Aquatic Sciences (2023) 85:74
https://doi.org/10.1007/s00027-023-00971-x

Aquatic Sciences

RESEARCH ARTICLE

Food web structure in the Xingu River rapids prior to operation of the Amazon's largest hydropower plant

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Received: 22 February 2023 / Accepted: 2 May 2023 / Published online: 22 May 2023

Abstract

The results of recent theoretical studies suggest that food webs are size-structured, with top predators coupling across different energy sources. However, evidence supporting this hypothesis is still scarce, especially in highly diverse tropical rivers. In the present study, we explored the association between body size, trophic position, and the use of allochthonous and autochthonous basal production sources in the Volta Grande rapids of the Xingu River, a major clearwater tributary of the Amazon River, during the period prior to operation of the Belo Monte Hydropower Plant (BMHP). This section of the river contains a maze of channels with rocky shoals that support dozens of endemic fishes, mollusks and other aquatic taxa that may be impacted by flow regulation by the Pimental Dam located upstream. During the low-water season, we surveyed fish, crustaceans, mollusks, sponges, aquatic and terrestrial insects, zooplankton, and basal production sources to obtain tissue samples for analysis of stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). The results indicated that the biomass of most aquatic organisms appears to be largely supported by riparian vegetation, highlighting the importance of the lateral connectivity between aquatic and terrestrial habitats. In contrast to expectation, we did not observe a gradual increase in the coupling of energy pathways with increasing body size and trophic position. These findings provide a baseline for the trophic ecology of this river under the natural flow regime that can be used for future impact assessments, and they also indicate that more complex food web models, potentially including additional functional traits (e.g., gut length) are needed to describe resource and habitat use in highly diverse tropical ecosystems.

Keywords Food chain length · Lotic ecosystem · Trophic ecology · Trophic level · Niche · Diet

Introduction

Over the past century, hydropower has been developed to meet the energy demands of growing populations and economies throughout the world (Zarfl et al. 2015, 2019). Although hydropower is promoted as clean energy, dams and reservoirs have profound impacts on fluvial and riparian ecosystems (Agostinho et al. 2008; Lees et al. 2016). Hydropower dams are barriers to fish migration and disrupt hydrological, sediment, and nutrient dynamics, resulting in change to the ecosystem structure and function downstream (Saunders et al. 2002; Maavara et al. 2017; Anderson et al. 2018; Sroczyńska et al. 2020). Under a natural flow regime, periodic flood pulses increase not only the volume of the aquatic habitat, but also inputs of allochthonous material from the floodplain, suspension and transport sediments, and access to floodplains and their resources for fishes and other aquatic organisms (Junk et al. 1989). The natural flood

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pulses provide large amounts of different energy sources to the consumers by coupling allochthonous and autochthonous food items (McCann 2011). Flow regulation by hydroelectric dams changes ecological dynamics, including the movement of matter and energy within aquatic food webs. Currently, there are 100 hydropower dams that are functional in the Amazon Basin (Tundisi et al. 2014), with a further 368 either planned or under construction (Zarfl et al. 2015, 2019); many of these are within areas of high biodiversity, including those with endemic aquatic species (Winemiller et al. 2016a). Hydropower projects are one of the principal agents responsible for losses of freshwater biodiversity and ecosystem services from rivers globally (Pringle 2003).

In tropical rivers, many fishes and other aquatic organisms exploit allochthonous resources (e.g., terrestrial invertebrates, fruits, seeds, leaves) from the floodplains, especially during the annual high-water period (Goulding 1980; Mérona and Rankin-de-Mérona 2004; Ou and Winemiller 2016; González-Bergonzoni et al. 2019). Allochthonous inputs to the aquatic food web are particularly important in oligotrophic systems (Goulding et al. 1988; Peterson et al. 2017; Correa and Winemiller 2018; Capitani et al. 2021). Many tropical river fishes enter floodplain habitats for feeding, refuge, and reproduction (Lowe-McConnell 1987; Winemiller and Jepson 1998). A large body of food web theory proposes that trophic interactions are size-structured, with vertical trophic position positively correlated with body size (Rooney et al. 2008; Woodward et al. 2005a, b). If the veracity of this pattern is assumed for tropical floodplain rivers, then dams likely disrupt food webs by restricting the seasonal movement of aquatic organisms, their access to habitats, and local assemblage structures, with ultimate impacts to food web structure and dynamics (McCann et al. 2005; Rooney et al. 2008). However, recent studies of tropical river fish assemblages have revealed only a weak relationship between trophic position and body size (Layman et al. 2005; Ou et al. 2017; Keppeler et al. 2020).

In the present study, we investigated associations between body size, vertical trophic position, and resource assimilation for aquatic macroinvertebrates and fishes in the Xingu River, a major Amazon tributary, prior the operation of the Belo Monte Hydropower Plant (BMHP) in 2016. The Xingu River drains the Brazilian Shield and is a major clearwater tributary of the Lower Amazon River. The middle section of the river has a relatively steep gradient and comprises a network of channels with rocky shoals and rapids which support a rich aquatic fauna, including many endemic species (Andrade et al. 2019). Aquatic communities of river rapids are known to be particularly sensitive to flow alterations from water impoundment, diversion, and flow alternation (Camargo et al. 2015). The BMHP provides a prime example of how poor site selection for hydropower development threatens not only local habitats and biodiversity, but also global biodiversity when endemic species are at risk (Winemiller et al. 2016a; Castro-Diaz et al. 2018; Jiang et al. 2018; Ribeiro and Morato 2020). We hypothesize that body size should be related to energetic pathway (terrestrial or aquatic), with larger taxa having broad diets derived from both terrestrial and aquatic basal resources, and smaller taxa having more specialized diets from either terrestrial or aquatic resources, depending on species traits. Therefore, the largest fishes are top predators and, consequently, the aquatic food web is strongly size-structured (i.e., trophic position is positively related to body size). To test this theory, we performed stable isotope analysis, which is considered to be an effective means for estimating the relative importance of production sources supporting consumers and the vertical trophic structure of communities (West et al. 2006; Dawson and Siegwolf 2011; Nagelkerken et al. 2020).

Material and methods

Study area

The study was conducted within the Volta Grande (Big Bend) of the middle Xingu River, a reach that now lies downstream from the Pimental Dam, a major component of the BMHP. The Xingu River arises in the Serra do Roncador in the central Brazilian state of Mato Grosso and flows 2050 km northward to its confluence with the Amazon in the state of Pará. The Xingu Basin encompasses 500,000 km^2 of the Brazilian Shield, an ancient geological formation that yields oligotrophic characteristics in the river, including low conductivity (mean = 30 μS/cm), low concentrations of suspended sediments and high transparency (Secchi depth = 1–5 m), and nearly neutral pH (mean = 6.7). The hydrological regime is strongly seasonal, with daily discharge ranging from 32,000 m^3 s^{-1} during the high-water period (January to May) to 500 m^3 s^{-1} during the low-water period (August to November). A strong elevational gradient (Goulding et al. 2003), combined with the region's numerous outcrops of metamorphic and igneous rocks, creates a complex maze of rapids in the middle reach.

Sampling

Surveys were conducted along a 10-km reach of the main channel within the Volta Grande reach approximately 45 km downstream from the town of Altamira (Fig. 1). Samples of common primary producers, macroinvertebrates, and fish were collected from the rapids near Paquiçamba (3°35′S; 51°50′W) during October 2012 when water levels were low. To minimize potential temporal and spatial bias in the interpretation of isotopic ratios of invertebrate and fish tissues, surveys were conducted during 1 week within an area of

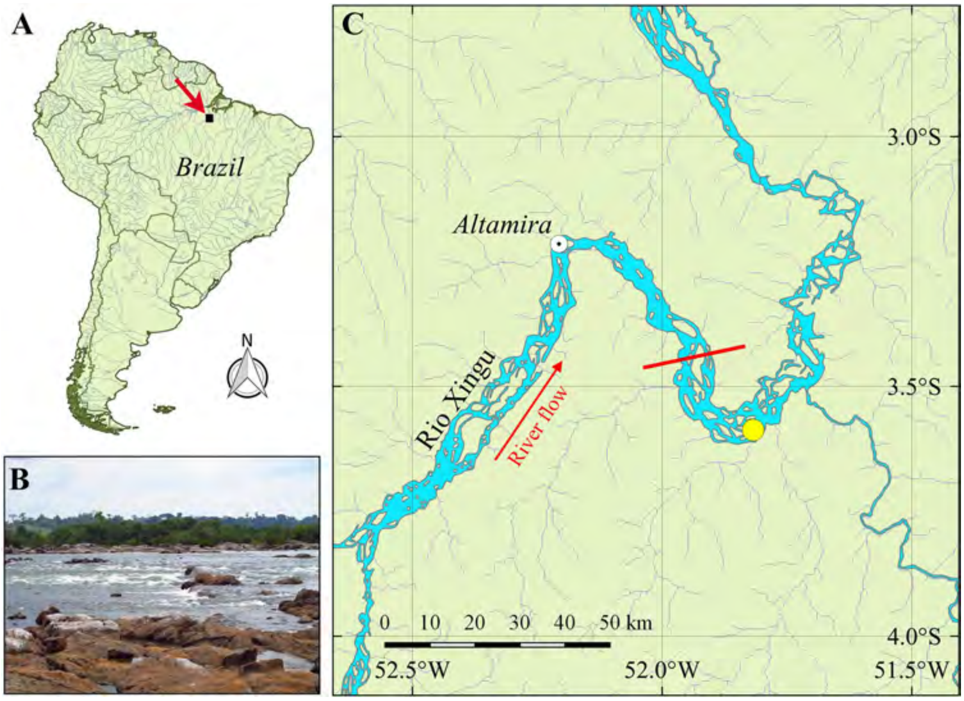

Fig. 1 The Volta Grande of the Xingu River prior to installation of the Belo Monte Hydropower Plant. **a** Location of the study area in South America, **b** rapids in Xingu River at Paquiçamba, **c** locations of the rapids at Paquiçamba (dot) and of the Pimental Dam (bar)

rapids covering approximately 24 km^2. At sites with fast-flowing currents, many rocks were covered with rheophilic macrophytes, especially species of Podostemaceae. Plants of the families Myrtaceae, Asteraceae, and Mimosaceae were common in areas with slower currents. The local riparian forests are flooded seasonally and provide feeding, spawning, and nursery habitats for many fish species (Zuluaga-Gómez et al. 2016; Fitzgerald et al. 2018; Andrade et al. 2019).

Fish, invertebrates (sponges, snails, microcrustaceans, crabs, and insects), and allochthonous (terrestrial vascular plants) and autochthonous (aquatic macrophytes, periphyton, and phytoplankton) basal production sources were sampled within the study reach. Fish were collected using gillnets of ten different mesh sizes (mesh size: 20–180 mm, stretched), cast nets (mesh size: 20–60 mm), and hand nets used while free diving. Fish specimens were identified to the lowest feasible taxonomic level using available ichthyological literature (Géry 1977; Planquette et al. 1996; Santos et al. 2004). Samples of aquatic insects were represented by larval stages, and crustaceans were mostly adult stages. Riparian vegetation and aquatic macrophyte samples were collected manually, and periphyton samples were scraped from rocks and submerged wood using forceps. Suspended fine particulate organic matter was collected by filtering the water through a 45-μm mesh seine, but we decided not to include these samples in subsequent analyses because these were composed of an unknown proportion of autochthonous and allochthonous resources (González-Bergonzoni et al. 2019). Samples were transported to the laboratory on ice and frozen until preparation for isotopic analysis. For fish, approximately 2 g of muscle tissue was collected from the dorsal flank region, with skin and scales removed. For a given fish species, specimens of a similar size range (adult) were selected to minimize any potential bias in isotopic ratios associated with ontogenetic niche differences. For mollusks and crustaceans, shell and carapace were removed, and only soft tissue was retained for analysis. We processed the whole body of insects for stable isotope analysis. Samples of plants and other basal sources included only fresh tissues. Stable isotope analysis was performed with a minimum of three samples for each species.

Methods for processing samples generally followed those described by Hoeinghaus et al. (2007) and González-Bergonzoni et al. (2019). Samples from animals and basal production sources were rinsed in distilled water, then dried to constant weight in an air-circulation oven at 60 °C, and finally homogenized into a fine powder using mortar and pestle that were cleaned in an acid bath between usages. Subsamples weighing from 1 to 26 mg were packed into Ultra-Pure tin capsules, and carbon (C) and nitrogen (N) isotope ratios were determined using a Delta-V isotope ratio mass spectrometer coupled to an NA1500 CHN Carlo Erba combustion analyzer via a Thermo Conflo III Interface (all Thermo Fisher Scientific, Waltham, MA, USA). Stable isotope ratios were expressed in standard delta (δ) notation and defined as parts per thousand (‰) relative to a standard reference as follows:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 10^3$$

where R_{sample} = the heavy to light isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) of the sample and $R_{standard}$ = the heavy to light isotope ratio of the standard reference. The $R_{standard}$ for $\delta^{13}C$ was Vienna Pee Dee Belemnite (VPDB) limestone formation, and the $R_{standard}$ for $\delta^{15}N$ was atmospheric N_2. For tissue samples with C/N ratios > 3.5 (Post et al. 2007), $\delta^{13}C$ values were corrected prior to analyses for lipid content using the following formula:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C : N$$

Body size measurements and trophic guilds

Fish specimens were weighed in the field using either a portable digital scale (precision: 0.01 g) when specimens were small, or spring scales (precision: 1 g) when specimens were large. We measured the carapace width of crabs, shell length of snails, and total length of insects. We estimated the length of three invertebrates (*Doryssa starkii*, zooplankton, and *Petrophila* sp.) that were not measured in the field using information from the literature (for more details, see Supplementary Information (SI) Table S1). Sponges (2 species in our dataset) are modular organisms, and specimens have variable sizes and shapes. Therefore, we decided to exclude this group from the morphological analyses.

To standardize body size measurements across organisms, we converted lengths to weights using the formula proposed by Keys (1928):

$$W = aL^b,$$

where W is the weight of individual i, L is the length of individual i, and a and b are the intercept and slope, respectively, of the length–weight relationship of individual i's population. Parameters a and b were obtained from the literature. Dry weights generated by the invertebrate length–weight relationships were later converted to wet weight using ratios obtained from literature. For more details on the protocol, see SI Table S1.

Fishes were classified into herbivorous/detritivorous, omnivorous, and carnivorous trophic guilds based on relevant literature and unpublished diet data obtained during the monitoring program in the region. This classification was necessary to define trophic discriminant factors in the stable isotope analyses (see below).

Data analysis

A permutational multivariate analysis of variance (PERMANOVA) using Euclidean distance was used to test the differences in stable isotope signatures between autochthonous and allochthonous basal production sources. We developed two baseline full Bayesian models (Quezada-Romegialli et al. 2018) to estimate the relative trophic position and contribution of autochthonous and allochthonous sources to biomass of the consumers. The model is based on two main equations:

$$\delta^{15}N_c = \Delta N\,(TP + \lambda) + \alpha\left(\delta^{15}N_{b1} + \delta^{15}N_{b2}\right) - \delta 15N_{b2}$$

and,

$$\delta^{13}C_c = \delta^{13}C_{b1}\alpha + \delta^{13}C_{b2}\,(1 - \alpha),$$

where $\delta^{15}N_c$, $\delta^{15}N_{b1}$, $\delta^{15}N_{b2}$ refer to the $\delta^{15}N$ values of consumers, baseline 1 (autochthonous sources), and baseline 2 (allochthonous sources), respectively; $\delta^{13}C_c$, $\delta^{13}C_{b1}$, and $\delta^{13}C_{b2}$ refer to the $\delta^{13}C$ values of consumers, baseline 1, and baseline 2, respectively. ΔN is the trophic position of the baseline, which was set to 1. ΔN is the trophic discriminant factor (TDF) for N. Previous studies indicated that ΔN values associated with carnivorous fishes are lower than those associated with herbivorous fishes (Mill et al. 2007; Lujan et al. 2011; Varela et al. 2011; Madigan et al. 2012). To account for these differences, we set ΔN as 1.77 ± 0.3 (standard deviation SD]) and 4.78 ± 1.30) for carnivorous and herbivorous/detritivorous fishes, respectively, following a previous literature synthesis (Bastos et al. 2017). We used intermediate ΔN values (3.28 ± 0.27) for omnivorous fish, which is a fair assumption given that ΔN decreases more-or-less linearly with the dietary $\delta^{15}N$ value (proxy for the trophic position of the food) (Hussey et al. 2014). Although ΔN may also vary with the diet of invertebrates, there are few studies that have explored ΔN differences among invertebrate groups. In addition, we have little information on the trophic ecology of many of the invertebrate groups sampled in our study. Thus, we set the mean ΔN of invertebrates as 3.02 ± 0.47), which is an average based on previous meta-analyses (Bastos et al. 2017). α is the contribution of baseline 1 to the consumers and is calculated following the equation below:

$$\alpha = \left(\delta^{13}C_{b2} - \left(\delta^{13}C_c + \Delta C\right)/TP - \lambda\right)/\left(\delta^{13}C_{b1} + \delta^{13}C_{b2}\right)$$

where ΔC is the TDF for carbon. Here, we set ΔC as 0.54 ± 0.53, an average based on previous meta-analyses (Bastos et al. 2017).

We explored the relationship between $\delta^{15}N$ and the relative trophic position with body mass using linear and quantile regressions (10th, 50th, and 90th quantiles), respectively. To test the association between resource use and body size and trophic position, we conducted linear regressions with trophic position and body size as response variables and the quadratic term of the α parameter (i.e., $\alpha + \alpha^2$), from the two baseline models, as a predictor following Keppeler et al.

(2022). The quadratic term assumes a dome-shaped relationship among the response and predictor variables, which is in line with the theory: consumers of high trophic level and large body size have intermediate α values (approx. 0.5) because they couple multiple energy sources (Keppeler et al. 2022). Models with the quadratic term were compared with alternative models containing a single linear term (i.e., α) and with intercept models (i.e., without any fixed effects: approx. 1). Model comparisons were based on the corrected Akaike information criterion (AICc). Analyses were performed in R 3.1.10 ® Development Core Team 2020).

Results

A total of 286 samples were analyzed, including 100 primary production sources and 186 animals. Allochthonous and autochthonous sources had significantly different stable isotope signatures (Pseudo-$F_{(1,\ 98)} = 345$, $P < 0.001$, $R^2 = 0.78$). Autochthonous resources were more enriched in ^{15}N and in ^{13}C than allochthonous resources (Fig. 2). In general, fishes had higher δ^{15}N values than invertebrates (Fig. 2). Fish and invertebrates revealed few differences in δ^{13}C and most taxa in both groups were estimated to have assimilated material derived from both autochthonous and allochthonous sources (Fig. 2).

The majority of aquatic animals were estimated to have assimilated a larger fraction of material from allochthonous production sources (38 species with $\alpha < 0.5$), with many fewer estimated to have assimilated material mostly from autochthonous resources (14 species with $\alpha > 0.5$) (Figs. 2, 3). The loricariid catfish *Baryancistrus chrysolomus* ($\alpha = 0.99$), leech (Hirudinea, $\alpha = 0.99$), zooplankton ($\alpha = 0.98$), and the pacu *Myloplus arnoldi* ($\alpha = 0.98$) were the taxa estimated to have assimilated the greatest fractions of material from autochthonous sources, whereas the snail *Doryssa starkii* ($\alpha = 0.001$), the loricariid catfish *Pseudancistrus nudiventris* ($\alpha = 0.003$), and the headstander *Leporinus* af. *fasciatus* ($\alpha = 0.004$), for example, were estimated to have assimilated material derived mostly allochthonous sources. δ^{15}N had a strong positive relationship with body size, which explained approximately 56% of the variation (Pseudo-$F_{(1,48)} = 62.31$, $P < 0.001$; Fig. 4a). Vertical trophic position was also associated with body size, but in this case, the relationship was steeper for the upper quantile (0.21, 95% confidence interval [CI]: 0.09, 0.24) than for the middle (0.07, 95% CI 0.03, 0.09) and lower quantiles (0.05, 95% CI 0.02, 0.10), forming a triangle shape relationship (Fig. 4b). The lowest δ^{15}N values and relative trophic position were observed for

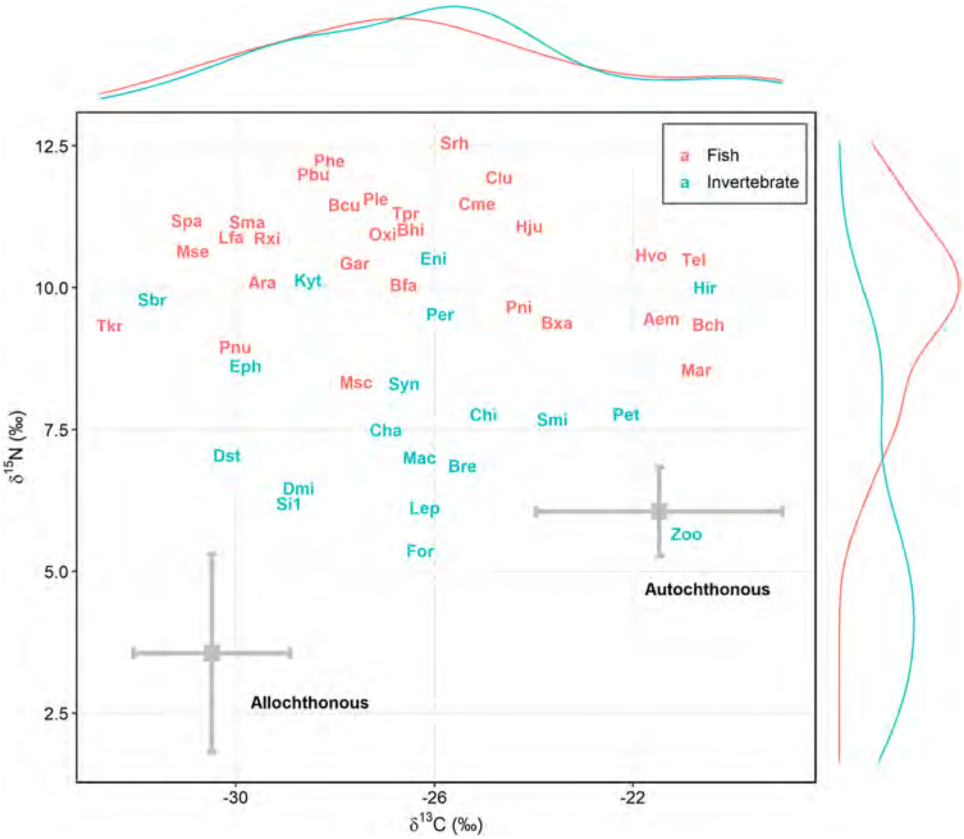

Fig. 2 Biplot with mean (± standard deviation) δ^{13}C and δ^{15}N of fishes, invertebrates, and allochthonous and autochthonous production sources. Color curves outside the box depict distributions of fishes and invertebrates across δ^{13}C and δ^{15}N gradients. Allochthonous and autochthonous sources are presented with mean and standard deviation (gray crosses) of the δ^{13}C and δ^{15}N. For the consumer acronyms, see SI Table S. δ^{C13}, $\delta^{15}N$ stable isotope ratios of carbon and nitrogen, respectively

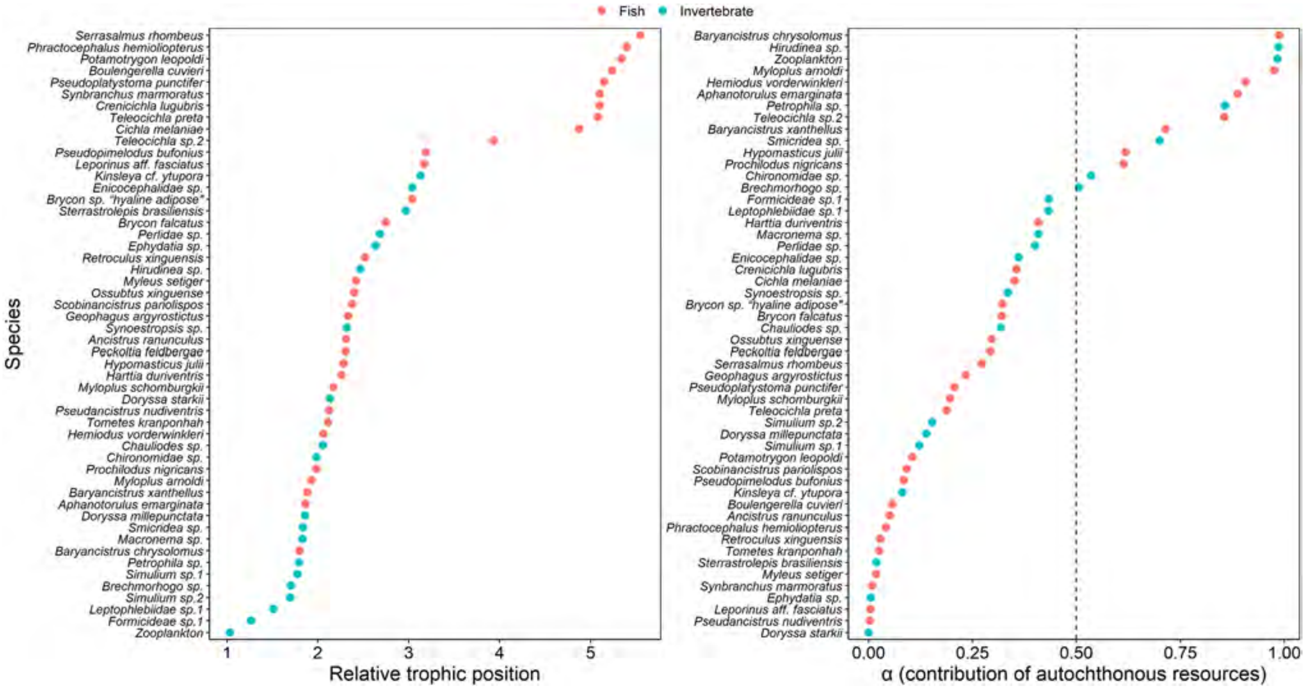

Fig. 3 Trophic positions and alpha values (i.e., relative assimilation of material from autochthonous sources) of fishes and invertebrates from rapids of the middle Xingu River estimated from stable isotopic ratios

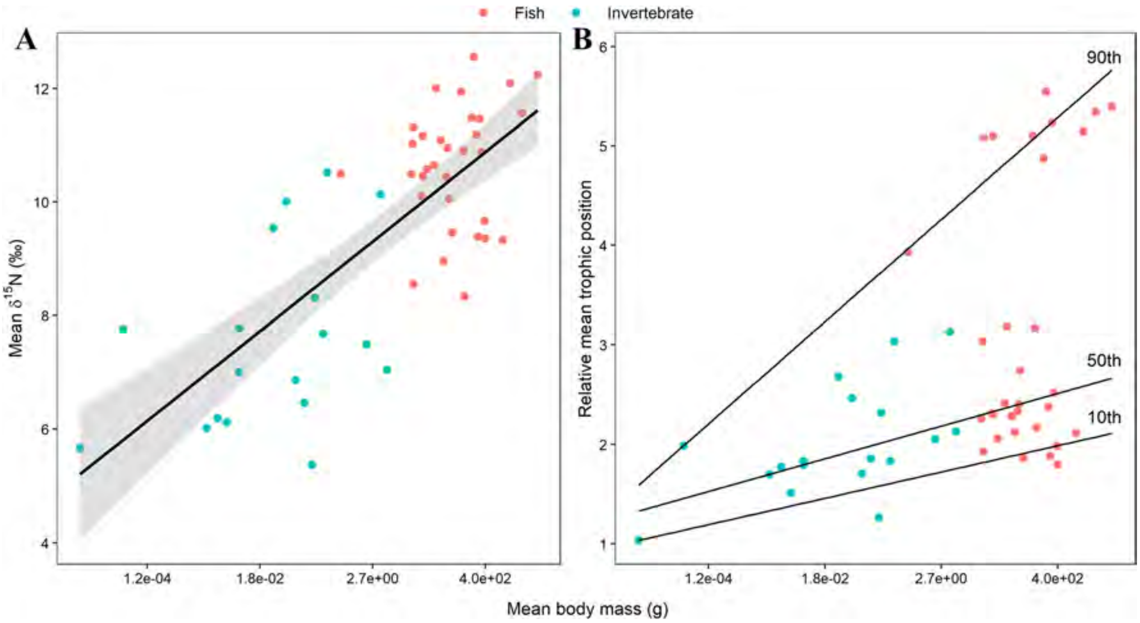

Fig. 4 Relationship between $\delta^{15}N$ (**a**) and trophic position (**b**) with biomass (in grams) of invertebrates and fishes from rapids of the middle Xingu River. **a** The trend line is based on a linear regression, **b**, the trend lines are based on a quantile regression. Body mass is shown in a log-scale

ants (Formicidae, $\delta^{15}N = 5.37$, relative trophic position [rTP] = 1.27) and zooplankton ($\delta^{15}N = 5.66$, rTP = 1.03), whereas highest values were recorded for the piranha *Serrasalmus rhombeus* ($\delta^{15}N = 12.56$, rTP = 5.55) and the redtail catfish *Phractocephalus hemioliopterus* ($\delta^{15}N = 12.25$, rTP = 5.40).

The parameter α did not have a dome-shaped relationship with body size ($t = 1.15$, $P = 0.26$) nor with trophic position ($t = -\ 0.05$, $P = 0.96$) (Fig. 5), as expected by food web theory. Instead, we found a weak negative association of both body size (Pseudo-$F_{(1,48)} = 5.68$, $P = 0.02$, $R^2 = 0.11$) and relative trophic position (Pseudo-$F_{(1,50)} = 7.49$, $P = 0.008$, $R^2 = 0.13$) with α. This is confirmed by our model comparisons, which indicated that models containing only the linear term α were more plausible (i.e., lower AICc) than quadratic-term models and intercept models (Table 1). Several large predators in the system were strongly associated with allochthonous sources, including the redtail catfish *Pharactocephalus hemioliopterus* ($\alpha = 0.04$), the pike characin *Boulengerella cuvieri* ($\alpha = 0.06$), and the stingray *Potamotrygon leopoldi* ($\alpha = 0.11$).

Discussion

The biomass of most aquatic organisms inhabiting the Volta Grande rapids of the Xingu River appears to be largely supported, either directly or indirectly, by riparian vegetation (Fig. 3). Allochthonous sources were particularly important in food chains supporting several species as well as the large predatory fishes, highlighting the relevance of the connectivity between marginal habitats and the river channel in clearwater rivers with low autochthonous production (Goulding et al. 1988). Aquatic food web structure did not conform to general predictions from food web theories. We found a weak relationship between trophic position and body size, and we did not observe a gradual increase in coupling of

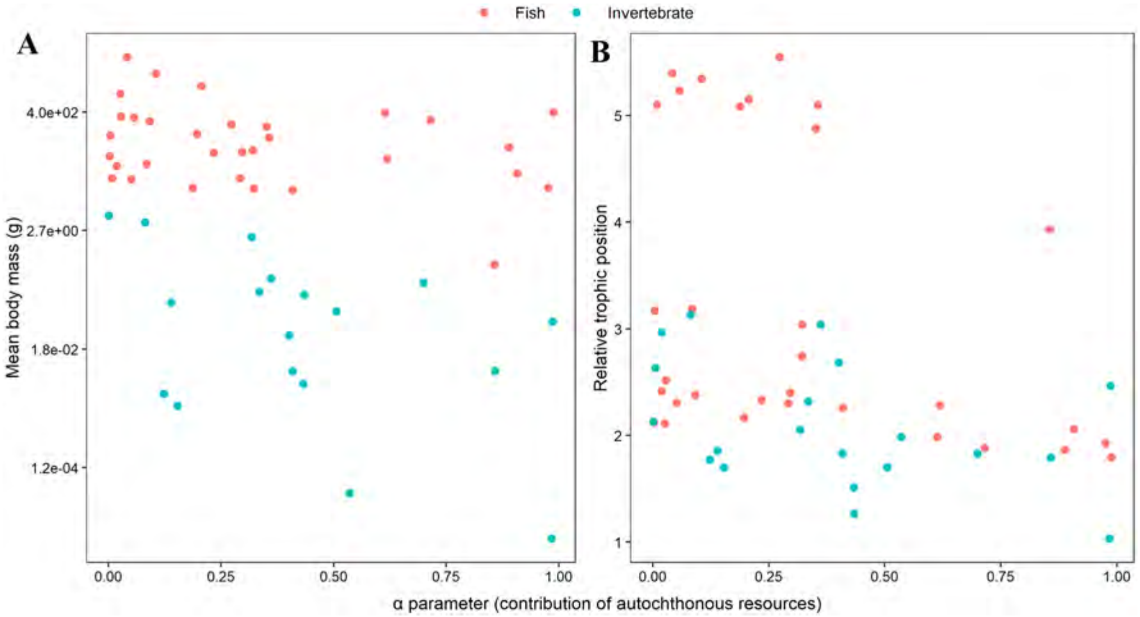

Fig. 5 Relationship between the α parameter with mean body mass (**a**) and relative trophic position (**b**) of fishes and invertebrates from rapids in the middle Xingu River. α values vary from 0, when the animal is completely supported by allochthonous production, to 1, when it is completely supported by autochthonous production

Table 1 Comparison of alternative models for the relationship between the α parameter with body mass and trophic position of invertebrates and fishes of the middle Xingu River

Response	Predictors	*df*	logLik	AICc	Delta	Weight
Body mass	α	3	− 144.68	295.89	0.00	0.56
	$\alpha+\alpha^2$	4	− 143.99	296.88	0.99	0.34
	~ 1	2	− 147.48	299.21	3.32	0.11
Relative trophic position	α	3	− 80.82	168.13	0.00	0.72
	$\alpha+\alpha^2$	4	− 80.81	170.48	2.35	0.22
	~ 1	2	− 84.45	173.14	5.01	0.06

Models are ranked according to AICc value

Comparison of alternative models for the relationship between the α parameter with body mass and trophic position of invertebrates and fishes of the middle Xingu River

AICc Corrected Akaike information criterion energy pathways with increasing body size and trophic position (Woodward et al. 2005a; Rooney et al. 2008).

After BMHP becomes operational, the flow regime will change, with multiple effects on ecological dynamics. Our findings provide baseline descriptions of trophic ecology for future impact assessments. Evidence of a strong dependence of aquatic fauna on allochthonous production sources is cause for concern. The availability of terrestrial food resources, such as leafs, fruits, seeds, and arthropods, is expected to decline with the commencement of BMHP operations, which will attenuate the seasonal flood pulse and channel–floodplain connectivity (Winemiller et al. 2016a; Timpe and Kaplan 2017). BMHP operations have already altered components of the flow regime in the Volta Grande reach, including the magnitude and duration of the seasonal flood pulse (Keppeler et al. 2022). Many aquatic organisms have been shown to shift feeding behavior according to food resources availability (trophic plasticity) (Layman et al. 2007; Jackson et al. 2013). Nonetheless, the energy inputs provided by terrestrial resources are important for supporting the biomass of aquatic organisms in the region. Evidence from other tropical rivers indicates that a loss in allochthonous inputs from forests reduces fish production (Arantes et al. 2019; Capitani et al. 2021). A reduction in fish abundance would strongly impact indigenous communities who are heavily dependent upon fish as their main source of animal protein (Bayley and Petrere 1989; Isaac et al. 2015; Begossi et al. 2018).

Reduced lateral connectivity during the annual flood pulse would impact populations of large predatory fishes supported by food chains originating from allochthonous production sources. This indirect dependence on allochthonous sources occurs because many prey (e.g., small fishes, crabs, shrimp) forage within littoral areas of the river channel as well as seasonally flooded areas in the floodplain. Other prey taxa are rheophilic habitat specialists that feed on resources, both autochthonous and allochthonous, within the rapids. If attenuation of the seasonal pulse were to reduce abundance of prey supported by allochthonous sources, this could, in the short-term, result in more intense exploitation of prey that are rapids specialists, some of which are endemic species. Studies of other South American rivers have shown that following the construction of hydroelectric dams, average fish size and food web length both declined, with large migratory predators strongly impacted (Hoeinghaus et al. 2007; Agostinho et al. 2016; Santos et al. 2017). The loss of large fish and predators is a global phenomenon (Winemiller et al. 2016b) that changes the structure and dynamics of aquatic communities and ecosystems due to trophic cascades (Estes et al. 2011).

We did not observe a significant trend of greater coupling of allochthonous and autochthonous energy channels with greater body size and trophic position, as predicted by food web theory (Rooney et al. 2008). Several large fishes seemed to depend mostly on one or the other energy channel, and several small invertebrates appeared to be strongly supported by both terrestrial and aquatic production sources. These patterns might result from multiple factors. Some large fishes move and feed among various habitats in the riverscape, including the main river channel and floodplain habitats (e.g., *Pseudoplatystoma punctifer*), but others are trophic specialists that are largely restricted to rapids (e.g., *Tometes kranponhah* that feed heavily on plants and fruits, and the Eaglebeak pacu *Ossubtus xinguense* that feed nearly exclusively on the aquatic macrophyte of the family Podostomaceae; Andrade et al. 2019). In addition, some aquatic organisms obtain energy direct or indirectly from detritus in the form of fine particulate organic matter (e.g., Chironomidae). This particulate organic matter often has an intermediate isotope signature reflecting a mixture of autochthonous and allochthonous source materials (González-Bergonzoni et al. 2019). Even during the dry season when the marginal habitats are not flooded, an allochthonous isotopic signal may be detected owing to accumulations of this material in the river channel.

We found a strong association between body size and δ15N, but a weaker and non-linear relationship between body size and vertical trophic position. Although δ15N is often considered to be a proxy for relative trophic position, δ15N also may be influenced by traits not directly associated with diet or body size (Villamarín et al. 2018). In our study, some herbivorous fish, such as *Ossubtus xinguense* and *Myleus setiger*, had δ15N as high as some carnivorous fish, such as *Synbranchus marmoratus* and *Boulengerella cuvieri*. In this case, the high δ^{15}N associated with herbivory may derive from several processes, including high rates of food consumption, low N absorption efficiency, and high excretion rates (Mill et al. 2007). Based on evidence from previous meta-analyses of trophic fractionation for fish feeding guilds provided by Bastos et al. (2017), we applied different trophic fractionation factors for herbivores and carnivores. However, more research is needed to assess trophic fractionation for consumers in tropical aquatic systems, especially for invertebrates.

Our analyses of food web structure included organisms with sizes spanning more than 10 orders of magnitude. The trophic position–body size relationship in the rapids of the Xingu River was best described by a constraint envelope, wherein the upper limit of the relationship had a steeper slope than the lower limit. Smallest invertebrates tended to have low trophic positions while fish of various sizes spanned a wide range of trophic positions, with some feeding directly on basal sources (e.g., plants, algae, detritus) and others. being omnivorous or carnivorous. This finding is consistent with recent studies of fish that indicate a positive association between body and trophic position for carnivores, but not for herbivorous/detritivorous species (Potapov et al. 2019; Keppeler et al. 2020). More complex models are needed to describe trophic interactions in tropical freshwaters, including those that incorporate functional traits (Keppeler et al. 2020).

The trophic position tended to be higher for fish than invertebrates, but there were exceptions. Despite being small, the crab *Kinsleya* cf. *ytupora* and gnat bugs (Enicocephalidae sp.) had higher trophic positions than many omnivorous and herbivorous fish. *Kinsleya* cf. *ytupora* is from a poorly know family of freshwater crabs (Pseudothelphusidae; Yang et al. 2020) that are likely to be omnivorous, feeding on both decaying plant material and animals. Decaying material contains bacteria and fungi that enrich the level of δ15N in the diet of detritivorous and ominivorous animals (Steffan et al. 2017), which could explain the high values observed in *Kinsleya* cf. *ytupora*. Enicocephalidae suck blood and other internal fluids from their prey, the identity of which remains unknown. We also found a relatively high trophic position for sponges. Freshwater sponges have endosymbiotic associations with green algae and also feed by filtering picoplankton, which is composed of both autotrophic and heterotrophic organisms (Reiswig et al. 2010). We speculate that the relatively high trophic position estimated for sponges indicate it is feeding mostly on heterotrophic bacteria.

The middle Xingu River is a hotspot for endemic aquatic biodiversity that now is threatened by impacts from the BMHP (Sabaj-Pérez 2015; Frederico et al. 2016). In the present study, we documented aspects of the trophic ecology in the rapids community under natural conditions prior to the commencement of BMHP operations and provide a baseline for future comparisons. Continued monitoring and analysis of aquatic community structure and ecosystem dynamics is essential both for advancing fundamental knowledge of tropical river ecology and to track environmental impacts of hydropower in the Amazon Basin.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00027-023-00971-x.

Acknowledgements MAZG, JC, and OL were funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) addressed to the Programa de Pós-Graduação em Ecologia Aquática e Pesca of the Federal University of Pará. KW acknowledges support from the US National Science Foundation (DEB 1257813 and IGERT 0654377) and the Estate of George and Carolyn Kelso via the International Sportfish Fund (KOW), and FWK acknowledges support from the Merit, Excellence, and Tom Slick fellowships from Texas A&M University. TG is funded by National Council for Scientific and Technological Development (CNPq #308528/2022-0). MCA received a grant from the "Centro de Triagem de Invertebrados" (UFPA/FADESP project #4390/ITV-DS project #R100603.CT.02). The study was funded by Norte Energia, Project P&D of the Agência Nacional de Energia Elétrica - ANEEL code PD-07427-0221/2021.

Author contributions Conceptualization: MCA, FWK, KW, TG. Developing methods: MCA, FWK. Data analysis: MCA, FWK. Preparation of figures and tables: MCA, FWK. Conducting the research, data interpretation, writing: MCA, FWK, MAZG, JWSC, OPL, RA, KW, TG.

Data availability The datasets used and/or analyzed during the current study are available as supplementary material.

Declarations

Conflict of interest The authors declared that they have no confict of interest.

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