UNIVERSIDADE FEDERAL DO PARÁ
NÚCLEO DE ECOLOGIA AQUÁTICA E PESCA
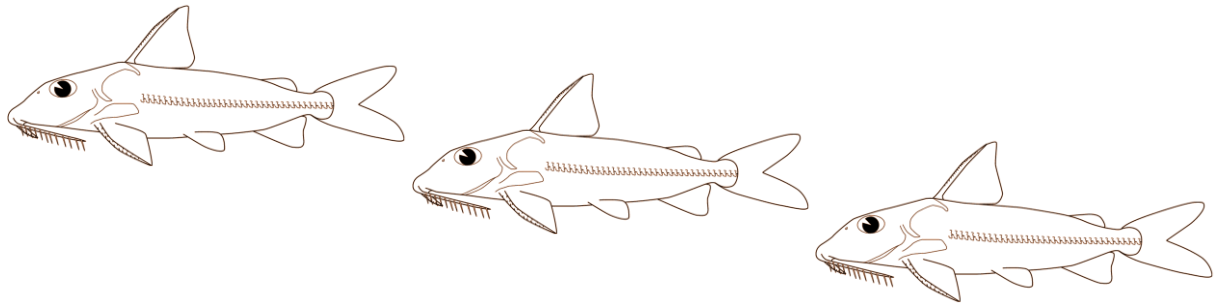PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA AQUÁTICA E PESCA

IZABELLA CRISTINA DA SILVA PENHA

Análises de conteúdo estomacal e isótopos estáveis indicam uma dieta especializada de *Doras higuchii* no trecho de vazão reduzida da barragem de Belo Monte, rio Xingu, Brasil

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Dissertação apresentado ao Programa de Pós-Graduação em Ecologia Aquática e Pesca da Universidade Federal do Pará, como requisito para a obtenção do título de Mestre em Ecologia Aquática e Pesca.

Orientador: Prof. Dr. Luciano Fogaça de Assis Montag
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RESUMO

A notável variação sazonal no nível da água durante as estações seca e cheia fazem do rio Xingu um sistema único, tanto em relação as suas paisagens quanto a biodiversidade. Essa dinâmica hidrológica é crucial na ecologia dos peixes, pois influencia diretamente na história de vida e nas estratégias biológicas das espécies. Assim, o objetivo deste estudo foi avaliar o efeito do pulso de inundação na ecologia alimentar do bagre *Doras higuchii* (Siluriformes: Doradidae) na área de influência da UHE Belo Monte, rio Xingu, Pará, utilizando 2 metodologias complementares, conteúdo estomacal e isótopos estáveis de C e N. As coletas ocorreram mensalmente entre dezembro/2020 e novembro/2021, utilizando redes de emalhar. Os indivíduos capturados foram medidos e pesados e eviscerados para remoção do estômago. Amostras de tecido muscular também foram extraídas para análises isotópicas. O conteúdo estomacal foi inspecionado, identificado e pesado para avaliação da composição de dieta, amplitude de nicho trófico e intensidade alimentar, testando a influência dos períodos hidrológicos nesses parâmetros por meio de Modelos Lineares Generalizados (GLM). A influência do pulso de inundação nas razões isotópicas de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$) dos indivíduos foi avaliada por uma ANOVA Two-Way, e a variação ontogenética de $\delta^{15}N$ por um GLM. Foram analisados 362 exemplares de *D. higuchii* (e 109 amostras de tecidos), constatando uma dieta baseada principalmente em sedimento (74,9% IAi) e insetos aquáticos (24,8%). Não foi observada variação da composição da dieta ao longo dos períodos hidrológicos, assim como na amplitude de nicho trófico. Por sua vez, os indivíduos apresentaram maior ingestão média de alimentos na cheia. A composição isotópica ($\delta^{13}C$ e $\delta^{15}N$) também não diferiu entre os períodos hidrológicos. Por fim, os espécimes não diferiram o $\delta^{15}N$ pelas ao longo do seu comprimento. Essas informações nos auxiliam na compreensão da interface entre fatores ambientais e biológicos, preenchendo lacunas no conhecimento da ecologia alimentar de peixes na Amazônia em um ambiente sobre influência de uma usina hidroelétrica de fio de água.

Palavras-chave: Alimentação, peixes, isótopos estáveis, pulso de inundação, Amazônia.

ABSTRACT

The remarkable seasonal variation in water level during the dry and flood seasons makes the Xingu River a unique system in terms of its landscape and biodiversity. These hydrological dynamics are crucial in fish ecology since they directly influence the species' life history and biological strategies. The objective of this study was to evaluate the effect of the flood pulse on the feeding ecology of the catfish *Doras higuchii* (Siluriformes: Doradidae) in the reduced flow section (RFS) of the Belo Monte dam, Xingu River, Pará. Collections were carried out monthly between December 2020 and November 2021 using gillnets. Individuals were measured and eviscerated to remove the stomach. Samples of muscle tissue were also extracted for isotopic analysis. Stomach contents were inspected, identified, and weighed to assess diet composition, trophic niche breadth, and feeding intensity, testing the influence of hydrological periods using Generalized Linear Models. Additionally, we evaluated the effect of the flood pulse on the isotopic ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) of individuals by a Two-Way ANOVA and the ontogenetic variation of δ^{15}N by GLM. A total of 362 specimens of *D. higuchii* were analyzed (tissues collected from 109 individuals), finding a diet based mainly on sediment (74.9% IAi) and aquatic insects (24.8% IAi), showing no variation among hydrological periods, as well as the range of trophic niche. On the other hand, we observed variation in feeding intensity, with higher average food intake in the flood period. The isotopic composition (δ^{13}C and δ^{15}N) did not differ across the hydrological periods either. Finally, the δ^{15}N did not vary by length classes. This information helps understand the interface between environmental and biological factors, filling gaps in the knowledge of feeding ecology of Amazonian fishes in an environment impacted by hydroelectric dam.

Keywords: Feeding, fish, stable isotope, flood pulse, Amazon.

APRESENTAÇÃO

A bacia Amazônica abriga a maior diversidade de peixes do mundo, com estimativas que podem chegar até 8.000 espécies (Santos *et al.* 2015; Reis *et al.* 2016). A elevada biodiversidade presente na região chega a corresponder cerca de 7% do total espécies de peixes encontradas no planeta (Hickman *et al.* 2014). Esta rica ictiofauna, assim como seus aspectos ecológicos, está fortemente relacionada com a dinâmica ambiental local, como a variação sazonal do nível de água dos rios, alta heterogeneidade ambiental, produtividade, dentre outras variáveis físico-químicas da água (Vannote *et al.* 1980; Junk *et al.* 1989; Freitas *et al.* 2010).

Os grandes tributários da bacia Amazônica, sofrem alterações sazonais no seu nível de água. Durante a estação cheia, os canais transbordam e alagam as vegetações marginais, formando as chamadas florestas de igapó ou várzea. Por sua vez, durante os períodos de seca, os canais dos rios sofrem um estreitamento. Esse fenômeno é chamado de pulso de inundação (Junk *et al.* 1989), que, em síntese, é definido como o fluxo natural das águas ou as mudanças sazonais no nível de vazão de água de um rio (Poff *et al.* 1997). As áreas alagadas por esse transbordamento dos rios proporcionam o aparecimento de novos locais para forrageio, reprodução e abrigo para organismos aquáticos, como os peixes. (Junk *et al.* 1989; Lowe-Mcconnell 1999). Desta forma, essa dinâmica hidrológica é crucial para a ecologia dessa fauna, uma vez que influencia diretamente na história de vida e nas estratégias biológicas das espécies (Junk 1980; Goulding *et al.* 2003; Freitas et al., 2022). Em suma, os ciclos hidrológicos possuem extrema importância no processo originário e de sustentabilidade das planícies de inundação. Com isso, o pulso de inundação se mostra como um dos principais fatores ambientais nas planícies amazônicas, fornecendo e modificando as condições abióticas desses locais, promovendo também alterações nas comunidades biológicas, produtividade, decomposição entre outros (Tundisi 2007).

Dentre os afluentes que compõe a bacia Amazônica, o rio Xingu destaca-se como o terceiro maior rio dessa drenagem e segundo maior tributário de águas claras da América do Sul (Wohl & Merritt 2001). O rio Xingu é caracterizado por possuir canais anastomosados ao longo de seu curso e extensos trechos de corredeiras que fluem sobre um leito rochoso (Camargo & Ghilardi 2009). Essas características, somadas a grande variação no nível da água durante a estação seca e cheia, fazem do rio Xingu um ambiente único, tanto com relação as suas paisagens quanto no âmbito da biodiversidade encontrada na região (Zuanon 1999; Acselrad *et al.* 2009; Nogueira *et al.* 2010). Atualmente, são registradas aproximadamente 500

espécies de peixes para a bacia do rio Xingu (Dagosta & De Pinna 2019), onde parte expressiva é considerada endêmica (Zuanon 1999; Sabaj-Pérez 2015). Os trechos do baixo e médio rio Xingu são as regiões onde essa riqueza se destaca (Camargo *et al.* 2004), com 367 espécies, sendo 87 endêmicas (Dagosta & De Pinna 2019).

As características do rio Xingu que regulam e favoreceram a ictiofauna, são as mesmas que evidenciaram um potencial de produção de energia elétrica na região (Fearnside 2006; Sabaj Pérez 2015). Nesse contexto, foi construída a Usina Hidrelétrica (UHE) de Belo Monte na região chamada Volta Grande do Xingu, entre os municípios de Altamira e Vitória do Xingu (Estado do Pará, Brasil), durante os anos de 2012 e 2016; em abril de 2016 começou a operar a primeira turbina (Norte Energia 2019). Apesar dos benefícios da produção energética, empreendimentos hidrelétricos produzem severos impactos ambientais, principalmente na dinâmica natural do pulso de inundação e, consequentemente, na biodiversidade (Junho 2008). Além das perturbações da fauna local, a implementação de uma UHE nos rios amazônicos pode causar a perda de conectividade nos trechos dos rios, retenção de nutrientes nos reservatórios, transmissão de doenças parasíticas a humanos, entre outros (Nobre *et al.* 2016).

Com o intuído de reduzir os impactos sociais e ambientais, o reservatório da UHE Belo Monte é do tipo fio d'água, com uma área alagada de aproximadamente 480 km² (Norte Energia 2019). Trata-se de uma tecnologia moderna e mais sustentável do que outros métodos de construção, porém, seus reservatórios menores tornam a geração de energia elétrica variável ao longo dos meses em função da sazonalidade de chuvas e outros fatores climáticos (Pereira 2015). Com o total barramento do rio e o início da sua operação comercial no início de 2016, a maior parte do fluxo de vazão do rio Xingu passou a ser desviada da região da Volta Grande para um canal de derivação, resultando em uma vazão residual que é controlada pela concessionária da barragem. Esse desvio causou uma redução de até 80% em relação à vazão natural do rio (Zuanon *et al.* 2019). Sendo assim, para o seu funcionamento, a concessionária foi obrigada a garantir a transmissão de uma quantidade mínima de água para a região da Volta Grande do Xingu, para garantir a continuidade dos processos biológicos dos organismos aquáticos e sociais das comunidades humanas tradicionais da região. Nesse contexto, foi apresentado uma proposta de volumes de vazão como medida de suavização para os impactos causados pelo empreendimento, que foi denominado de "Hidrograma de Consenso". Seu principal objetivo é reproduzir, mesmo que artificialmente, o pulso sazonal de subida e descida do nível de água do rio (Eletronorte 2002, Agência Nacional de Águas 2009), na tentativa de reduzir assim os impactos diretos no ciclo de vida da fauna local.

Especialmente para os peixes, o barramento de rios ou as condições de fio d´água afeta as rotas de migração, ciclos reprodutivos, dinâmica alimentar e as interações intra e/ou interespecíficas da biota (Tundisi 1978; Agostinho *et al.* 1992; Larinier 2000). Desta forma, estudos ecológicos de peixes em áreas de influência de hidrelétricas são de grande relevância para ciência, uma vez que fornecem dados sobre como os organismos respondem ao impacto e ao novo ecossistema formado. Tais informações podem subsidiar estratégias mais eficientes de conservação e manejo dos estoques populacionais.

Dentre as espécies de peixes amazônicos, os bagres da família Doradidae são um dos mais representativos nos grandes rios da região (Sabaj Pérez *et al.* 2007). São peixes que ocorrem, em sua maioria, nas bacias da América do Sul; cerca de 70% das espécies ocorrem na bacia Amazônica (Eler *et al*. 2007). Os indivíduos pertencentes a esta família são facilmente identificados pelas ossificações bem desenvolvidas na linha lateral, que formam um apêndice espinhoso (Higuchi *et al*. 2007). As espécies podem variar de tamanho, desde espécies com aproximadamente três centímetros de comprimento do gênero *Physopyxis* a peixes do gênero *Oxydoras* que podem atingir até um metro de comprimento e 20 kg (Higuchi 1992; Ferreira *et al*. 1998). Quanto a biologia alimentar, o conhecimento existente aponta os doradídeos como animais onívoros, com uma dieta baseada em detritos e insetos aquáticos imaturos, moluscos, frutos, entre outros (Casatti *et al.* 2005; Cardone *et al.* 2006; Sá-Oliveira & Isaac 2013; Barbosa & Montag, 2015).

Diante do exposto, essa dissertação objetivou descrever a dieta de *Doras higuchii* Sabaj Pérez & Birindelli, 2008 (Figura 1) (Siluriformes: Doradidae) e avaliar o efeito do pulso de inundação na dinâmica alimentar da espécie na Volta Grande do rio Xingu, trecho que está sob influência direta da UHE Belo Monte. Essa espécie é amplamente distribuída nos tributários do baixo rio Amazonas (Sabaj Pérez & Birindelli 2008) e pode atingir cerca de 30 cm de comprimento (Froese & Pauly 2021). Na região do estudo, é popularmente conhecida como "botinho" entre os ribeirinhos e pescadores. Até o momento, a literatura acerca da biologia e ecologia de *D. higuchii* é escassa ou inexistente, e desta forma, esse estudo trará dados cruciais (se não inéditos) sobre aspectos ecológicos dessa espécie, contribuindo o preenchimento de lacunas de conhecimento sobre os doradídeos.

Por fim, o presente estudo está formatado como um manuscrito científico, e posteriormente será submetido à revisão para língua inglesa e submetido a revistas especializadas (e.g., Ecology of Freshwater Fish, Marine and Freshwater Research, Aquatic Ecology). Tal pesquisa contou com a participação da colaboradora Lídia B. Seabra, que nos auxiliou na rotina de laboratório e análises dos isótopos estáveis, do Professor David

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Figura 1: Exemplar de *Doras higuchii* Sabaj Pérez & Birindelli, 2008 (Doradidae: Siluriformes), coletado na região do médio rio Xingu, Pará, Brasil. Foto: Leandro M. Sousa.

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MANUSCRIPT

Analysis of stomach contents and stable isotopes indicate a specialized diet of Doras higuchii in the reduced flow section of Belo Monte dam, Xingu River, Brazil

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INTRODUCTION

Studies on the trophic dynamics of fishes support our understanding of how these organisms use the resources available in the environment (Neves et al. 2020; Costa et al. 2021). This relationship is directly influenced by environmental variables - such as temperature and precipitation - and biotic interactions (Petraitis & Latham 1999; Winemiller & Layman 2005). One of the leading agents of environmental change in floodplains is the successive cycles of rising and falling river water levels (Junk et al. 1989). This dynamic, termed flood pulse, is one of the main ecological predictors of aquatic organisms (Junk et al. 1989; Liebhold et al. 2004; Yang et al. 2008).

In the Amazon, a region with extensive floodplains, the effects of the flood pulse on the landscape and species' life history are also notable (Junk et al. 1989). For instance, the rivers overflow during the high-water periods, flooding the adjacent terrestrial environments,

originating in the "igapó" or floodplain forests (Goulding 1980; Junk et al. 1989). One of the essential features of these flooded environments is the increased input of allochthonous nutrients into the aquatic habitats, such as terrestrial invertebrates, fruits, and detritus carried into the main channels (Lowe-McConnell 1999). Such items become available for aquatic organisms, especially fish (Junk et al. 1989; Freitas et al. 2011).

Thus, these hydrological dynamics directly influence the feeding ecology of species (Hahn & Delariva 2003; Bayley et al. 2018; Castello et al. 2019). Such influence is reported in studies conducted in the Amazon, which observed that water level variations affect the food web, exerting pressure for adaptation in many species (Reis & Caramashi 1999; Soares & Yamamoto 2005; Merona & Rankin-Demérona 2004; Rebelo et al. 2010; Prudente et al. 2016). Although this knowledge is consolidated, given the extensive literature available, the feeding strategy of Amazonian fish species facing the flood pulse is still far from being widely known due to the vast diversity in the region. In this context, the flood pulse effects are more conspicuous and better documented for species that feed primarily on allochthonous items (Freitas et al. 2022). On the other hand, our comprehension of how the flood pulse affects diets based on autochthonous items (e.g., crustaceans and insect larvae) is relatively unknown because the impacts of these hydrological dynamics on their availability are only partially known.

In recent decades, studies on fish trophic ecology have been enhanced by the advent of stable isotope analysis (Fry 2006), especially the isotopic signature of carbon (C) and nitrogen (N) (Layman et al. 2007; Shipley & Matich 2020). This approach highlights the assimilation process and energy flow of resources consumed by the organisms, elucidating the origin of organic matter and their trophic level (Layman et al. 2007; Brito et al. 2006; Neres-Lima et al. 2016; Zandonà et al. 2017). The isotopic composition analysis on the resources and consumers, combined with the inspection of stomach contents, has shown remarkable contributions in

reconstructing the animals' diets in their natural habitats (Zandona et al. 2017; Shipley & Matich 2020).

Given the above, the present study aims to evaluate the effect of the flood pulse on the feeding ecology of the catfish *Doras higuchii* Sabaj Pérez & Birindelli, 2008 from the middle Xingu River region, a stretch directly affected by the construction of the Belo Monte Hydroelectric Power Plant (HPP Belo Monte) (Pará, Brazil). This species, a Doradidae family (Siluriformes) representative, is widely distributed in the large tributaries of the Eastern Amazon (Sabaj Pérez & Birindelli, 2008), and data on its biological and ecological aspects are scarce or absent. To understand the effect of local variation of water levels on the diet of *D. higuchii,* we combined the inspection of stomach contents with stable isotope analyses, aiming to answer two main questions: i) how does the flood pulse affect the diet composition and trophic niche breadth? ii) how does the flood pulse influence the species' feeding intensity? We expect that the water level variation of the Xingu River directly influences the trophic dynamics of *D. higuchii,* promoting changes in the diet composition, trophic niche, and feeding intensity along the hydrological periods. Additionally, we expect that the species shows a more significant variability of food items during high-water periods, resulting in a more generalist diet and greater food consumption for this period. Finally, in addition to filling crucial knowledge gaps about the trophic ecology of doradid fishes, we also expect to provide data on the diet of a species from a recently impacted area by a hydroelectric dam.

MATERIAL AND METHODS

Study area

Samplings were carried out in the Volta Grande do Xingu (VGX), in the middle Xingu River, Pará, Brazil. This area shows a reduced flow section (RFS) which extends from the Pimental Dam (3°25'33.0" S, 51°57'03.3" W) to the Belo Monte Dam (3°06'44.8" S,

51°46'39.3" W), the reduced flow section is about 100 km long. (Figure 2). The climate type is *Am* according to the Köppen-Geiger classification (PEEL et al. 2007), described as a sub-equatorial or tropical wet climate (Barbosa et al. 2018). Since the complete damming of the Xingu River in 2016, the RFS's water flow has been controlled by the Pimental Dam. During the study period (December/2020 to November/2021), the average flow varied from 8,215.9 m³/s in March to 707.8 m³/s in October (data provided by the concessionaire Norte Energia) (Figure 3). This variation, although artificially controlled, allows the distinction of four hydrological periods: filling (December to February), flood (March to May), receding water (June to August), and dry (September to November).
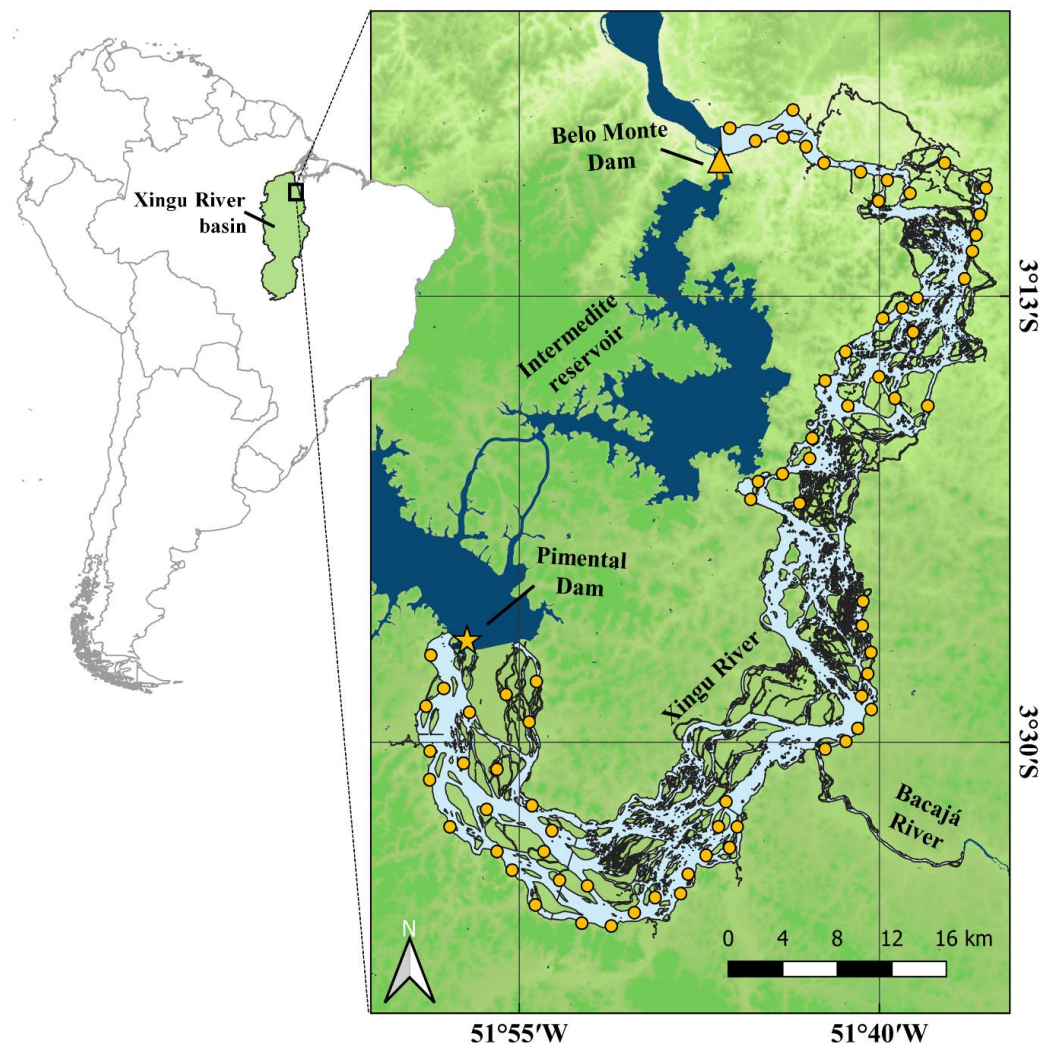
Figure 1: Sampling sites of *Doras higuchii* (Doradidae: Siluriformes) in Volta Grande do Xingu (VGX), middle Xingu river (Pará, Brazil), from December/2020 to November/2021. The yellow circles can represent more than one location, since they are the places where the fishing nets were placed.
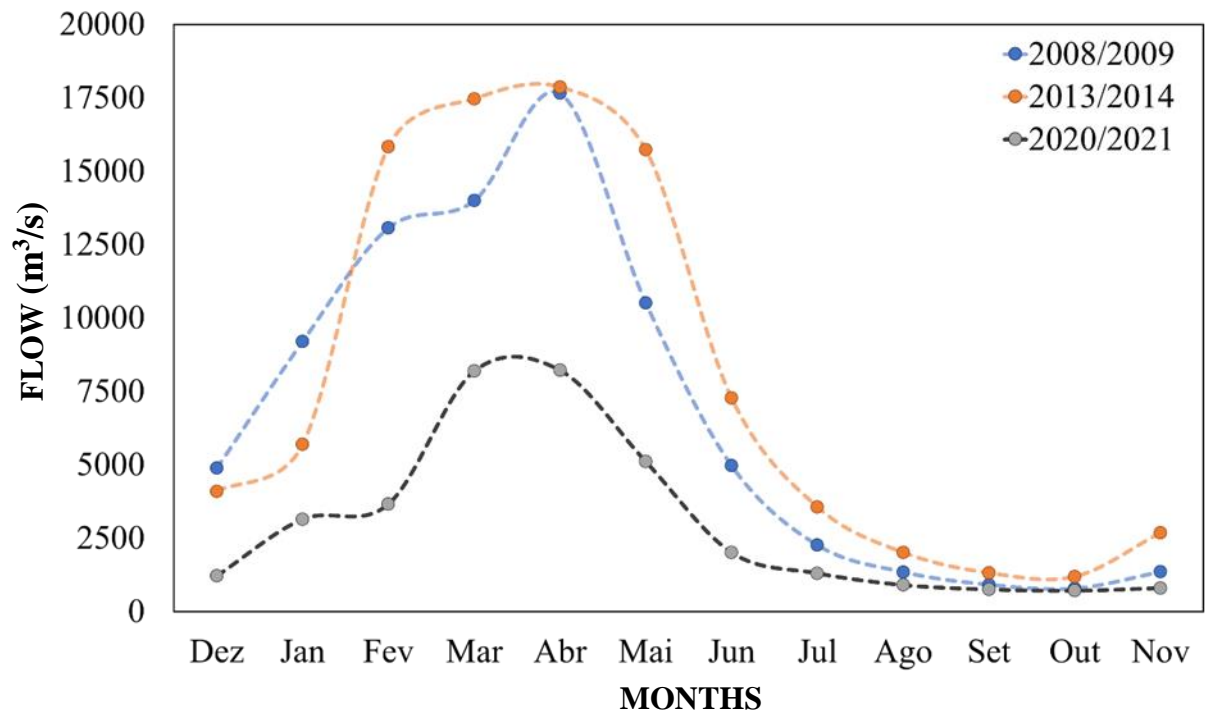
Figure 3: Monthly average of water flow in the Volta Grande do Xingu (VGX) (Pará, Brazil) in the pre (2008/2009 and 2013/2014) and post-dam period (2020/2021).

Collection of biological material

Specimens collections occurred monthly between December 2020 and November 2021, where each field campaign lasted approximately fifteen days. To capture the fish, we used gill nets with different mesh sizes (2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 16, and 18 cm between opposite knots), each measuring 20 meters long and one meter high. The set of these nets formed a single battery; on each collection day, three batteries were used. With the fishermen's guidance, the net batteries were exposed to each other by approximately 2 km from 5:00 pm to 9:00 pm. Each

day, a new location was sampled to cover as much of the VGX as possible at the end of the field campaigns.

After collection, still in the field the fish were measured for standard length (Ls; in centimeters; 0.1 cm precision) and total mass (Mt; in grams; 0.01 g precision). They were then dissected, had their stomachs removed, and weighed (Me; in grams; 0.001 g precision). The stomachs were stored in 70% alcohol and sent to the Ecology and Conservation Laboratory (LABECO) of the Universidade Federal do Pará (UFPA, Guamá Campus). Witness specimens were fixed in 10% formalin for 48h, transferred to 70% alcohol, and will be incorporated into the ichthyological collection of the Universidade Federal do Pará (Belem, Pará). The procedures for capturing and transporting biological material were authorized by IBAMA (ABIO No. 1267/2020) and the UFPA Ethics Committee (CEUA No. 8293020418).

After biometry, three specimens of *D. higuchii* were selected per day to remove a muscle fragment from the dorsal region for isotope analyses. These tissues were stored separately in aluminum foil and frozen. Additionally, samples of potential food resources of the species were collected, such as sediment, particulate organic matter (POM), periphyton, plant fragments, microphytoplankton, and aquatic and terrestrial invertebrates. Each resource was sampled individually, stored in plastic tubes, and frozen. Combining the isotope analysis of the consumers and food resources allows us to estimate the contribution of each assimilated item, demonstrating the diet over previous weeks or months due to the renewal rate of muscle tissue (Sacramento et al. 2016, Nielsen et al. 2018). The collection, processing, and storage of all samples followed the protocol described in Levin & Curry (2012).

Processing of the biological material

In the laboratory, stomach contents were inspected using a stereomicroscope. The food items were identified to the lowest taxonomic level possible using specific literature (Costa &

Simonka 2006; Mugnai et al. 2010) and consultations with specialists. Finally, each item was weighed on a precision electronic scale (0.0001 g).

For each food item, we calculated the Frequency of Occurrence (FOi%) (Hyslop 1980) and Mass Percentage (M%) (HYNES 1950), combining them into the Alimentary Index (Ai%; modified from Kawakami & Vazzoler 1980). The importance of each item in the species diet was obtained by the formula: $Ai\% = [(FOi\% * M\%)/(\sum FOi\% * M\%)] * 100$. Subsequently, the recorded items were grouped into six feeding categories (aquatic insects, terrestrial insects, aquatic molluscs, fish, terrestrial plants, and sediment) and had their respective FOi%, M%, and Ai% values also calculated.

For the isotopes, the samples were thawed, washed separately with distilled water, and placed in glass Petri dishes sterilized for 24h in a 10% hydrochloric acid solution. Then, samples were dehydrated at 60ºC for 48 hours. After cooling with a desiccator, samples were macerated using a porcelain gral until their total homogenization (transformed into powder) and stored in Eppendorf tubes. Samples were analyzed at the Center for Nuclear Energy in Agriculture of the University of São Paulo (CENA/USP). Precise aliquots of 0.5 g of each sample were stored in tin capsules and submitted to a mass spectrometer (Isotope Ratio Mass Spectrometers) for the determination of carbon ($^{13}C/^{12}C$) and Nitrogen ($^{15}N/^{14}N$) isotope ratios.

Data analysis

Diet composition

The diet composition, expressed by the Ai% values of the feeding categories, was evaluated using GLMs ("quasibinomial" family) models (McCullogh & Searle, 2001) to test the influence of the water level on the variation of Ai% values of the main trophic categories consumed by *D. higuchii.* In this approach, we used the IAi% values calculated from the set of

individuals collected on each day in each expedition. Furthermore, we assigned a monthly average value of water level for the individuals collected in a given month.

Trophic Niche breadth

We used the IAi% values of food items to assess the trophic niche range of the species over hydrological periods through the standardized Levin (Ba) index (Hurlbert 1978). This index is expressed by the formula $Ba = [(\sum j\ P2) - 1 - 1] * (n - 1) - 1$, where Ba is the standardized Levin index, Pij is the proportion of the food resource (j) and n is the number of food resources used (Krebs 1989). In this index, it is possible to visualize the range of the trophic niche through the estimated distribution of food items found in the stomach of the species, as well as to inform about the degree of diet specialization (Fugi et al. 2008). The Ba values can range from 0 when the species is characterized as a specialist (e.g., a unique feeding habit) to 1 when the species is described as broadly generalist. To test the influence of the flood pulse (flow) on the niche range of *D. higuchii*, the values of Ba were evaluated using a GLM ("quasibinomial" family). For this analysis, we used the Ba values calculated from the IAi% values obtained from the individuals collected per month.

Feeding intensity

The feeding intensity, or the amount of food ingested by an individual, was evaluated by the Repletion Index (IR). The IR, calculated individually for each specimen, is given by the formula $IR = (Me/Mt) * 100$ (Santos, 1979), where Me is the total mass of items found in the stomach, and Mt is the total mass. To investigate the influence of hydrological periods on the feeding intensity of *D. higuchii*, we evaluated the variation of IR values versus the water levels using GLM (quasibinomial" family). For each individual, a monthly average value of the water flow was assigned, corresponding to the month it was collected.

Stable isotopes

Isotopic ratios (δ) are expressed in parts per thousand (‰) relative to the Pee Dee Belemnite (PDB) standard for $\delta^{13}C$ and the standard atmospheric nitrogen for $\delta^{15}N$ (Lajtha & Michener 1994), following the following equation: $\delta^{13}C\ ou\ \delta^{15}N = [(R_{sample}/R_{standard}) - 1] * 10^3$, where R corresponds to the ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Initially, we visually explored the carbon/nitrogen ratios of food sources and *D. higuchii* specimens for each hydrological period, using means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ in biplot graphics. From this investigation, it was possible to demonstrate the proportional contributions of food resource sources to consumer trophic enrichment factors (TEFs), also analyzing whether (or not) a given food source can be assimilated by the consumer (Parnell et al. 2010). This estimation was performed using a Bayesian mixture model (polygon) for stable isotopes in the *siar* package (Stable Isotope Analysis in R) of the R Studio program (R Core Team 2021).

We also evaluated the influence of hydrological periods on the carbon and nitrogen isotope ratios of *D. higuchii* through a two-factor Analysis of Variance (Two-Way ANOVA). Additionally, we evaluated the nitrogen isotopic signature of each specimen to investigate possible ontogenetic effects on the trophic positioning. We used a GLM ("quasibinomial" family) to assess the variation of $\delta^{15}N$ versus the specimens' standard length. For all GLMs performed in this study, we used the *glm* function from the *stat* package of R Studio (R Core Team 2021).

RESULTS

The stomach contents of 362 specimens were analyzed, 63 from the filling period, 61 from the flood period, 116 from the receding water period, and 122 individuals from the dry period. From this total, 220 stomachs presented at least one item (60.8%), and 142 were empty (39.2%). The captured individuals ranged from 7.0 cm to 34.4 cm in length (mean = 18.05 cm)

and weighed between 5.5 g and 244.0 g (mean = 130.9 g).

Diet composition and niche breadth

In general, specimens of *D. higuchii* fed predominantly on sediment (74.9% Ai%), followed by aquatic insects (24.8% Ai%), indicating an omnivorous feeding habit with a tendency to detritivory. The other feeding categories (terrestrial insects, aquatic molluscs, fish, and terrestrial plants) represented less than 1% of the diet (Table 1). We did not observe the influence of the water level on the Ai% values of the two main feeding categories consumed by *D. higuchii*: sediment (GLM: t = 0.042; p = 0.966) and aquatic insects (GLM: t = 0.643; p = 0.522). For the niche breadth, the Levin index ranged from 0.006 to 0.069 and did not vary according to the average water level of the Xingu River (GLM: t = 0.669; p = 0.519), highlighting that the species tends to maintain a specialist trophic niche throughout the seasons.

Feeding intensity

The Repletion Index (RI) ranged from 0.0001 to 0.0221 (0.0025 ± 0.0039), with higher values during periods of high water, indicating more significant feeding activity in times of flooding. This pattern was observed both when considering the whole set of individuals (GLM: t = 4.468; p < 0.001; Figure 4A) and the monthly average values of IR (GLM: t = 2.417; p = 0.036; Figure 4B).
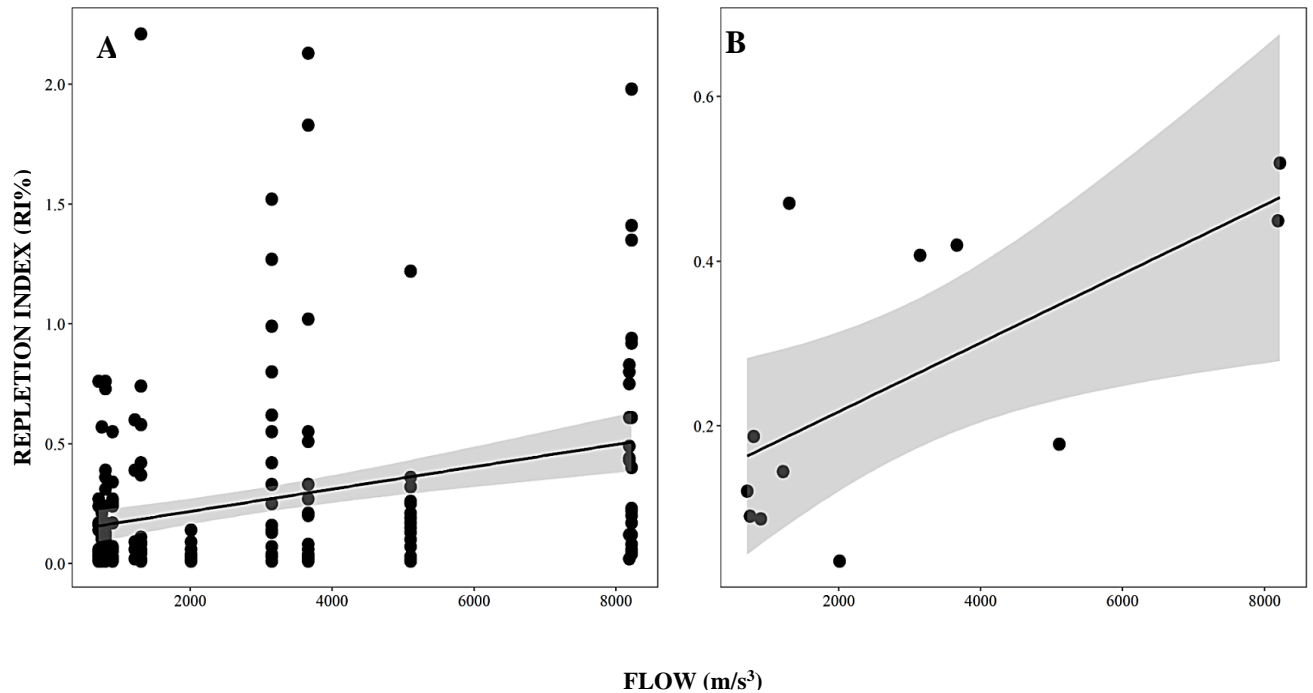
Figure 2: Repletion index (RI), indicating the feeding intensity of *Doras higuchii* (Doradidae: Siluriformes) captured in the Volta Grande do Xingu (VGX) (Pará, Brazil), from December 2020 to November 2021. (A = whole set of individuals; B = monthly average values of IR)

Isotopic composition

We analyzed 497 samples for stable isotopes, of which 388 were of potential food resources (sediment, aquatic insects, terrestrial insects, organic matter, microphytoplankton, periphyton, and terrestrial plant) and 109 muscle samples of *D. higuchii* (Table 2). Of the latter, 26 were from the filling period, 30 from the flood, 30 from the receding water, and 23 from the dry period.

The average nitrogen isotopic composition of the species was 11.24 ‰ ($\pm$ 0.63) in the filling, 11.13 ‰ ($\pm$ 0.51) in the dry, 11.01 ‰ ($\pm$ 0.47) in the flood and 10,84 ‰ ($\pm$ 0.46) in the receding water (Table 2). Regarding potential food resources, the highest $\delta^{15}N$ mean was observed to sediment (8.67 $\pm$ 2.37), followed by aquatic insects (8.43 $\pm$ 0.54) and molluscs (7.5 $\pm$ 0.92) (Table 2). These results suggest that *D. higuchii* feeds on these non-basal resources throughout the hydrological periods.

Table 1: Alimentary Index (Ai%) of items and feeding categories of *Doras higuchii* (Doradidae: Siluriformes) collected from December/2020 to November/2021 in the Volta Grande do Xingu (VGX), middle Xingu river (Pará, Brazil). n = number of stomachs with items.

Food items	Filling			Flood			Recending Water			Dry		
	Dec/20 (n = 8)	Jan/21 (n = 18)	Feb/21 (n = 18)	Mar/21 (n = 10)	Apr/21 (n = 17)	May/21 (n = 21)	Jun/21 (n = 13)	Jul/21 (n = 17)	Aug/21 (n = 31)	Sep/21 (n = 25)	Oct/21 (n = 17)	Nov/21 (n = 25)
AUTOCHTHONOUS												
Aquatic insects	0.14	0.16	0.12	0.37	0.30	0.11	0.67	0.64	0.28	0.24	0.10	0.18
Diptera (immature)			<0.01		<0.01	<0.01	0.04			<0.01		<0.01
Diptera (Ceratopogonidae; immature)	0.14	0.10	0.37	0.15	0.06	0.54	0.27	0.27	0.24	0.06	0.16	0.11
Diptera (Chironomidae; immature)		<0.01	<0.01									
Diptera (Tipulidae; immature)						<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Coleoptera (immature)					<0.01		<0.01			<0.01	<0.01	
Coleoptera (Elmidae; immature)		<0.01										
Ephemeroptera (immature)					<0.01							
Ephemeroptera (Polymitarcyidae; immature)					<0.01	<0.01						
Hemiptera (immature)					<0.01							
Hemiptera (Naucoridae; immature)		<0.01										
Trichoptera (immature)					<0.01	0.03	0.05			<0.01	<0.01	<0.01
Trichoptera (Ecnomidae; immature)					<0.01		<0.01	<0.01	<0.01	<0.01		<0.01
Trichoptera (Hydropsychidae; immature)		<0.01										
Trichoptera (Leptoceridae; immature)					<0.01							
Trichoptera (Polycentropodidae; immature)							<0.01		<0.01			
Odonata (immature)		<0.01										
Plecoptera (immature)		<0.01										
Insect fragment	<0.01	0.01		0.04	<0.01	<0.01	<0.01	<0.01	<0.001	<0.01		<0.001
Insect fragment (immature)					<0.01	<0.01					<0.001	
Aquatic molluscs			<0.01	<0.01	<0.01	<0.01	<0.01		<0.01			
Bivalve		<0.01	<0.01			<0.01		<0.01				
Gastropoda		<0.01	<0.01	<0.01	<0.01	<0.01						
Fish	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01			
Scale		<0.01			<0.01							<0.01
Fish fragments			<0.01		<0.01	<0.01		<0.01				
Sediment	0.86	0.84	0.88	0.63	0.70	0.89	0.32	0.36	0.72	0.75	0.89	0.82
Detritus	0.86	0.82	0.63	0.80	0.93	0.42	0.63	0.73	0.75	0.94	0.84	0.88
Stone/Sand		0,05										
ALLOCHTHONOUS												

Terrestrial insects		<0.01										
Ephemeroptera		<0.01										
Terrestrial Plants	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	0.01	<0.01	<0.01
Plant fragments	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	0.01	<0.01	<0.01	<0.01	<0.01	0.01

Table 2: Mean and standard deviation (± sd) of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic signatures of *Doras higuchii* (Doradidae: Siluriformes)

and trophic resources collected in the Volta Grande do Xingu (VGX), middle Xingu river (Pará, Brazil). n = number of samples analyzed.

Sample	Filling			Flood			Recending Water			Dry		
	δ^{15}N	δ^{13}C	n	δ^{15}N	δ^{13}C	n	δ^{15}N	δ^{13}C	n	δ^{15}N	δ^{13}C	n
Doras higuchii	11.24 (± 0.63)	-27.41 (± 0.53)	26	11.01 (± 0.47)	-26.52 (± 0.95)	30	10.84 (± 0.46)	-26.63 (± 0.51)	30	11.13 (± 0.51)	-27.5 (± 1.91)	23
Aquatic insects	8.43 (± 0.54)	-31.3 (± 1.59)	-	-	-	12	7.22 (± 0.6)	-36.66 (± 2.57)	34	7.69 (± 0.87)	-33.77 (± 2.92)	5
Terrestrial insects	6.48 (± 1.81)	-28.11 (± 3.07)	5	5.45 (± 1.4)	-28.27 (± 1.08)	7	5.9 (± 2.02)	-29.3 (± 2.91)	17	6.73 (± 2.48)	-28.23 (± 2.65)	10
Organic matter	2.27 (± 1.26)	-31.39 (± 1.22)	8	1.8 (± 1.31)	-30.84 (± 0.46)	10	2.63 (± 1.78)	-30.24 (± 1.16)	5	4.06 (± 1.94)	-30.36 (± 1.3)	7
Microphytoplankton	-	-	14	5.4 (± 0.44)	-28.63 (± 0.79)	-	-	-	12	6.05 (± 1.38)	-30.75 (± 1.98)	-
Molluscs	7.22 (± 1.17)	-28.54 (± 4.46)	5	7.5 (± 0.92)	-25.28 (± 5.08)	5	7.21 (± 1.24)	-26.32 (± 4.72)	25	7.09 (± 1.1)	-29.18 (± 3.76)	11
Periphyton	-	-	4	5.18 (± 0.55)	-25.43 (± 1.56)	-	-	-	7	6.38 (± 1.84)	-26.92 (± 1.95)	-
Terrestrial plants	5.18 (± 2.62)	-29.78 (± 2.26)	28	5.24 (± 2.57)	-28.29 (± 2.35)	30	3.58 (± 2.39)	-28.41 (± 1.89)	19	3.58 (± 2.39)	-28.41 (± 1.89)	26
Aquatic producers	7.46 (± 1.42)	-29.52 (± 4.19)	-	3.25 (± 1.85)	-29.21 (± 1.71)	-	-	-	-	3.99 (± 0.55)	-30.23 (± 7.09)	-
Sediments	8.67 (± 2.37)	-26.93 (± 2.37)	22	4.54 (± 1.33)	-28.39 (± 1.6)	23	6.06 (± 1.71)	-28.85 (± 1.25)	25	7.81 (± 1.92)	-28.96 (± 1.3)	12
Total			112			117			174			94

Based on the food items identified in the stomach content combined with the results found in the biplot (Figure 5), we selected three resources from each hydrological period to perform the mixing models analysis (polygons), also with samples of *D. higuchii*.
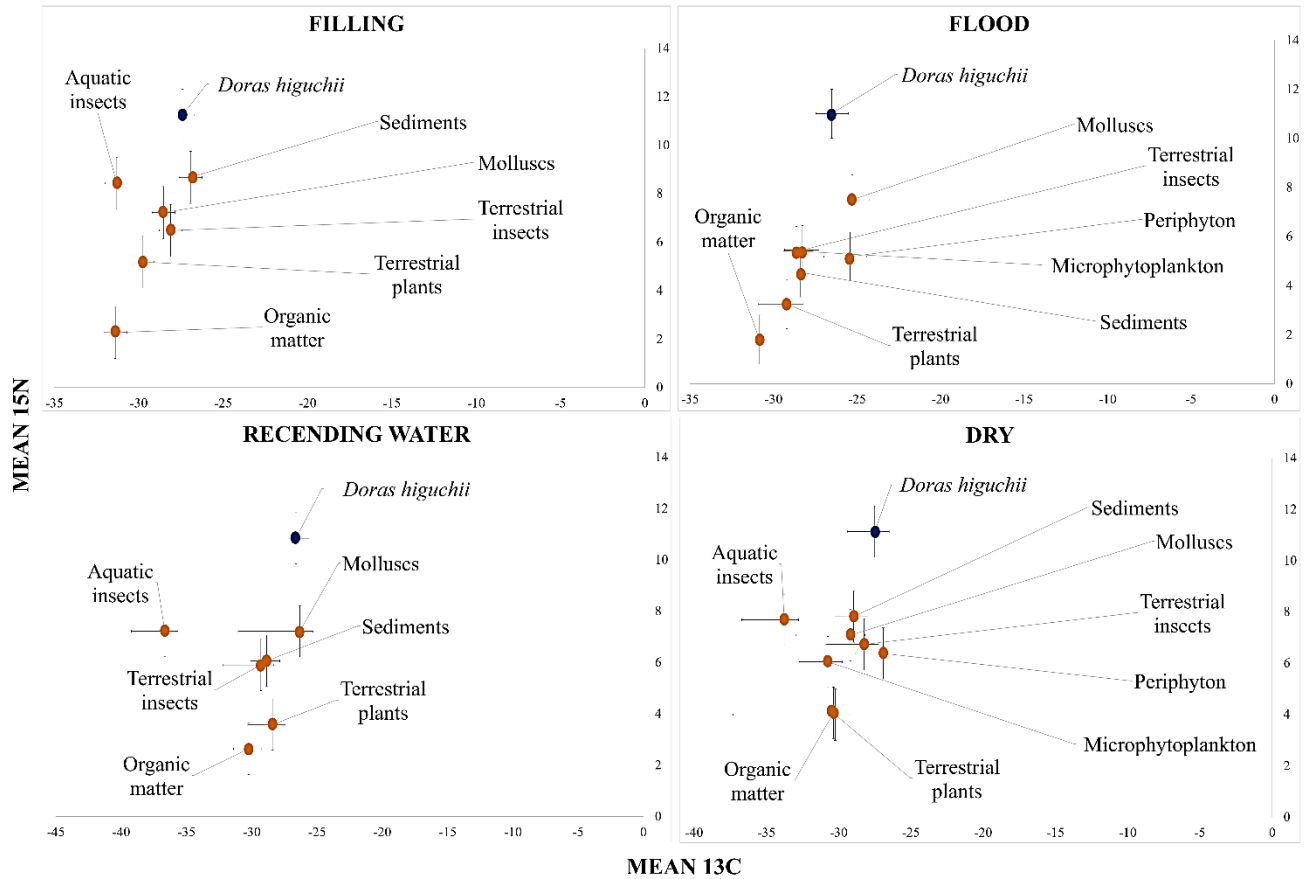
Figure 5: Biplot with averages and deviations of resources and muscle of Doras higuchii in each hydrological period for the selection and subsequent analysis of mixing models, collected from December/2020 to November/2021 in the Volta Grande do Xingu (VGX).

Thus, we observed that in the flood and receding water periods (Figure 6A-6C), the fish samples were entirely placed within the polygon, confirming the isotopic signature of the resources consumed by the fish. On the other hand, some fish samples obtained during the dry and flood periods (Figures 6B and 6D) remained outside the polygon. It suggests that *D. higuchii* may feed on a broader range of trophic resources (e.g., plant parts, aquatic insects).
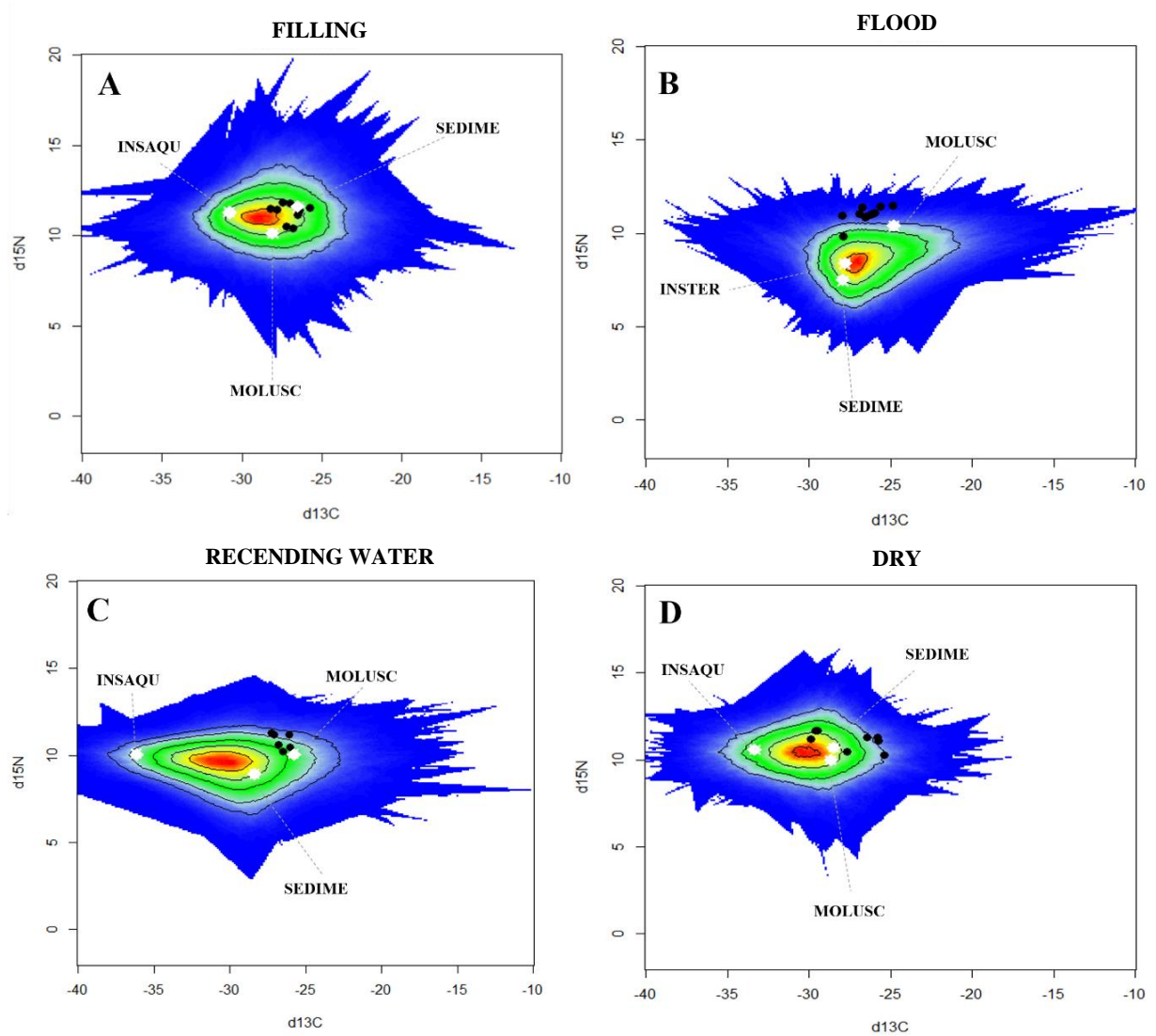
Figure 6: Mixture models (polygons) of *Doras higuchii* (Doradidae: Siluriformes) samples and its food resources, collected from December/2020 to November/2021 in the Volta Grande do Xingu (VGX), middle Xingu river (Pará, Brasil). Mean $\delta^{13}C/\delta^{15}N$ values of fish samples are indicated in black on the polygon, and the trophic resources in white. Probability contours are 5%. Aquatic insect (INSAQU), Terrestrial insect (INSTER), Sediment (SEDIME), and Molluscs (MOLLUSC).

The contribution of trophic resources ($\delta^{13}C/\delta^{15}N$) in the diet of *D. higuchii* evidenced the importance of aquatic insect consumption in the filling (31.6%), receding water (23.5%) and dry (24%); aquatic molluscs in the filling (28.2%), flood (35.6%), receding water (46.5%)

and dry (27.1%); and sediments in the filling (40.1%), flood (26.5), receding water (30%) and dry (48.9%) seasons. These results corroborate those obtained from the inspection of stomach contents. As a caveat, we did not sample aquatic insects in the flood period due to logistical limitations. Thus, in this period, the model estimated terrestrial insects as one of the important items for the contribution of the diet (37.9% - Table 3). Additionally, we highlight the importance of molluscs in the isotopic signature of the individuals, despite their low occurrence in the stomach analysis.

Table 3: The contribution of trophic resources ($\delta^{13}C/\delta^{15}N$) in the diet of *D. higuchii.*

	Aquatic inv.	Terrestrial inv.	Molluscs	Sediment
Filling	31.6%	-	28.2%	40.1%
Flood	-	37.9%	35.6%	26.5%
Receding water	23.5%	-	46.5%	30%
Dry	24%	-	27.1%	48.9%

The isotopic signatures of $\delta^{15}N$ and $\delta^{13}C$ of *D. higuchii* specimens did not differ along the hydrological periods (p = 0.212 and p = 0.728, respectively), indicating similar average values throughout the flood pulse. Still, it suggests that *D. higuchii* may consume similar resources at different periods and that these resources are potentially available during the hydrological cycle. This result is corroborated by data from the stomach contents analysis, which showed no deviation in the diet composition along the flood pulse. Finally, we did not observe relationships between the nitrogen isotopic signature ($\delta^{15}N$) and length of individuals (GLM: t = 0.963; p = 0.344), suggesting that the species may maintain the trophic position throughout its growth.

DISCUSSION

The diet of *D. higuchii* from the middle Xingu river was predominantly composed of sediment and aquatic insects, indicating an omnivorous habit with a tendency to detritivory. Through analysis of stomach contents, we observed that different water flow levels did not

influence the dietary composition and trophic niche breadth of *D. higuchii*. In turn, specimens fed more intensely during high water periods. The isotopic signature analyses (δ^{15}N and δ^{13}C) corroborated the results of stomach contents inspection, indicating the consumption of similar items throughout the hydrological periods. Finally, the δ^{15}N of *D. higuchii* did not vary according to the specimens' size, suggesting no ontogenetic variation in the trophic position occupied by the species.

Omnivory, and its various tendencies (e.g., herbivory, insectivory, and detritivory), is commonly described for Doradidae species: consumption of plant material and insects by *Pterodoras granulosus* (Valenciennes, 1821) in the Paraná River (Arantes 2009); consumption of fruits and aquatic macroinvertebrates by *Lithodoras dorsalis* (Valenciennes, 1840) in the estuarine region of the Amazon River (Barbosa et al. 2015); sediment and mollusc ingestion by *Hassar affinis* (Steindachner, 1881) in lakes of the Mearin River basin (Barros et al., 2021). Generally, the detritivore habit is also suggested for *Doras* species, also feeding on immature aquatic insects in the soft substrates (van der Slenn & Albert, 2017), but no specific study on these fishes have been performed until now.

For fishes, diet composition can vary seasonally for different reasons (Piorski et al. 2005). These variations may result from changes in food availability caused by habitat modifications and changes in intrinsic biological patterns (Wooton 1990). In this sense, the flood pulse natural dynamics is one of the main agents of environmental transformation in the Amazonian rivers, producing effects on the aquatic and terrestrial trophic chain (Junk et al. 1989; Freitas et al. 2022). However, in the present study, the diet of *D. higuchii* did not vary temporally, which leads us to suggest that the current flood pulse in the region does not affect the availability of food sources. On the other hand, the reduced water flow in this study area may be producing an environmental homogenization, accompanied by the less natural variability of potential food resources for the consumers.

The similar diet composition of *D. higuchii* along the hydrological periods was accompanied by an unchangeable trophic niche breadth. The low values observed for Levin's Index (0.006 to 0.069) indicate a tendency to a more specialized feeding habit. On the contrary, some studies have shown that the generalist/opportunistic character is more recurrent in Neotropical fishes (Santos & Ferreira 1999; Resende 2000; Freitas et al. 2022), especially for organisms inhabiting environments marked by seasonal variations such as Amazonian floodplains (Lowe-McConnell 1999). In these environments, fish tend to adapt their diets, ingesting what becomes more available throughout the seasons (Gerking 1994). In this sense, we suggest, once again, that the water flow variation (artificially controlled) recorded for the VGX may not affect the availability of the main resources consumed by *D. higuchii*.

Although the diet composition did not vary temporally, the feeding intensity of *D. higuchii* was higher in the flood periods. In this case, the interaction between terrestrial and aquatic environments, promoted by the flood pulse, may increase the input of the main food items of *D. higuchii* in the Volta Grande do Xingu (e.g., sediments and aquatic insects). For instance, as the river floods, sediment accumulation in the main channels is greater, promoting the reproduction of insects with aquatic juveniles (Bayer 2010).

Studies on fish trophic ecology usually apply the inspection of the stomach contents, providing information on what was consumed by the organisms in recent times (Esteves et al. 2021). However, evaluating diets using stable isotope techniques complements this scenario by aggregating medium to long-term past information (Fry 2006). For the present study, the analysis of the isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) highlighted the importance of aquatic insects and sediment in the diet of *D. higuchii*, corroborating the results observed in the stomach contents. However, the isotope data revealed the extent of mollusc consumption, despite not being a recurrent item in the stomach analyses. The consumption of molluscs by doradid fishes has already been observed in some studies: *Oxydoras niger* (Valenciennes, 1821)

in Mamoré River, Bolivia (Lauzanne & Loubens 1985); *Trachydoras paraguayensis* (Eigenmann & Ward, 1907) in Paraná River, Brazil (Hahn et al. 1991); and *Hassar affinis* in Mearin River (Barros et al., 2021). Some studies with poecilid fishes have also evidenced that the predominant items in the stomach were not necessarily the most assimilated (isotope analysis) (Trinidad & Bastos et al. 2017; Zandonà et al. 2017).

Additionally, we observed no relationship between the $\delta^{15}N$ and the standard length of the specimens, which may indicate no ontogenetic effects on the trophic level of *D. higuchii*. Our results contradict some studies that associate feeding flexibility throughout fish growth as an adaptive life-cycle trait (Agostinho et al. 2003; Novaes et al. 2004; Guedes et al. 2015). Often, it is a strategy to face natural changes in food availability (Dill 1983; Joblin 1996). Although some studies also demonstrated no ontogenetic effects on the diet (Fagundes et al. 2007; Freitas et al. 2011), information on this subject is still lacking for doradid fishes. Thus, additional studies regarding the trophic ecology of these fishes are essential to discuss life strategies and the evolution of feeding habits.

In summary, the hydrological variations in the VGX region resulted in few effects on the trophic ecology of *D. higuchii*, contrary to what has been expected and observed for species from the same region (Freitas et al., 2022) and species inhabiting other floodplains (Welcomme, 1979; Gerking, 1994). Based on this observation, we suggest two scenarios; first, regardless of local hydrological variations, the diet of *D. higuchii* in this area is naturally based on few resources (e.g., detritus, aquatic insect larvae, molluscs); second, the drastic reduction of the water flow in the Volta Grande do Xingu due to the Belo Monte Dam, and the consequent reduction of the flood pulse effects, may have affected the availability of food resources used by *D. higuchii*. Thus, the specimens must adapt to a new scenario of available resources. A combination of these scenarios is also possible and even more likely.

Finally, we emphasize that filling gaps in the feeding ecology of doradids, especially in the Amazon region, is necessary to provide data on their life history. Despite providing ecological data on *D. higuchii* for the first time, the results obtained here can be useful to better understand the conservation status of this species in the Xingu river basin, given the environmental changes caused by the construction of a hydroelectric dam in this important Amazonian tributary.

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