

Trophic dynamics of a carnivorous catfish under dam-regulated flood conditions in the Amazon



Antonio Augusto Jardim Jr^{1,2}, Erival Gonçalves Prata¹,
Lais Martins Silva¹, João Pedro da Silva Moraes¹,
Lucas Pires de Oliveira^{1,2}, Luciano Fogaça de Assis Montag^{1,2} and
Tiago Magalhães da Silva Freitas³

Correspondence:
Antonio Augusto Jardim Jr
biosantosjr@gmail.com

This study investigates the trophic dynamics of *Pinirampus pinirampu* under an altered flood pulse regime, using stomach content and stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Monthly sampling was carried out in the Xingu River (Amazon basin) from January to November 2021. In total, 135 stomachs (40 with identifiable contents) and 23 muscle tissue samples were collected, alongside representative samples of potential autochthonous food sources. Stomach content analysis revealed a diet primarily composed of aquatic insects, with no significant variation in niche breadth or feeding intensity across hydrological periods. However, isotopic data indicated that the main assimilated carbon sources derived from crustaceans, fish, and mollusks, reflecting a consistently high trophic position throughout the hydrological cycle. These findings highlight the importance of integrating complementary trophic assessment methods to gain a more comprehensive understanding of fish ecology under controlled flow conditions. Furthermore, the results provide insights to guide conservation and management strategies aimed at mitigating the ecological impacts of hydroelectric developments on Amazonian fish assemblages.

Keywords: Pimelodidae, *Pinirampus pinirampu*, Stable isotope, Trophic ecology, Xingu River.

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¹ Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará, Rua Augusto Corrêa, 01, 66075-110, Belém, PA, Brazil. (AAJ) biosantosjr@gmail.com (corresponding author), (EGP) erival.gprata@gmail.com, (LMS) lais.martins.silva@icb.ufpa.br, (JPSM) jopedromoraes@gmail.com, (LPO) lucspires10@gmail.com, (LFAM) lfamontag@gmail.com.

² Programa de Pós-Graduação em Ecologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Rua Augusto Corrêa, 01, 66075-110, Belém, PA, Brazil.

³ Laboratório de Zoologia, Faculdade de Ciências Naturais, Campus Universitário do Marajó-Breves, Universidade Federal do Pará, Alameda IV, 3418, 68000-000, Breves, PA, Brazil. (TMSF) freitastms@gmail.com.

Este estudo investiga a dinâmica trófica de *Pinirampus pinirampu* sob um regime de pulso de inundação alterado, utilizando análise de conteúdo estomacal e isótopos estáveis ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$). Amostragens mensais foram realizadas no rio Xingu (Bacia Amazônica) de janeiro a novembro de 2021. No total, 135 estômagos (40 com conteúdo identificável) e 23 amostras de tecido muscular foram coletadas, juntamente com amostras representativas de potenciais fontes de alimento autóctones. A análise do conteúdo estomacal revelou uma dieta composta principalmente de insetos aquáticos, sem variação significativa na amplitude do nicho ou na intensidade alimentar ao longo dos períodos hidrológicos. No entanto, dados isotópicos indicaram que as principais fontes de carbono assimilado derivaram de crustáceos, peixes e moluscos, refletindo uma posição trófica consistentemente alta ao longo do ciclo hidrológico. Essas descobertas destacam a importância da integração de métodos complementares de avaliação trófica para obter uma compreensão mais abrangente da ecologia de peixes em condições de fluxo controlado. Além disso, os resultados fornecem insights para orientar estratégias de conservação e manejo que visem mitigar os impactos ecológicos dos empreendimentos hidrelétricos nas assembleias de peixes da Amazônia.

Palavras-chaves: Ecologia trófica, Isótopos estáveis, Pimelodidae, *Pinirampus pinirampu*, Rio Xingu.

INTRODUCTION

The flood pulse is a seasonal natural phenomenon essential for the functioning of Neotropical River systems, driving ecological interactions between aquatic and terrestrial environments (Junk *et al.*, 1989; Tockner *et al.*, 2000). For fish, during high-water periods, floodplain inundation enhances connectivity among watercourses, enabling migration routes, providing predator refuges, and creating spawning and nursery areas (Goulding, 1980; Barbosa *et al.*, 2018). This process also expands foraging opportunities by providing allochthonous resources such as terrestrial macroinvertebrates, fruits, and seeds, which mainly benefit frugivorous, insectivorous, omnivorous, and herbivorous species (Freitas, Garcez, 2004; Barbosa *et al.*, 2018; Freitas *et al.*, 2022).

In contrast, during low-water periods, the reduction in wetted areas increases the relative availability of autochthonous resources, including aquatic macroinvertebrates, zooplankton, phytoplankton, crustacean, mollusk, and macrophytes, which may become more accessible and easier to capture. This contraction of the main river channel also raises the density of aquatic organisms, favoring carnivorous species due to the greater aggregation of prey (Luz-Agostinho *et al.*, 2009; Pereira *et al.*, 2017; Barbosa *et al.*, 2018).

Many studies have evaluated the effects of ecological processes such as the flood pulse on fish trophic ecology through direct analysis of stomach contents (Silveira *et al.*, 2020; Freitas *et al.*, 2022; Penha *et al.*, 2024). This method involves the visual inspection of gastrointestinal contents, providing short-term information on diet composition that can be used to infer feeding intensity and trophic niche breadth, for instance (Amundsen,

Sánchez-Hernández, 2019; Silveira *et al.*, 2020). A complementary approach involves the analysis of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes (Peterson, Fry, 1987; Fry, 2006; Davis *et al.*, 2012). The $\delta^{13}\text{C}$ values help trace the basal sources of organic matter assimilated by consumers, whereas $\delta^{15}\text{N}$ provides estimates of a species' trophic position within the food web (Albrecht *et al.*, 2021; Winemiller *et al.*, 2023). The isotopic data from these stable elements not only complement stomach content analyses but also offer integrated, long-term information about dietary assimilation, allowing the assessment of whether the items found in stomach contents correspond to those effectively assimilated (Prata *et al.*, 2025; Seabra *et al.*, 2025a).

Integrating stomach content and stable isotope analyses improves our understanding of how floodplain dynamics, particularly those impacted by anthropogenic disturbances, shape fish feeding behavior (Penha *et al.*, 2024; Prata *et al.*, 2025; Seabra *et al.*, 2025a). Among such disturbances, hydropower development poses a significant threat to Neotropical fish assemblages (Fitzgerald *et al.*, 2018), as it alters natural flow regimes and leads to habitat loss, environmental homogenization, and changes in sediment transport and water quality (Winemiller *et al.*, 2016; Arantes *et al.*, 2019).

A notable example is the Xingu River, a highly biodiverse tributary of the Amazon basin (Camargo *et al.*, 2004; Barbosa *et al.*, 2015). Following the commissioning of the Belo Monte Hydroelectric Dam in 2016 (Zuanon *et al.*, 2019), the river's natural discharge was reduced by approximately 80% downstream (Zuanon *et al.*, 2019; Penha *et al.*, 2024), potentially compromising ecological interactions with terrestrial environments during flood events (Winemiller *et al.*, 2016). This new hydrological configuration may lead to changes in the composition of macroinvertebrate assemblages, an important food resource for many fish species (Fjellheim, Raddum, 1996; Richardson *et al.*, 2002) and consequently alter fish diets in response to shifts in prey abundance and taxonomic composition. Moreover, interspecific competition and predation rates may increase if available food resources become limited, potentially leading to a higher frequency of empty stomachs (Baumgartner, 2007).

Among the diverse Neotropical fish fauna, the family Pimelodidae stands out, comprising approximately 30 genera and 117 species widely distributed throughout South America (Fricke *et al.*, 2025). One of its representatives in the Xingu River is the catfish *Pinirampus pinirampu* (Spix & Agassiz, 1829), locally known as “barba-chata” (Dagosta, de Pinna, 2019). Siluriforms possess highly developed chemosensory and tactile systems that allow them to locate and capture prey even under low-light or turbid-water conditions (Barthem, Goulding, 1997; Freitas *et al.*, 2020). These traits are particularly relevant for *P. pinirampu*, a medium-sized nocturnal piscivore that primarily consumes small fish and forages both in the water column and near the bottom (Barbarino Duque, Winemiller, 2003; Carolsfeld *et al.*, 2003). This species also represents an important food resource for traditional local populations and is highly valued in some riverine communities (Valdelamar-Villegas, Olivero-Verbel, 2020). As a predatory catfish with access to a diverse prey base, *P. pinirampu* is likely influenced by fluctuations in floodplain connectivity and prey availability across hydrological periods, owing to its short-range lateral migration behavior (Lima *et al.*, 2023).

Given this context, the present study aimed to investigate the trophic dynamics of *Pinirampus pinirampu* under the influence of the regulated flood pulse in the Xingu River. We hypothesized that (1) the contrast between high- and low-water periods under a

regulated flow regime would not lead to major shifts in dietary composition, feeding intensity, or trophic niche breadth of *P. pirinampu*; (2) the isotopic structure ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the population would remain relatively stable between hydrological periods due to consistent availability of autochthonous resources; and (3) the contributions of assimilated basal sources, as well as isotopic niche area and overlap, would show little variation between periods, reflecting a stable trophic strategy. By identifying the stability of feeding patterns in a carnivorous predator under a regulated flow regime, this study provides insight into how hydrological control can influence energy pathways and trophic interactions in Amazonian River systems.

MATERIAL AND METHODS

Study area. This study was conducted in the Reduced Flow Section (RFS) of the Xingu River, located in the Volta Grande region, Pará State, Brazil. The study area lies between the Pimental and Belo Monte dams and includes sampling sites corresponding represented by collection dates (Fig. 1). Since the construction of the Belo Monte Hydroelectric Complex in 2016, this section of the river has been subject to hydrological regulation, with flow regimes controlled according to environmental guidelines established by IBAMA and ANA, which define fixed limits for minimum and maximum discharge. Consequently, the alteration of the natural seasonal dynamics caused by dam construction has resulted in an approximately 80% reduction in downstream flow, significantly modifying the river's hydrological and ecological processes (Fitzgerald *et al.*, 2018; Zuanon *et al.*, 2019; Bertassoli *et al.*, 2021).

The region is classified as having a tropical monsoon climate (Am) according to the Köppen-Geiger system and is dominated by dense evergreen ombrophilous forest (Peel *et al.*, 2007; Barbosa *et al.*, 2018; Montag *et al.*, 2025). The river channel in this section features clear waters, heterogeneous depth profiles, and a mosaic of rocky outcrops and sandy substrates, which together contribute to high habitat heterogeneity and complexity (Fitzgerald *et al.*, 2018).

Flow data revealed pronounced seasonal variation, with peak flows of 8,215.9 m³/s in March (high-water season) and 707.8 m³/s in October (low-water season) (Penha *et al.*, 2024). Based on this seasonal pattern, we defined two distinct hydrological phases: the high-water period (December to May) and the low-water period (June to November) (Freitas *et al.*, 2022; Lima *et al.*, 2023; Montag *et al.*, 2025). These phases were used as categorical variables to assess the trophic ecology of *Pirinampus pirinampu* under regulated flow conditions.

Sampling procedures and processing biological material. Specimens were collected monthly from January to November 2021 using monofilament nylon gillnets with mesh sizes of 2, 8, 10, 12, 16, and 18 cm (measured between opposite knots). Each net measured 20 m in length and 1 m in height, and multiple nets were deployed sequentially to form standardized sampling sets. At each event, three gillnet sets were installed at sites spaced approximately 5 km apart. Captures from the three sets were pooled per sampling event for subsequent analyses. Nets were deployed at 16:00 and retrieved at 21:00 on the same day to ensure consistent sampling effort across sites and months.

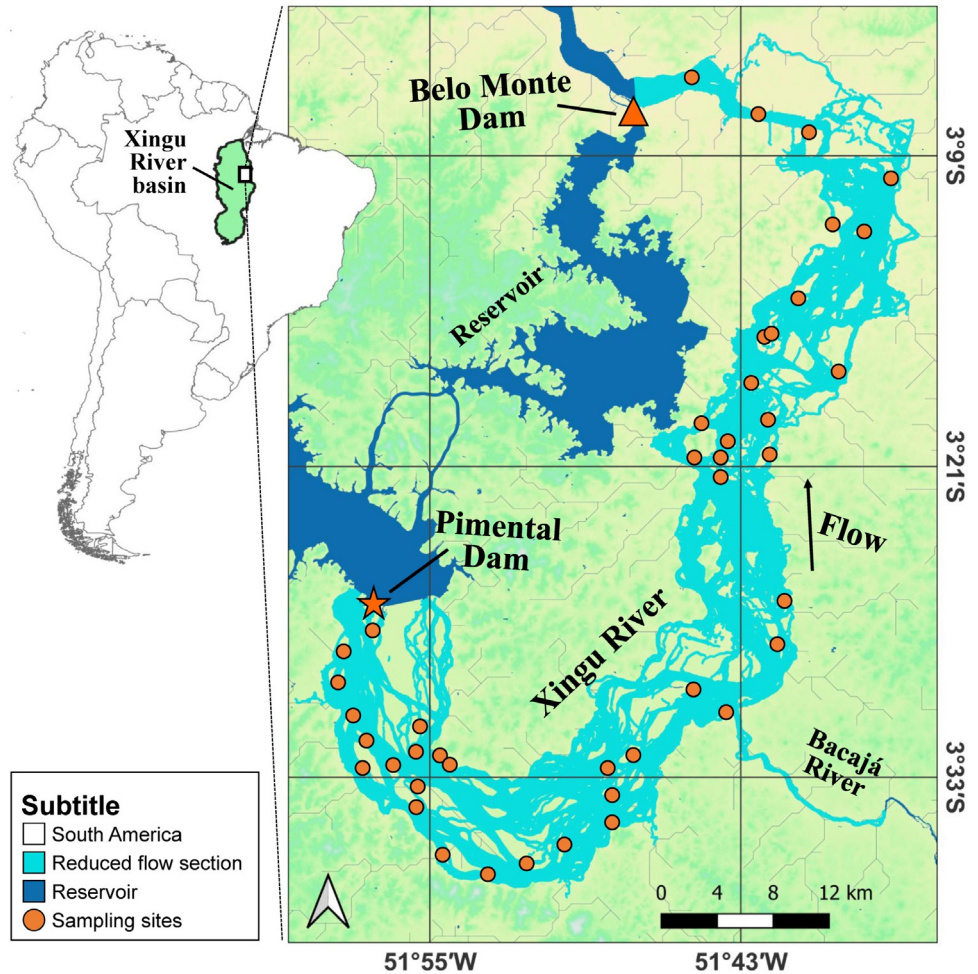


FIGURE 1 | Sampling locations for *Pinirampus pirinampu* in the Volta Grande do Xingu (VGX), middle Xingu River (Pará, Brazil), from January to November 2021.

After collection, a subset of individuals of *Pinirampus pirinampu* was selected, from which dorsal muscle tissue samples (without skin, scales, or spines) were collected from the right flank. In addition, tissue samples were obtained from individuals of other fish species, and other sources that could represent potential prey items were also sampled (see Tab. S1). Tissue samples were immediately stored on ice and later processed for stable isotope analysis.

Fish were anesthetized using benzocaine (0.1 g/L) and euthanized following the ethical guidelines of the Brazilian National Council for the Control of Animal Experimentation (CONCEA). Standard length (SL, in cm, to the nearest 0.1 cm) and total weight (TW, in g, to the nearest 0.01 g) were recorded for each specimen. Stomachs were removed via ventral incision, preserved in 70% ethanol, and sent to the Laboratory of Ecology and Conservation (LABECO) at the Universidade Federal do Pará (UFPA, Guamá Campus) for dietary analysis. Voucher specimens were fixed in 10% formalin for 48 h, transferred to 70% ethanol, and deposited in the ichthyological collection of the Zoological Museum at Universidade Federal do Pará (MZUFPA, Belém), under catalog number MZUFPA 891.

Samples of autochthonous sources (crustaceans and mollusks) were collected during each hydrological period. Crustaceans (shrimp and crab) and mollusks (bivalves) were captured through active search on rocks in rapids or rocky areas. Shrimps were kept in aquaria for 24 h to allow gut clearance; afterward, the samples were wrapped in aluminum foil and stored on ice.

All samples were rinsed with distilled water to remove inorganic debris and kept chilled to preserve their physicochemical integrity. Subsequent laboratory processing and stable isotope analysis were conducted at LABECO (UFPA), following standardized protocols to ensure analytical accuracy.

In the laboratory, stomach contents were examined under a stereomicroscope (up to 32× magnification). Food items were identified to the lowest possible taxonomic level using specialized literature (Buckup *et al.*, 2007; Mugnai *et al.*, 2010; Hamada *et al.*, 2019) and with expert assistance. Each item was weighed on a high-precision analytical balance (± 0.0001 g) and assigned to one of six trophic categories: aquatic insects, aquatic crustaceans, aquatic mollusks, fish (autochthonous), plant fragments, and terrestrial insects (allochthonous).

For stable isotope analysis, all tissue and primary source samples were thawed, rinsed with distilled water, and placed in Petri dishes previously sterilized with a 10% diluted hydrochloric acid (HCl) solution for 24 h to remove inorganic carbonates. Samples were then oven-dried at 60 °C, with drying times varying by material type: fish muscle tissues, crustacean, and mollusk were dried for 24 h. Dried samples were ground into a fine powder using a porcelain mortar and pestle, stored in labeled Eppendorf tubes, and sent to the Center for Nuclear Energy in Agriculture (CENA) at the University of São Paulo (USP, Piracicaba) for isotopic analysis. At CENA, approximately 0.5 mg of each sample was encapsulated in ultra-pure tin capsules (4 × 6 mm), and stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were determined using an isotope ratio mass spectrometer (IRMS). All samples were analyzed in duplicate, and analytical precision, based on repeated measurements of internal laboratory standards, was better than $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ (Pinnegar, Polunin, 1999).

Data analysis. A total of 135 individuals of *P. pirinampu* were analyzed, with SL ranging from 11.8 to 58.5 cm (mean \pm standard deviation = 37.30 ± 9.60 cm) and body weights from 17.85 to 64.60 g (11.13 ± 10.69 g). Of these, 95 had empty stomachs and were excluded. The remaining 40 individuals were analyzed for diet composition, trophic niche breadth, and feeding intensity. Based on the smallest length at first maturity regardless of sex ($C_{50} = 53.6$ cm; Peixer *et al.*, 2006), most of the analyzed individuals were classified as juveniles, with only two adults (Fig. S2).

To quantify dietary composition, the weight (g) of each food item was converted to a percentage based on its proportion of total items per stomach (Hynes, 1950). The Frequency of Occurrence (FO) (Hyslop, 1980) was also calculated to derive the Alimentary Index (Ai), using the modified formula proposed by Kawakami, Vazzoler (1980):

$$A_i = [(FO_i \times M_i) / \Sigma(FO_i \times M_i)] \times 100$$

Where A_i represents the relative importance of food item i , FO_i is its frequency, and M_i is its mass percentage. The A_i was calculated for grouped individuals, both across the entire study and per sampling date.

The A_i values of the trophic categories were square-root transformed and used in two main analyses. First, differences in diet composition between hydrological periods were assessed using Permutational Multivariate Analysis of Variance (PERMANOVA) via *adonis2* function from the *vegan* package (Oksanen *et al.*, 2024) in RStudio (R Development Core Team, 2024). Second, variation in trophic niche breadth was tested using Permutational Analysis of Multivariate Dispersion (PERMDISP), employing the *vegdist* and *betadisper* functions, both from the *vegan* package. This analysis quantifies the average distance of each sample to its group centroid, thereby comparing dispersion across the two hydrological phases. The unit of replication for both analyses was the pooled A_i values from individuals collected per sampling month per hydrological period.

Feeding intensity was evaluated using the Repletion Index (RI), calculated for each specimen according to the formula by Zavala-Camin (1996):

$$RI = (ME / MT) \times 100$$

Where ME is the stomach content mass (including identifiable items and digested material) and MT is total body mass before dissection. Differences in RI values between phases were tested using a *t*-test (*t.test* function, *stats* package in RStudio). Normality and homogeneity of variances were verified using the Shapiro-Wilk and Levene's tests. All statistical analyses, including the following tests, adopted $\alpha = 0.05$ (Zar, 2010) and were conducted in RStudio (R Development Core Team, 2024).

Isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ were expressed in parts per thousand (‰) relative to international standards: Pee Dee Belemnite (PDB) for carbon and atmospheric nitrogen (AIR) for nitrogen, following the conventions established by Peterson, Fry (1987):

$$\delta^{13}C(\text{‰}) = \left[\left(\frac{{}^{13}C / {}^{12}C}{\text{sample}} \right) / \left(\frac{{}^{13}C / {}^{12}C}{\text{standard}} \right) - 1 \right] \times 1000$$

and

$$\delta^{15}N(\text{‰}) = \left[\left(\frac{{}^{15}N / {}^{14}N}{\text{sample}} \right) / \left(\frac{{}^{15}N / {}^{14}N}{\text{standard}} \right) - 1 \right] \times 1000$$

To correct lipid-related bias, we applied mathematical normalization using measured ‰C and C:N ratios as proxies for lipid content. For fish tissue with C:N ratios > 3.5, we applied the correction following Post *et al.* (2007):

$$\Delta\delta^{13}C = \delta^{13}C_{\text{extracted}} - \delta^{13}C_{\text{untreated}}$$

To evaluate differences in isotopic composition between hydrological phases, independent *t*-tests were applied to $\delta^{13}C$ and $\delta^{15}N$ values. The isotopic niche area and overlap between hydrological phases were estimated using the Standard Ellipse Area corrected for small sample sizes (SEAc), expressed in ‰². Twenty thousand iterations were performed, with 1,000 discarded as burn-in, a thinning factor of 10, and two

independent chains, resulting in 3,800 posterior samples for each ellipse parameter. This Bayesian-based metric allows for robust estimation of trophic niche breadth and overlap in bivariate isotopic space (Jackson *et al.*, 2011; Syväranta *et al.*, 2013) and was implemented using the *SIBER* package (Stable Isotope Bayesian Ellipses in R) in RStudio. Isotopic niche overlap (IOv) was also calculated based on SEAc values (Jackson *et al.*, 2011; Syväranta *et al.*, 2013).

Before applying mixing models, we assessed source-consumer compatibility through simulations of the isotopic mixing space (Smith *et al.*, 2013; Phillips *et al.*, 2014). All tissue samples fell within the 95% mixing envelope, indicating no outliers and no need for sample exclusions (Fig. S3). Polygon simulations were performed using the *sp* (Pebesma *et al.*, 2025) and *splanx* packages (Bivand *et al.*, 2022) in RStudio.

Finally, to assess variations in the contribution of assimilated basal resources between hydrological phases, Bayesian isotopic mixing models were implemented using the *simmr* package (Parnell *et al.*, 2010). The models were fitted using Dirichlet priors and Markov Chain Monte Carlo (MCMC) simulations. For each model, 10,000 iterations were run, with 10% discarded as burn-in. We applied the Gelman-Rubin and Geweke diagnostic tests, targeting convergence values equal to 1 as recommended by Parnell (2021). Ninety-five percent of credible intervals were used for result interpretation. To perform the mixing polygon and model analyses, we used the mean \pm 1 SD of the trophic discrimination factor (TDFs): $0.47 \pm 1.23\text{‰}$ for $\delta^{13}\text{C}$ and $2.92 \pm 1.78\text{‰}$ for $\delta^{15}\text{N}$, following Zanden and Rasmussen (2001), values previously applied in studies of Amazonian ichthyofauna (Penha *et al.*, 2024, 2025; Prata *et al.*, 2025; Seabra *et al.*, 2025a,b).

RESULTS

Diet composition. The diet of *Pirinampus pirinampu* (Tab. 1; Fig. 2) comprised 11 distinct food items, with larvae of aquatic insects representing the dominant component, accounting for 91% of the diet (Ai). When categorized by a trophic group, aquatic insects alone contributed 92% to the overall diet, reinforcing the insectivorous feeding habit of the species. All remaining food items combined contributed only 8% of the total diet (Tab. 1).

Food consumption varied among months and between high- and low-water periods. During the high-water period, overall food consumption was higher, with pronounced peaks in May for aquatic insect fragments and bivalves. In the low-water period (June), there was a higher consumption of Blattodea (termites) (Fig. S4).

No significant differences in diet composition were detected between high- and low-water periods (PERMANOVA; Pseudo-F = 1.052, $p = 0.35$), nor in trophic niche breadth (PERMDISP; $F = 0.64$, $p = 0.43$), indicating dietary consistency across hydrological phases. Likewise, feeding intensity, as measured by the Repletion Index (RI), showed no significant variation between periods ($t = 0.08$, $df = 37.363$, $p = 0.93$; $n = 26$ for the high-water period and $n = 14$ for the low-water period), suggesting that *P. pirinampu* maintains a similar feeding activity throughout the hydrological cycle.

TABLE 1 | Alimentary index (Ai) of food origin, items, and category for the diet of *Pinirampus pinirampu* collected monthly and across hydrological periods in the middle Xingu River, Eastern Amazonia, Brazil. n = number of stomachs with food content.

Categories/Food items	2021											Total n = 40
	High-water					Low-water						
	Jan n = 2	Feb n = 1	Mar n = 8	Apr n = 5	May n = 10	Jun n = 7	Jul n = 1	Aug n = 2	Sep n = 1	Oct n = 2	Nov n = 1	
AUTOCHTHONOUS												
Aquatic insect												0.92
Aquatic insect fragment	0.11									0.5		
Aquatic insect (larva)	0.89		1	0.87	0.98	0.56	1	1	1	0.53	1	
Corydalidae (Immature)		1	<0.01							0.29		
Aquatic crustacean												<0.01
Zooplankton (Cladocera)	1											
Aquatic mollusk												0.01
Bivalve				0.13	0.27							
Fish												<0.01
Scale					0.11							
ALLOCHTHONOUS												
Plant fragments												<0.01
Plant fragments				0.93								
Terrestrial insect												0.07
Blattodea (termite)			0.28			0.44				0.29		

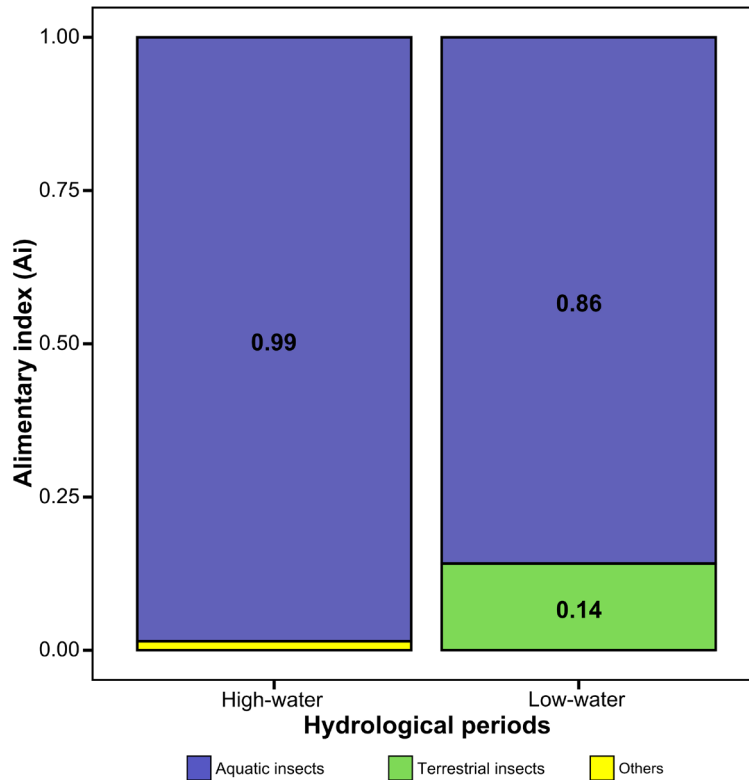


FIGURE 2 | Alimentary index (Ai) of the diet of *Pinirampus pinirampu* collected across hydrological phases in the middle Xingu River, Eastern Amazonia, Brazil.

Stable isotopes. A total of 824 samples were analyzed for stable isotope composition. Of these, 23 were muscle tissue samples from *P. pirinampu*, with 11 collected during the high-water period and 12 during the low-water period. The remaining 801 samples represented basal resources, including fish, crustaceans, and mollusks (Tab. 2).

Mean $\delta^{13}\text{C}$ values of *P. pirinampu* differed significantly between hydrological periods ($t = 2.210$; $df = 20.778$; $p = 0.038$; Fig. 3), indicating a shift in the assimilated carbon source. Individuals sampled during the low-water period exhibited more depleted $\delta^{13}\text{C}$ values (-29.1‰), while those from the high-water period showed less depleted values (-28‰), resulting in an absolute difference of approximately 1‰ ($\Delta\delta^{13}\text{C} \approx 1\text{‰}$). Conversely, $\delta^{15}\text{N}$ values remained stable across periods ($t = 0.363$; $df = 16.586$; $p = 0.72$), averaging $12.58 \pm 0.56\text{‰}$ during the high-water period and $12.50 \pm 0.35\text{‰}$ during the low-water period (Tab. 2), suggesting no significant change in trophic position.

TABLE 2 | Number of samples, means, and standard deviations (\pm SD) of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values for *Pirinampus pirinampu* and basal resources collected across hydrological periods in the middle Xingu River, Eastern Amazonia, Brazil. n = number of tissues sampled.

Species/Resource	High-water					Low-water				
	Mean		SD		n	Mean		SD		n
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
<i>Pirinampus pirinampu</i>	-28	12.58	1.13	0.56	11	-29.1	12.5	1.12	0.35	12
Fish	-27.3	10.59	2.91	1.36	359	-27.8	10.57	2.69	1.26	344
Crustacean	-28.8	9.9	2.11	0.46	17	-29.2	9.9	1.99	1.13	35
Mollusk	-25.8	7.36	4.66	1.04	10	-29	7.13	3.93	1.11	36
Total					397					427

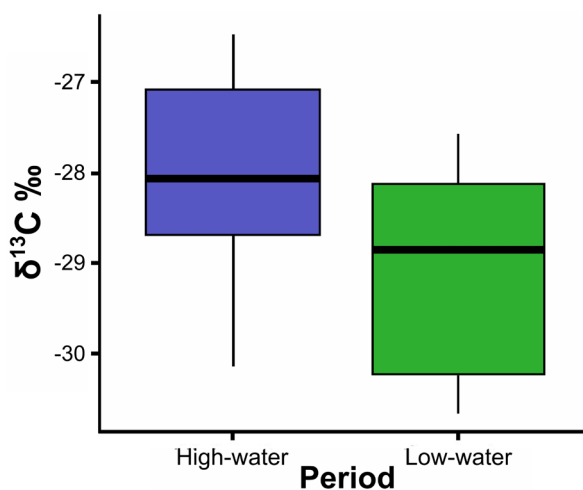


FIGURE 3 | Boxplots of $\delta^{13}\text{C}$ values for *Pirinampus pirinampu* between hydrological phases in the reduced flow stretch in the middle Xingu River. The median is represented as a horizontal line within the box; box limits represent the first and third quartiles; whiskers indicate minimum and maximum values; dots indicate outliers. Mean $\delta^{15}\text{N}$ values did not show a statistically significant difference.

The relative contributions of assimilated carbon sources by *P. pirinampu* varied between hydrological periods, with crustaceans as the primary contributors (Fig. 4). Values represent posterior means from Bayesian mixing models implemented in MixSIAR. During the high-water period, crustaceans accounted for 53%, followed by fish (29%), while mollusk contributed 18%. During the low-water period, the contribution of crustaceans (45%) decreased slightly, fish remained relatively stable (31%), and mollusks increased (24%).

Mixing model analyses revealed minimal changes in the relative assimilation of carbon sources between hydrological phases (Fig. 5). In both periods, crustaceans were the dominant sources, followed by fish, with mollusks contributing to a lesser extent.

We observed variation in isotopic niche areas between hydrological periods. The largest Standard Ellipse Area corrected for small sample size (SEAc) occurred during the high-water period (2.22‰²), while the low-water period exhibited a reduced isotopic niche area (1.17‰²) (Fig. 6). The overlap between periods, calculated using SEAc-based ellipses in SIBER, was 0.65‰², representing 19.13% of the total combined isotopic niche area.

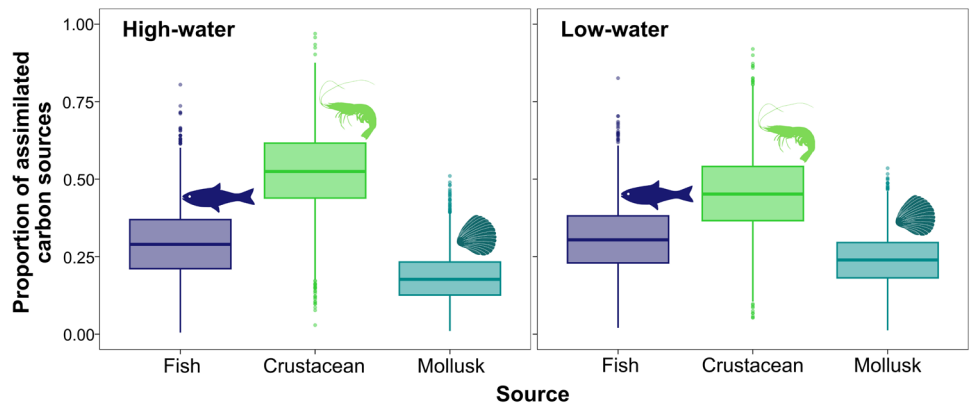


FIGURE 4 | Proportional contributions of assimilated basal resources by *Pinirampus pirinampu* across hydrological phases in the reduced flow stretch of the middle Xingu River, Eastern Amazonia, Brazil.

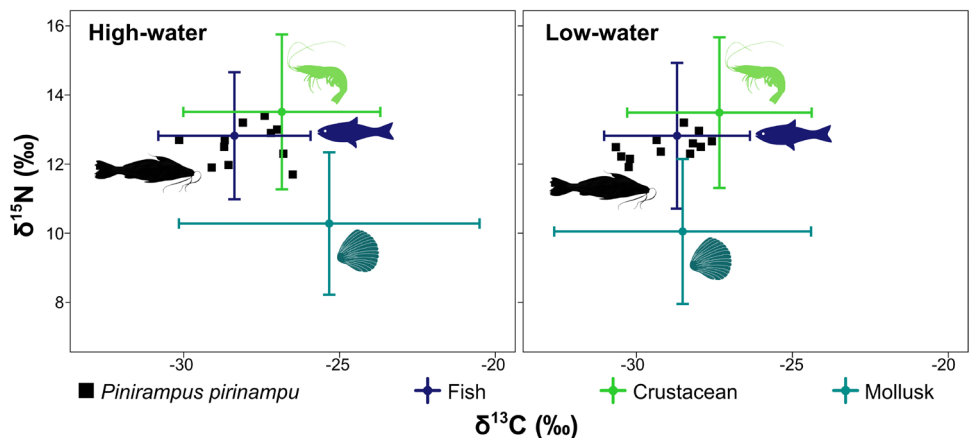


FIGURE 5 | Mix model outputs for *Pinirampus pirinampu* and associated resources collected from January to November 2021 in the Volta Grande do Xingu, Pará, Brazil. Trophic Discrimination Factors (TDF): 0.47 ± 1.23 for $\delta^{13}\text{C}$ and 2.92 ± 1.78 for $\delta^{15}\text{N}$ (Zanden, Rasmussen, 2001).

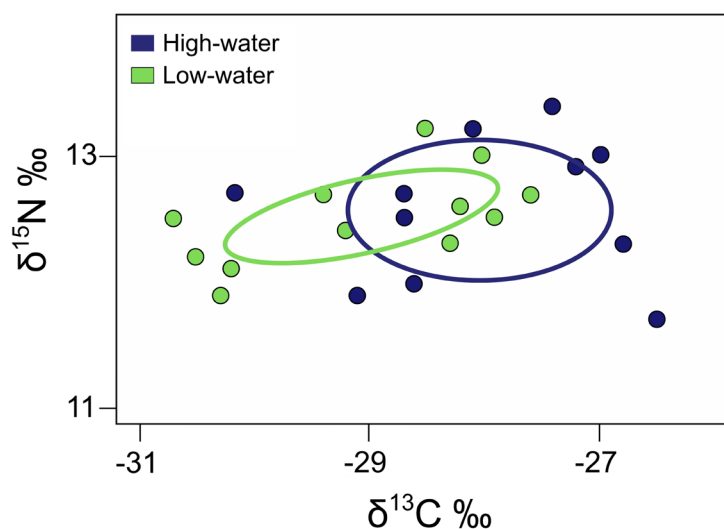


FIGURE 6 | Isotopic niche area of *Pinirampus pirinampu* across hydrological phases in the reduced stretch flow in the middle Xingu River. Solid lines represent SEAc (40% credibility interval). The overlap between periods representing 19.13% of the total combined isotopic niche area.

DISCUSSION

Our results demonstrate that *Pinirampus pirinampu* maintains a consistent insectivorous feeding strategy throughout the high- and low-water periods. No significant differences were observed in diet composition, trophic niche breadth, or feeding intensity between periods, supporting the initial hypothesis that variations in water volume would not markedly alter the species' feeding parameters. Despite the relatively small number of stomachs analyzed, the patterns observed were statistically coherent across individuals and periods, which could be further confirmed by future studies with larger sample sizes.

In contrast, the hypothesis regarding isotopic stability was only partially supported. While $\delta^{15}\text{N}$ values remained stable between the high- and low-water seasons, indicating a consistent trophic position and sustained assimilation of prey from higher levels of the food web, $\delta^{13}\text{C}$ values varied significantly between periods. Although the absolute difference in $\delta^{13}\text{C}$ values was modest ($\approx 1\text{‰}$), such variation can still be ecologically meaningful in Amazonian floodplain systems, where even small isotopic shifts may reflect changes in the balance between allochthonous and autochthonous carbon inputs. In this context, the observed pattern likely reflects seasonal adjustments in assimilated carbon sources, driven by changes in prey use in response to fluctuations in the relative availability of fish, crustaceans, and mollusks. Additionally, the broader trophic niche space (inferred from the SEAc) observed during the high-water period, together with moderate isotopic niche overlap (19.13%), suggests that the species can exploit a wider range of carbon sources when connectivity and habitat diversity increase during floods.

Carnivorous fish are known to adjust their diets according to prey availability, as documented in studies across the Amazon basin (Moreira-Hara *et al.*, 2009; Prata *et al.*, 2025). In the study region, crustaceans, fish (likely juveniles), and aquatic insects represented the most abundant and accessible prey items. Supporting this, Prata *et al.* (2025), working concurrently in the same area, also reported that these groups

dominated the diet of another carnivorous fish species. Similar to our findings for *P. pirinampu*, that species exhibited limited seasonal dietary variation, suggesting that high prey availability and broad foraging flexibility contribute to the trophic stability of carnivorous fishes in floodplain environments.

Despite the relatively high number of individuals captured, the high proportion of empty stomachs observed in *P. pirinampu* can be considered a common feature among carnivorous fishes (Freitas *et al.*, 2020). This pattern is often attributed to intermittent feeding behavior and the rapid digestion of soft-bodied prey, both of which reduce the likelihood of detecting food remains (Manko, 2016; Jiao *et al.*, 2023; Skjoldal *et al.*, 2025). In addition, factors such as capture-related stress, seasonal variation in prey availability, and the low feeding frequency of larger individuals may also contribute to this outcome (Almeida *et al.*, 1997; Vignon, Dierking, 2011; Gupta, Banerjee, 2014; Ferreira *et al.*, 2024).

Although *P. pirinampu* has traditionally been described as a piscivorous species (Barbarino Duque, Winemiller, 2003; Bennemann *et al.*, 2011; Röpke *et al.*, 2025), our results revealed a predominance of aquatic insects in its diet, with fish and other prey groups occurring less frequently. Given that most of the analyzed individuals were juveniles (Peixer *et al.*, 2006), this feeding pattern likely reflects ontogenetic effects, in which greater trophic plasticity and the consumption of small, abundant prey constitute an energetically efficient foraging strategy (Almeida *et al.*, 1997; Qin *et al.*, 2024; Skjoldal *et al.*, 2025). Thus, the predominance of autochthonous benthic resources such as aquatic insects suggests that juvenile *P. pirinampu* intensively exploit shallow margins and substrates during the high-water period, when prey availability increases substantially (Duarte *et al.*, 2019; Brito *et al.*, 2021; Röpke *et al.*, 2025).

Our findings suggest that the trophic strategy of *P. pirinampu* aligns with the Optimal Foraging Theory, which posits that predators maximize their net energy intake by targeting prey that are both abundant and energetically efficient to capture and handle (MacArthur, Pianka, 1966; Stephens, Krebs, 1986). The predominance of crustaceans in assimilated resources, which are generally easier to capture than juvenile fish (Carvalho *et al.*, 2006; Carvalho *et al.*, 2020), and the significant consumption of aquatic insects during the high-water period, as discussed above, support this interpretation. Therefore, *P. pirinampu* exhibits a foraging strategy adapted to local environmental conditions, prioritizing prey that are both abundant and easily captured.

Discrepancies between stomach content analysis and stable isotope data observed in this study are not uncommon and have been documented in other predatory fishes worldwide (Beaudoin *et al.*, 1999; Jensen *et al.*, 2012), where ingestion of invertebrates was common but isotopic signatures reflected assimilation of higher-trophic-level prey (*e.g.*, fish). Conversely, an opposite pattern has been reported, where stable isotope analysis of a previously known piscivorous species revealed aquatic invertebrates' signatures, resulting in a lower trophic position (Gerber *et al.* 2023). This discrepancy likely reflects the different temporal scales of both methods: stomach content analysis represents recent feeding, whereas isotopes integrate assimilated diet over weeks or months (Pinnegar, Polunin, 1999; Post, 2002). In our study, stomach contents indicated a mainly insectivorous diet, while isotopes suggested greater assimilation of crustacean-derived carbon, especially during high water, highlighting the complementary nature of both approaches.

The broader isotopic niche observed during the high-water period likely reflects increased food availability and access to expanded habitat, including flooded forests. This pattern is consistent with the Flood Pulse Concept (Junk *et al.*, 1989), which predicts greater trophic generalism during floods due to higher resource heterogeneity and increased foraging opportunities (Winemiller, 1996; Azevedo *et al.*, 2022). Even under an altered flood regime, the seasonal rise in water levels still appears sufficient to expand the diversity of assimilated carbon sources.

Moreover, the moderate overlap observed between isotopic niches, together with the broader niche area during the high-water period, supports the interpretation of dietary plasticity, allowing *P. pirinampu* to adjust to seasonal shifts while maintaining reliance on core prey groups. Such trophic flexibility is a common adaptive strategy among predatory fishes (Barbosa *et al.*, 2018; Weiss *et al.*, 2025) and may be essential for species persistence in environments subjected to hydrological alterations.

It is also important to note that, following the reduction of flood pulses after the construction of the Belo Monte Hydroelectric Dam in 2016, monitoring in the Volta Grande do Xingu has revealed changes in the spatial dynamics of organic matter deposition (Utsunomiya *et al.*, 2024; Quaresma *et al.*, 2025). Such altered hydrological regimes are known to reduce the biomass of marginal and benthic biomass of macroinvertebrates and to disrupt both the timing and extent of allochthonous and autochthonous prey inputs into adjacent habitats, consequently affecting prey availability for juvenile foragers (Baumgartner, 2007; Pereira *et al.*, 2017). The feeding data obtained here may reflect subtle ecological shifts associated with these hydrological changes, indicating variations in benthic productivity and the use of nearshore resources (Vinson, Angradi, 2011; Baker *et al.*, 2014; Han *et al.*, 2020; Ng *et al.*, 2021; Poiesz *et al.*, 2024). Reservoir impoundment and flow regulation often simplify riparian vegetation and benthic communities, altering the distribution and abundance of insect prey (Fjellheim, Raddum, 1996; Richardson *et al.*, 2002), factors that have been shown to drive changes in the diets and trophic niches of predatory fishes in regulated rivers (Richardson *et al.*, 2002).

In summary, our results revealed a distinct trophic dynamic of *P. pirinampu*, a carnivorous species influenced by the hydrological regulation imposed by the Belo Monte Dam. Seasonal variations in assimilated carbon sources suggest flexible foraging behavior in response to altered prey availability, reflecting the feeding plasticity that supports the species' resilience and the maintenance of its functional role within the food web. However, the apparent stability in the feeding dynamics (*e.g.*, stomach contents) may also represent an adaptive response to ongoing environmental changes rather than an absence of impact. Such adjustments underscore the importance of long-term monitoring and the integration of complementary trophic approaches to better assess the environmental consequences of flow regulation in Amazonian rivers.

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AUTHORS' CONTRIBUTION 

Antonio Augusto Jardim Jr: Conceptualization, Formal analysis, Writing–original draft, Writing–review and editing.

Erival Gonçalves Prata: Conceptualization, Formal analysis, Writing–original draft, Writing–review and editing.

Lais Martins Silva: Formal analysis, Writing–original draft.

João Pedro da Silva Moraes: Formal analysis, Writing–original draft.

Lucas Pires de Oliveira: Formal analysis, Writing–original draft.

Luciano Fogaça de Assis Montag: Conceptualization, Funding acquisition, Methodology, Project administration, Writing–original draft, Writing–review and editing.

Tiago Magalhães da Silva Freitas: Conceptualization, Data curation, Methodology, Writing–original draft, Writing–review and editing.

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Experiments were approved by the Ethical Committee for Animal Use in Experiments of the Universidade Federal do Pará (CEUA number 8293020418/2020) and Collection Licenses of SISBIO number 1267/2020.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

AI STATEMENT

The authors did not use any AI-assisted technologies in the creation of this manuscript or its figures.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

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PEER REVIEW

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