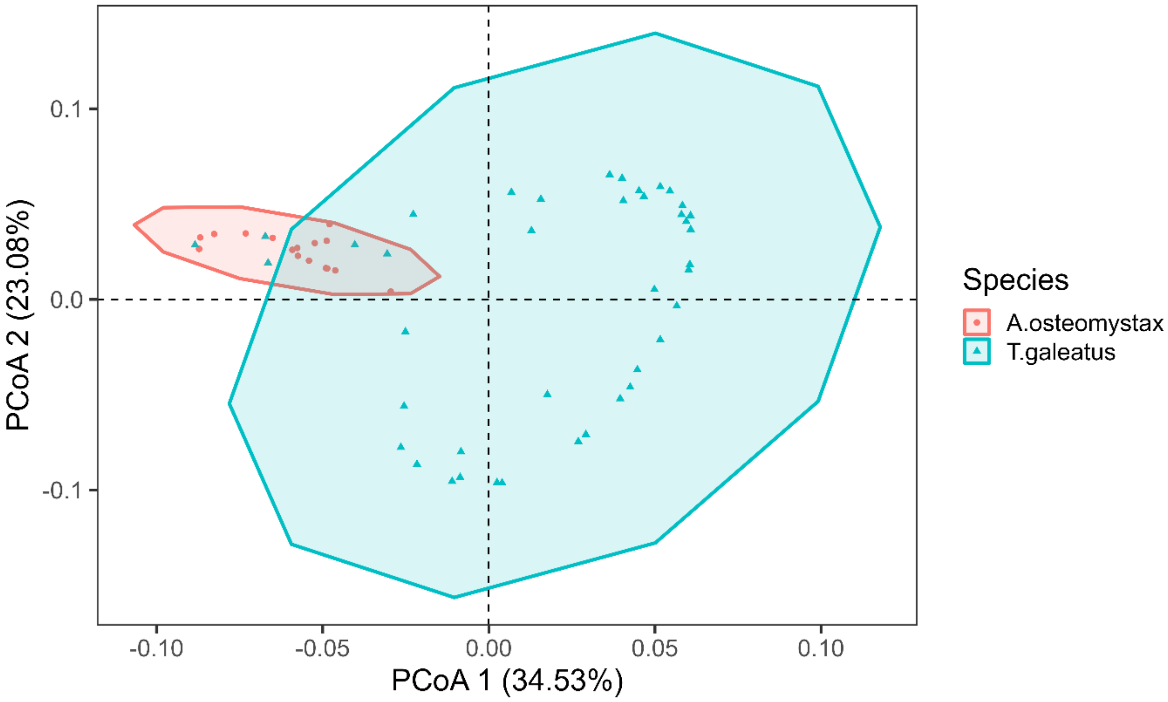

Figure 19 (7). Ordination diagram of the first two PCoA axes for the diet of *A. osteomystax* (●) and *T. galeatus* (Δ). Total variation explained by axis 1 and axis 2 = 57.61%. Some points may overlap due to the values.

4.2.15 Discussion

Despite *A. ostemystax* and *T. galeatus* are phylogenetically related and occur in the same environments in their native distribution, our results showed morphological and dietary segregation between non-native populations. Thus, there is a difference in dietary niche breadth and low overlap, indicating a mild competition for resources. Morphological differences related to swimming and foraging could favour the coexistence between these species, even in a new environment where they are non-native. Morphology and diet correlations in fishes are constantly observed (Neves *et al.*, 2015; Pease *et al.*, 2018; Baldasso *et al.*, 2019), which supports the idea that the first influences the second (Garcia *et al.*, 2020). In this sense, sympatric species tend to differ in habitat use and feeding ecology to avoid competitive exclusion (Hardin, 1960; Schoener, 1974). This pattern was also observed in 12 Cichlids in Mexico (Pease *et al.*, 2018), fours Auchenipterids (including the genera *Auchenipterus* and *Trachelyopterus*) in the Brazilian Amazon (Freitas *et al.* 2017), three Characids in the Iguaçu River (Mise *et al.*, 2013), two Characids (Carniatto *et al.*, 2017) and two Serrasalmids (Alvez *et al.*, 2017) in the Upper Paraná River, and two Heptapterids in the Lower Paranapanema River, our study area (Garcia *et al.*, 2020). Although, the most concrete example must be the feeding segregation at deeper levels and divergent spatial distribution between the non-native predators *Plagioscion squamosissimus* (Heckel, 1840) and *Cichla monoculus* (Spix & Agassiz, 1831) in the neighboring Capivara Reservoir, avoiding competition (Capra & Bennemann, 2009).

In our study, morphological indexes such as body compression, aspect ratio and relative area of fins, relative length of head, and area of eye were the main segregators of the species. These differences may demonstrate how the species occupy and exploit the habitats. For *A. ostemystax,* a higher area of eyes (as well as your position on the head), is demonstrated as visual acuity for detecting food and a superior position in the water column (Kirchheim & Goulart, 2010; Tonella *et al.* 2018), while the smaller eyes of *T. galeatus* show us that this species can inhabit deeper sites and explore the bottom (Gatz Jr., 1979; Oliveira *et al.*, 2010). Likewise, the *A. osteomystax* higher area of the fins is related to species that live in habitats with flow requiring fins for stabilization, sudden turns, and acceleration (Gatz Jr., 1979; Breda *et al.*, 2005; Oliveira *et al.*, 2010), especially because the species presented bifurcated caudal fin (Gatz Jr., 1979). On the other hand, *T. galeatus* high body compression denotes the occupation of lentic habitats (Gatz Jr., 1979; Watson & Balon, 1984), being the high aspect ratio of fins (in special of anal and pelvic fins) related to maneuverability capacity and relationship with the bottom, most common in benthic species (Breda *et al.*, 2005). Thus, several authors assume that *T. galeatus* inhabits structured lentic environments, such as bottoms with leaves, rock crevices, and submerged plants and wood (De Souza *et al.*, 2016; Freitas *et al.*, 2017; Souza *et al.*, 2017).

It should be noted that *T. galeatus* showed a large morphological variation. To the Pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), the morphological variations in non-native populations could be related to the strategy of invasion of new environments (Vila-Gispert *et al.*, 2007). To populations of Neotropical Cichlids inhabiting lotic and lentic sites of the Upper Paraná River, was verified the selection of traits to better help individuals to swim in these sites, which also influenced their diet (Sampaio *et al.*, 2013). In this sense, *T. galeatus* morphological range may also be an advantage in biological invasion and habitat exploitation over *A. osteomystax*, which maintained narrow morphological traits, reflecting in your spatial distribution and feeding ecology. In the Brazilian Amazon, Freitas *et al.* (2017) observed the preference of some *Auchenipterus* to inhabit flow habitats, while *Trachelyopterus* was more related with lentic sites. To the Upper Paraná River, was verified that *A. osteomystax* occurs in rivers, channels and lagoons connected to lotic habitats, however it is not usually present in isolated lagoons, as *T. galeatus* (Oliveira *et al.* 2010). *Trachelyopterus galeatus* can survive in habitats with low oxygen concentrations, distributing itself in abundance in lentic environments such as lagoons (Soares *et al.*, 2006; De Souza *et al.*, 2016). Many studies showed that the species is favored in flooded and backwater habitats (Soares *et al.*, 2006; Peretti & Andrian, 2008; De Souza *et al.*, 2016), such as impoundments (Garcia *et al.*, 2018b, Garcia *et al.*, 2020). In contrast, *A. ostemystax* could present lower abundance in reservoirs, as verified in the Brazilian Pantanal (Barilli *et al.*, 2012). Since spatial distribution and morphology were different, it could have influenced diet segregation. Even though both species feeding on insects, we found a segregation at deeper levels, same result observed in the Capivara reservoir for two coexisting non-native predators (Capra & Bennemann, 2009).

A*uchenipterus ostemystax* revealed a narrower niche breadth with restrict diet mostly composed by aquatic insects (autochthonous resources), suggesting specialist behaviour supported by morphological traits of eye, mouth position and body shape (Barilli *et al.*, 2012; Tonella *et al.*, 2018). However, these same traits seem to not influence the species to consume allochthones resources in the water column, as expected. In some regions of Amazon, species of *Auchenipterus* showed preference of terrestrial insects (Freitas *et al.*, 2016), while in others they keep the preference of autochthonous resources even during different seasons (Freitas *et al.*, 2022). Thus, or results also displayed a slight flexibility of diet (consuming terrestrial insects and microcrustaceans in low proportions), which may have ensured the success of its colonization in the Upper Paraná River (Barili *et al.* 2012; Tonella *et al.*, 2018). This flexibility could be related with the food availability (Carniatto *et al.*, 2017; Baldasso *et al.*, 2019), since a previous study with *A. osteomystax* in the same reservoirs observed the use of microcrustaceans in sites that did not provide many insect resources (Garcia *et al.* 2018b). In the other hand, the exclusive use of autochthonous resources could be a response to the presence of the sympatric *T. galeatus* to avoid interspecific competition (Nieto *et al.*, 2023), pattern also presented by congeneric species of *Astyanax* in the Iguaçu River (Mise *et al.*, 2013), and to *Moenkhausia* species (Carniatto *et al.*, 2017), and heptaperids species (Garcia *et al.*, 2020) in the same watershed.

Trachelyopterus galeatus showed a broader niche breadth but preferred terrestrial invertebrates and plants (allochthonous resources). The morphology and maneuverability capacity could allow the species to explore different habitats, capturing food both on the surface and at the bottom (Peretti & Andrian, 2008; Souza *et al.*, 2017). The species has a cylindrical body, protractible mouth and barbels that help in the foraging (Ferraris Jr., 2003;

Ota *et al.*, 2018). However, the head length and the mouth width may be the morphological trait which most influences the diet, since allow the capture of larger preys (Freitas *et al.*, 2017, Souza *et al.*, 2017), as verified to species of *Rhamdia* in the Iguaçu River (Baldasso *et al.*, 2019). So, several studies reported the diet composition of the species, demonstrating the adaptive capacity and the generalist/oportunistic strategy of *T. galeatus* in different environments (Santos, 2005; Peretti & Andrian, 2008; Ximenes *et al.*, 2011; Garcia *et al.* 2018b, 2020b). We found larger winged Coleoptera and Hymenoptera (40 mm of length), as well as fruits and seeds (30 mm of length) whole inside the stomach of fish. So, was denoted the oportunistic behavior (Garcia *et al.*, 2020b; Bianchi-Costa *et al.*, 2023) since winged insects performs sudden reproductive flights (Galinha & Hahn, 2004) and plants release fruits and seeds only in short periods (Correa *et al.*, 2015). Nevertheless, this behaviour is only possible due to the presence of suitable morphology (Kirchheim & Goulart, 2010), and favoured by the inhabit of lentic habitats due to proximity to the surroundings and higher influx of terrestrial preys (Soares *et al.*, 2006; De Souza *et al.*, 2016). In contrast, *A. ostemystax* prefer flow habitats (Oliveira *et al.* 2010) and has a smaller snout and narrow mouth (Ferraris Jr., 2003; Ota *et al.*, 2018), which could limit its capacity of capture larger preys (Kirchheim & Goulart, 2010). In this way, morphological variations influenced the spatial distribution and diet of fish, contributing to the trophic segregation and avoiding exclusive competition by species (Barros *et al.*, 2017; Baldasso *et al.*, 2019; Garcia *et al.*, 2020; Nieto *et al.*, 2023).

Although our study was not able to evaluate this, the interference of both non-native species on similar native species and native fish assemblage in general must be considered. For example, native species of Auchenipteridae to the Upper Paraná River such as *Tatia neivai* (Ihering, 1930) and *Ageneiosus militaris* Valenciennes, 1835 may suffer directly with the presence of *A. osteomystax* and *T. galeatus*. The small catfish "noivinha" *T. neivai* has behavior and diet very similar to the results obtained for *A. osteomystax*, that is, capturing of small prey in the water column and surface (Severo-Neto *et al.*, 2023). On the other hand, the medium-sized "palmito" *A. militaris* feeds on larger preys (Hahn *et al.*, 2004), where the generalist/opportunistic behavior of *T. galeatus* may be a threat. In addition, the feeding behavior and spatial distribution of *T. galeatus* in the structured marginal zone can results in competition with several small-sized species with similar habits and diet, such as representatives of Characidade and Cichlidae (Hahn *et al.*, 2004). Finally, the cryptic coloration of *T. galeatus* may contribute to the capture of prey and avoid of predators in these environments (Bulla *et al.*, 2011), a capacity not presented by *A. osteomystax*.

Concluding, our results revealed morphological differences between the sympatric non-native auchinepterids, which can be determinant in the spatial segregation and diet divergence. Although both species are insectivorous, they present particularities in the food resources use which resulted in low dietary niche overlap. *Auchenipterus ostemystax* probably occupied flow habitats behaving as a specialist of narrow dietary niche, while *T. galeatus* may occupied lentic habitats with higher dietary niche breadth and acted as opportunist/generalist, exploring since the bottom until the surface. Thus, these factors seem to be essential to coexisting species in the invaded environments, avoiding competitive exclusion. However, this ability can threaten the structure of the native assemblage, as they can compete with fish that have similar spatial distribution and feeding, as well as other species in the aquatic community. So, new studies on morphological and dietary relationships are important to better understand the interactions between Neotropical fish, especially non-native species in reservoirs that display a range of strategies to colonize these man-made environments.

4.2.16 Acknowledgment

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4.2.18 Supplementary Material

4.2.19 Material and Methods

4.2.20. Samplings

Our samplings were performed quarterly from September 2018 to September 2020: Rosana Reservoir – site 1 (22.601220 S, 52.165324 W), site 2 (22.601569, 52.160614), site 3 (22.600590, 52.160098), site 4 (22.636232, 52.161589), site 5 (22.612902, 52.162611), site 6 (22.636299, 52.158774), and site 7 (22.599940, 52.159673). Taquaruçu Reservoir - site 1 (22°39’15.0”S 51°40’42.0”W); site 2 (22°39’37.0”S 51°37’53.8”W); site 3 (22°41’24.7”S 51°34’50.5”W); site 4 (22°41’10.8”S 51°32’20.9”W), site 5 (22.676369 S, 51.714037 W), site 6 (22.667733 S, 51.683496 W), and site 7 (22.657963 S, 51.658144 W).

4.2.21 Results

Table 16 (S1). Prey items of the diet of *A. osteomystax* and *T. galeatus* from the Lower Paranapanema River, Paraná and São Paulo states. Prey items with frequency of occurrence equalto to zero was excluded.

Prey item		**Species**			
		A. osteomystax		*T. galeatus*	
		n 30		**n** 54	
		Frequency of occurrence (%)	Volume (%)	Frequency of occurrence (%)	Volume (%)
Arachnid	Terrestrial Acari	0.0	0.00	5.1	0.01
	Araneae	5.9	1.56	5.1	0.05
Insect	Aquatic Insect Fragment	0.0	0.00	10.0	0.09
	Blattodea Adult	0.0	0.00	10.0	0.09
	Coleoptera Adult	23.5	2.97	69.2	48.66
	Coleoptera Larvae	0.0	0.00	2.6	1.59
	Diptera Adult	41.2	0.09	5.1	0.04
	Ephemeroptera Nymph	17.6	28.24	2.6	0.04
	Hemiptera Adult	17.6	4.10	15.4	0.74
	Hymenoptera Adult	11.8	0.05	89.7	33.63
	Lepidoptera Adult	0.0	0.00	2.6	0.04
	Odonata Nymph	35.3	58.23	7.7	11.63
	Thysanoptera Adult	5.9	0.04	0.0	0.00
	Trichoptera Nymph	5.9	0.01	0.0	0.00
Myriapoda	Diplopoda	0.0	0.00	10.0	0.88

Prey item		**Species**			
		A. osteomystax		*T. galeatus*	
		n 30		**n** 54	
		Frequency of occurrence (%)	Volume (%)	Frequency of occurrence (%)	Volume (%)
Crustacean	Cladocera	17.6	0.82	0.0	0.00
	Copepoda	5.9	3.90	0.0	0.00
	Decapoda (Shrimp)	0.0	0.00	15.4	0.52
Mollusc	Gastropoda	0.0	0.00	10.0	0.01
Fish	Fish Scale	0.0	0.00	10.0	0.04
Algae	Filamentous Algae	0.0	0.00	10.0	0.12
Terrestrial Plant	Plant Fragment (fruit)	0.0	0.00	25.1	0.75
	Plant Fragment (leaf and stick)	0.0	0.00	15.4	0.87
	Plant Fragment (seed)	0.0	0.00	20.6	0.06
Detritus	Organic Detritus	0.0	0.00	10.0	0.12
Sum		100.00	100.00	100.00	100.00

4.3 CAPÍTULO 3

MORPHOLOGICAL DEFORMITIES IN NON-NATIVE CATFISH *TRACHELYOPTERUS GALEATUS* (LINNAEUS, 1766) IN THE UPPER PARANÁ RIVER, BRAZIL: A SIGN OF HUMAN IMPACT?

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BRIEF COMMUNICATION

JOURNAL OF FISH BIOLOGY

Morphological deformities in the invasive driftwood catfish *Trachelyopterus galeatus* in the Upper Paraná River basin, Brazil: a sign of human impact?

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4.3.1 Tittle - Morphological deformities in non-native catfish *Trachelyopterus galeatus* (Linnaeus, 1766) in the Upper Paraná River, Brazil: a sign of human impact?

4.3.2 BRIEF COMMUNICATION

4.3.3 Morphological deformities in non-native catfish *Trachelyopterus galeatus* (Linnaeus 1766) in the Upper Paraná River, Brazil: a sign of human impact?

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4.3.6 CORRESPONDENCE

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4.3.7 FUNDING INFORMATION

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4.3.8 ABSTRACT

Here we report the presence of morphological deformities in *Trachelyopterus galeatus* (Auchenipteridae), a non-native catfish occurring in the Upper Paraná River basin, Brazil. The frequency of anomalous individuals reached 18.5% of all catches. X-ray images have showed anomalies, or total absence of structures, in the pelvic girdle. Also, we observed the absence of the adipose fin and mental barbells. Recording these findings is of extreme importance for evidencing the human impact in aquatic communities since this sort of information can be used in the management systems and environmental monitoring.

Keywords: Basin fragmentation, Cascade of reservoirs, Contaminants, Paranapanema River, South America.

Morphological deformities have been described for different species of fish around the globe in marine (Gangan *et al.,* 2018; Jawad *et al.,* 2018), and freshwater ecosystems (Rutkayová *et al.*, 2016; Da Silva and Casas, 2020). The development of abnormal bones and anomalies in the morphology of fish occurs during their early life stages, nearly in any case, associated with environmental conditions (Sfakianakis *et al.* 2004), endogamy (Tave *et al.,* 1983), or pollution (Browder *et al.,* 1993; Lemly, 2002). Hence, the recording of anomalies in the morphology of individuals may evidence human impact on aquatic communities (Browder *et al.,* 1993; Lemly, 2002).

Trachelyopterus galeatus (Linnaeus, 1766) is a non-native species occurring in the Upper Paraná River (Orsi *et al.*, 2016). Its introduction was favored by the establishment of the Itaipu reservoir, which in 1982 eliminated the geographical barrier of the Sete Quedas Falls (Júlio Júnior *et al.*, 2009). Deformities related to fins have been well documented for both captive (Sfakianakis *et al.,* 2004), and wild individuals (Jawad *et al.,* 2018). However, we observed wild individuals of *T. galeatus* displaying alterations in the pelvic and adipose fins, as well as in the barbells, which are records less common in nature (Gangan *et al.,* 2018), and specially less common in Brazil (Mise *et al.,* 2017; Da Silva and Casas, 2020).

During the monitoring of ichthyofauna in the Lower Paranapanema River (Project nº 11218/2018), 54 individuals of *T. galeatus* were captured between spring 2018 and spring 2019 with the help of gill nets in the Taquaruçu (22°32'37.22"S-52° 0'0.58"O), and Rosana reservoirs (22°36'3.15"S-52°52'15.75"O). Individuals were anesthetized and euthanized by overexposure to clove (oil 1g/ml), kept in formalin 10% for 48 hours and further transferred to alcohol 70%. The collection license (license number 16578), and the Animal Ethics Committee have authorized the field sampling (CEUA Nº 30992.2014.33).

The study of fish deformities was based on the comparison between external morphology and X-ray images of anomalous and a normal individual (*e.g.*, MZUEL-20791). Morphological alterations caused by capturing, handling, or the attack of other organisms were not considered. The frequency of anomalous individuals reached 18.3% for both reservoirs, and it was arranged into five categories where some individuals have showed more than one anomaly (Table 1).

Table 17 (1). Morphological deformities and observed frequency (%) in *Trachelyopterus galeatus* of the Lower Paranapanema River between spring 2018 to spring 2019.

Recorded deformity	**Reservoir**		**%**	**Voucher**
	ROS	TAQ		
Total absence of the pair of the pelvic fins	X	X	5.5%	MZUEL-20787; MZUEL-20782
Total absence of the adipose fin	X		5.5%	MZUEL-20787
Total absence of one of the pelvic fins and total absence of one of the posterior mental barbel	X		3.7%	MZUEL-20787
Total absence of one of the pelvic fins and one of the pelvic fins with malformation		X	1.8%	MZUEL-20786
Total absence of one of the anterior mental barbel	X		1.8%	MZUEL-20787

Abbreviations: ROS, Rosana Reservoir; TAQ, Taquaruçu Reservoir.

Based on the morphological and x-ray images, it was possible to visualize the pelvic girdle in its normal condition displaying its morphological structures in the MZUEL-20791 specimen (Figure 1a, Figure 2a). In the MZUEL-20787 specimen (Figure 1b, Figure 2b), the left pelvic fin did not have the pelvic-fin rays. In both fins of the MZUEL-20786 specimen (Figure 1c, Figure 2c), it was unfeasible to identify some bones such as the basipterygium, anterolateral process and anteromedial process, since they were in a state of malformation as well as the pelvic-fin rays (right pelvic fin), which were reduced in size and smaller in numbers. Moreover, the pelvic girdle was completely absent in the MZUEL-20787 specimen (Figure 1d, Figure 2d). In the MZUEL-20791 specimen (Figure 1e), was possible to visualize the adipose fin in its normal condition, while in the MZUEL-20787 specimen the structure was completely absent (Figure 1f). In the MZUEL-20791, the pairs of the anterior and the posterior mental barbells were present (Figure 1g), while in the MZUEL-20787 one of the posterior (Figure 1h), or anterior (Figure 1i), mental barbell was absent.

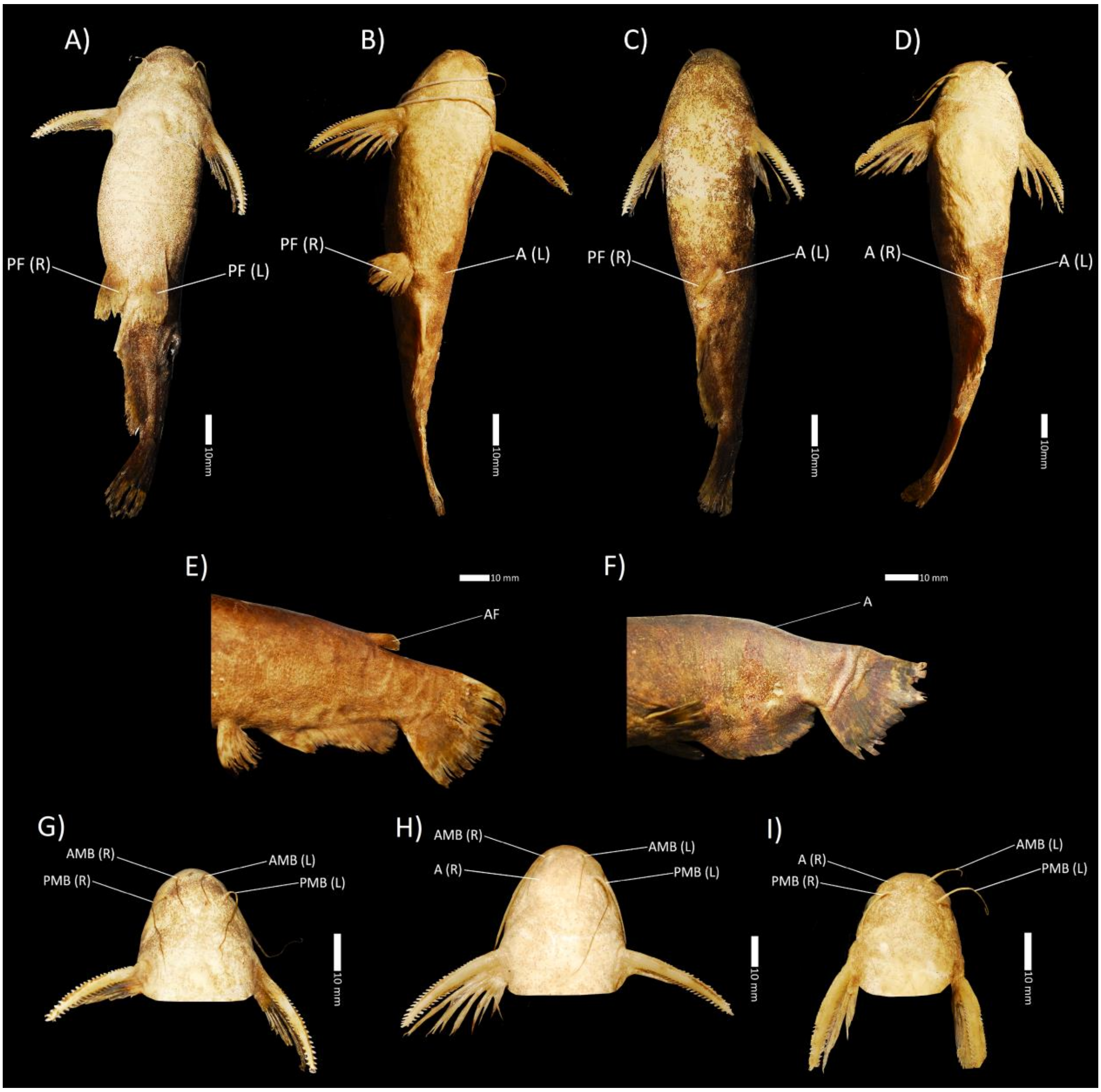

Figure 20 (1). *Trachelyopterus galeatus* specimens in ventral view. a, e, g) MZUEL-20791, 137.62 mm SL; b, h) MZUEL-20787, 152.79 mm SL; c) MZUEL-20786, 12.00 mm SL; d) MZUEL-20787, 141.09 mm SL; f) MZUEL-20787, 136.52 mm SL; i) MZUEL-20787, 143.64 mm SL. L, left; R, right; PF, pelvic fin; AF, adipose fin; AMB, anterior mental barbell; PMB, posterior mental barbell; A, absent. Scale bars equal 10 mm.

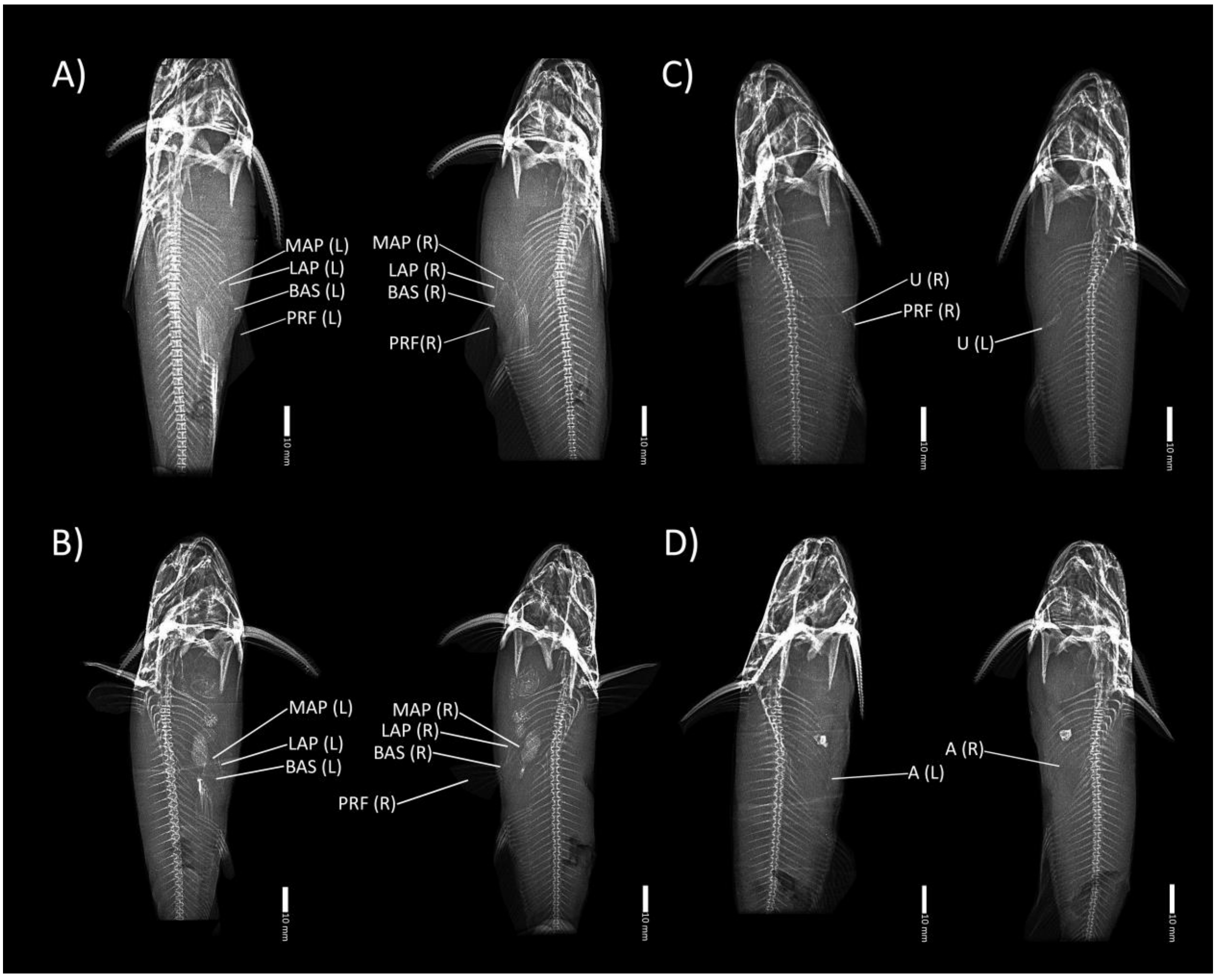

Figure 21 (2). *Trachelyopterus galeatus* specimens x-ray with deformation. Pelvic girdle in left oblique and right oblique views. a) MZUEL-20791, 137.62 mm SL; b) MZUEL-20787, 152.79 mm SL; c) MZUEL-20786, 12.00 mm SL; d) MZUEL-20787, 141.09 mm SL. L, left; R, right; BAS, basipterygium; LAP, anterolateral process; MAP, anteromedial process; PFR, pelvic-fin rays; U, undefined; A, absent. Scale bars equal 10 mm.

Studies in the Guaíba Lake demonstrated alterations in the rays and spines dysplasia in ossified fins of several groups of fish (Malabarba *et al.,* 2004; Flores-Lopes and Reuss-Strenzel, 2011), while for the Iguaçu River these alterations were also found in the adipose fin of Callichthyidae individuals (Mise *et al.,* 2017). However, serious alterations, such as the total absence of pelvic fins and bones of pelvic girdle, have been recorded only in freshwater Elasmobranchii individuals in the Liberdade River (Da Silva and Casas, 2020). Thus, the partial or complete absence of pelvic girdle structures is a new record for the Actinopterygii individuals in Brazil and in the Upper Paraná River, having such alterations just been showed over controlled experiments in the United States (Tave *et al.,* 1983).

The absence of pelvic fins may harm the ecology of *T. galeatus*, since these structures are important for the body stabilization during swimming, especially in slow speeds swimming (Standen, 2010). Also, these species feed in lentic environments of high complexity (with leaves, rocks, macrophytes and driftwood), which that require from fish good maneuverability (Freitas *et al.*, 2017). In addition, the absence of pelvic fins may result in a decrease of the evasion ability when facing a predator (Kawabata *et al.*, 2016). These losses may be increased by the absence of the adipose fin, since it is known that these structures can help the caudal fin during the swimming (Reimchen and Temple, 2004), and performing a sensorial function (Aiello *et al.*, 2016).

The pelvic fins may also be used during the fertilization process and protection of the eggs (Py-Daniel and Fernandes, 2005), while its absence can result in changes in the density of the eggs during spawning (Ostrander *et al.*, 1985). Auchenipteridae individuals can exhibit alterations in the pelvic fins and barbells for breeding purposes (Py-Daniel and Fernandes, 2005), where the deformed individuals can suffer disadvantages during reproductive periods. Additionally, the deformities in the barbells can harm sensorial functions of survival, feeding, and swimming stabilization in the larval stage (Godinho *et al.*, 2003).

The populations of *T. galeatus* in the Lower Paranapanema River may have been isolated by the construction of the Rosana (1987) and Taquaruçu Dams (1989) (Orsi *et al.*, 2016), thus, restricting the gene flow and increasing endogamy which have led to the presence of deformities (Browder *et al.*, 1993; Lemly, 2002). Moreover, the incidence of deformities above 15% is pertinent (Tave *et al.*, 1983), giving evidence to the high degree of environmental impact. Deformed individuals have difficulties in reaching the adulthood, as they become more susceptible to predation (Gangan *et al.*, 2018). However, deformed individuals can reach maturity in environments without predators (Lemly, 2002), which may have been occurred in the Lower Paranapanema River since the Rheophilic predators are currently reduced by the fragmentation of the basin (Orsi *et al*., 2016).

Deformities may also be related to teratogenic processes generated by chemical pollutants, such as heavy metals arising from human activities (Browder *et al.*, 1993; Lemly, 2002). In this sense, it is known that the surroundings of the Rosana and Taquaruçu reservoirs are exposed to agriculture, livestock, and discharge of domestic and industrial effluents (Cunico *et al.*, 2006; Vidotto-Magnoni *et al.*, 2015). Therefore, this record of fish deformities here might denote the poor water quality in these environments (Mise *et al.*, 2017), which may also compromise the native fish communities (Malabarba *et al.*, 2004; Flores-Lopes and Reuss-Strenzel, 2011). On the other hand, the water might become unsuitable for human use (Mise *et al.*, 2017), while the reservoirs are currently being exploited for fishing, sporting fishing, irrigation, and recreation (Orsi *et al.*, 2016). Thus, further analysis should be carried out to clarify the factors that are influencing the deformities observed here (Rutkayová *et al.*, 2016; Jawad *et al.*, 2018).

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4.3.10 CONTRIBUTIONS

All authors contributed to manuscript preparation. J.D.F, D.A.Z.G., A.C.R.C.: fish collection, project conception and design, data analysis and interpretation of data; J.R.L.: fish collection, data analysis and interpretation of data; F.S.A., M.L.O.: project conception and design, interpretation of data and funding.

4.3.11 SIGNIFICANCE STATEMENT

Here we reported morphological deformities in a species from the Upper Paraná River, superior to 15%. We performed comparisons between anomalous and normal fish using morphological and x-rays images. Hence, we observed the absence of barbells, adipose fin, pelvic fins, and absence of structures of the pelvic girdle. Our findings might be related to the human impacts in the environment, being such results of great importance to management systems and environmental monitoring.

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4.3.13 REFERENCES

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5. CONCLUSÃO GERAL

A dieta, ecologia alimentar e ecomorfologia da ictiofauna de dois reservatórios vizinhos foram avaliadas e encontradas divergências que podem estar relacionadas com a heterogeneidade ambiental. Sendo assim, a assembleia de peixes do reservatório de Rosana explora mais recursos alóctones e apresenta comportamento tendente à especialização, enquanto a assembleia de peixes do reservatório de Taquaruçu tende ao uso de recursos autóctones, porém com espécies apresentando comportamento generalista na exploração deste recurso. Em adição, houve alta sobreposição de nichos alimentares impulsionada por espécies não-nativas, especialmente no reservatório de Taquaruçu. As espécies alteraram sua dieta entre os reservatórios, o que demonstra plasticidade alimentar, todavia, as espécies nativas apresentaram menor flexibilidade alimentar do que as espécies não-nativas, reforçando a capacidade das últimas em colonizar novos ambientes.

Conclui-se que as populações do reservatório de Rosana responderam mais próximas daquelas dos trechos livres de barragem da planície de inundação do Alto Rio Paraná, enquanto as do reservatório Taquaruçu se comportam como a maioria presente nos reservatórios brasileiros, corroborando a tendência de compartimentalização na cascata de reservatórios. A partir disso, a análise de ecomorfologia demonstrou que mesmo espécies não-nativas aparentadas possuem diferenças morfológicas para a exploração ambiental e alimentação, bem como variações em sua plasticidade alimentar. Esses fatores parecem ser essenciais para a coexistência de não nativos nos ambientes invadidos, ao evitar a competição exclusiva. Ainda, a análise morfológica proporcionou o registro de anomalias. Esta descrição é extremamente importante, visto que pode denotar o grau de impacto ambiental sobre os ambientes estudados vindo a influenciar inclusive a potabilidade da água na região. Portanto, mais estudos sobre dieta e morfologia são importantes para melhor compreender as interações entre peixes Neotropicais, especialmente relações entre espécies nativas e não-nativas sob diferentes graus de influência do barramento.