Trophic ecology of a small characid reflects the degradation of a basin after the rupture of an ore tailings dam

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STATEMENTS AND DECLARATIONS

Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

Ethics approval

The sampling, euthanasia, and transportation of organisms were authorized by the Ministério do Meio Ambiente (MMA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Sistema de Autorização e Informação em Biodiversidade (SISBIO, number 80532-1), and the ethics committee of the Federal University of Viçosa (number 7982018).

Credit authorship contribution statement

Larissa C. Paiva: Conceptualization, Methodology, Data curation, Investigation, Writing (original draft, review & editing); Débora R. Carvalho: Conceptualization, Methodology, Data curation, Statistical Analysis, Investigation, Writing (review & editing); Frederico F. Ferreira: Conceptualization, Methodology, Investigation, Writing (review & editing); Jorge A. Dergam: Funding acquisition, Project administration, Writing (review & editing); Marcelo Z. Moreira: Methodology, Writing (review & editing); Carlos F. Sperber: Investigation, Writing (review & editing); Paulo S. Pompeu: Conceptualization, Methodology, Funding acquisition, Investigation, Project administration, Writing (review & editing).

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Summary

Knodus moenkhausii is a small characid widely distributed and abundant in the Doce River basin, which experienced the largest socio-environmental disaster in Brazil. This species is also recognized for its broad dietary response to various levels of degradation, making it a potential indicator of the ecosystem's impacts resulting from the rupture of the Fundão iron mining dam in 2015. Thus, the objective of this study was to investigate the trophic ecology of *K. moenkhausii* in the Doce River basin by analyzing its carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions. Samplings of *K. moenkhausii* individuals and their potential food resources were conducted at three sites affected by the rupture of the ore tailings dam and at three unaffected (control) sites, which were distributed across the upper, middle, and lower regions of the basin. The $\delta^{13}C$ values of *K. moenkhausii,* within each evaluated region, no differences were observed in compositions between the affected and their respective control sites. The $\delta^{15}N$ was different between regions for the control sites, but similar between the affected sites, indicating possible homogenization of the river channel conditions due to the impact. In control sites, *K. moenkhausii* individuals fed on more nutritious resources, such as invertebrates, while in affected sites, they assimilated more algae and periphyton. We also confirmed the importance of the regional context when assigning control sites and verified that the $\delta^{15}N$ values were more effective in reflecting the degradation of the Doce River basin.

Keywords: *Knodus moenkhausii;* stable isotopes; isotopic niche; Doce River, Fundão Dam.

Introduction

Knodus moenkhausii (Eigenmann & Kennedy, 1903) is a small characid described from the Paraguay River basin, mainly inhabits structurally simple, small streams without marginal vegetation (Souza, Oliveira, and Pereira 2016), but they are also found in larger rivers (de Carvalho, Alves, Moreira, et al. 2020). This species is known for its broad dietary plasticity in environments with different levels of degradation (de Carvalho et al. 2019), which may be related to its wide distribution and abundance in different basins (Casatti, de Ferreira, and Carvalho 2009). In the Doce River basin, one of the main river basins in southeastern Brazil, there are records of the occurrence of approximately 114 species of native fish and around 39 non-native ones, which corresponds to more than 25% of its ichthyofauna (Bueno et al. 2021). As for the nature of *Knodus moenkhausii*, ongoing genetic microsatellite analysis on large samples from the Lower Doce River suggests that the Doce River populations have moderate levels of variation (Dergam's unpublished data). This pattern may indicate either that this species is native, or it was introduced in rather large stocks in the basin. The increasing record of *K. moenkhausii* in Brazilian basins (Bueno et al. 2021; Souza et al. 2016) and its ability to change its diet according to the environment in which it lives, makes this a species of great interest in ecological studies (Brambilla, Uieda, and Nogueira 2018; Zanini et al. 2017), especially those that aim to evaluate the effects of anthropogenic activities on the aquatic environment (de Carvalho et al. 2019). Furthermore, recent samplings indicate an increase in the number of records of this species throughout the Doce River basin (authors' observations), highlighting the assessment of *K. moenkhausii*'s biology as an alternative for providing information on the environmental conditions of this basin affected by Brazil's largest environmental disaster.

The collapse of the Fundão dam, which occurred in 2015, affected a large part of the Doce River basin, with 663.2 km of water bodies being directly impacted by a mud composed of ore tailings (IBAMA, 2015). The impacts on the ichthyofauna ranged from mortality caused by the sediment transport to effects observed on smaller scales, such as histopathological alterations (Eduardo et al. 2022; Kelvin et al. 2020), accumulation of heavy metals (Andrades et al. 2021; Ferreira et al. 2020), behavioral changes (such as changes in eating habits) (Andrades et al. 2020), among others. When assessing trophic changes, stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) emerge as promising tools. They offer valuable insights into the acquisition and transfer of energy between resources and consumers, thereby reflecting an individual's diet (Barriviera Furuya et al. 2002). The $\delta^{13}C$ values provide information about the basal carbon sources preferentially assimilated by fish, while the $\delta^{15}N$

values provide an estimate of the trophic position occupied by them (Fry 2006). As they are elements present in ecosystems and with natural distribution, stable isotopes reflect the physical and metabolic processes of the environment, being an important tool for tracing patterns, verifying physiological mechanisms in organisms and tracing energy flows in food chains (Pereira 2001; Peterson and Fry 1987). Together, these isotopes can be used to reconstruct food webs (Garcia et al. 2006), assessment of carbon flow (Pereira 2001), niche estimates (Phillips and Gregg 2003) and trophic diversity (Eurich et al. 2019), among others. This tool facilitates the study of trophic characteristics from an individual level to the community level, thereby aiding in the assessment of anthropogenic impacts on aquatic ecosystems.

Knowing that *K. moenkhausii* has great dietary plasticity and can change its diet in the face of different anthropogenic impacts (de Carvalho et al. 2019), the objective of this work was to investigate the trophic ecology of this species throughout of the Doce River. With this objective, the present study evaluated the trophic structure, trophic niches and carbon sources assimilated by individuals of *K. moenkhausii* in three regions of the basin (upper, middle and lower), including affected and unaffected/control sites (tributaries that flow into the region of the three affected sites) by the collapse of the Fundão dam. We aim to test the hypothesis that *K. moenkhausii* will exhibit distinct dietary preferences and, consequently, different trophic niches between sites affected and sites not affected by the collapse of the ore tailings dam, especially in the regions closest to the rupture. We also expect that the isotopic signatures of affected and unaffected sites are naturally different between the sampled regions, highlighting the importance of local geographic constraints. In addition to contributing to the understanding of the impacts caused by the collapse of the Fundão dam, we aim for our results to offer supplementary insights into the feeding behavior of this increasingly abundant species in Brazilian river basins.

Materials and methods

<u>Study area</u>

This study was carried out in the Doce River watershed, in southeastern Brazil. The river is 853 km long, covering 230 municipalities in the states of Minas Gerais and Espírito Santo, until it flows into the Atlantic Ocean. The basin is located in the Atlantic Forest and Cerrado biomes (Matos, Davis, and Candido 2015). The soil in the basin is characterized by intensive use in agriculture and livestock farming, the climate is humid tropical, characterized by climatic variability. Floods occur between December and March and low waters between August and September (Coelho 2009). In November 2015, the basin was affected by the rupture of the Fundão dam, releasing approximately 39.2 million m^3 of tailings (Sánchez et al. 2018). These tailings traveled 22 kilometers until reaching the Doce River, ultimately reaching the mouth of the Atlantic Ocean, impacting a total of 663.2 kilometers of water bodies directly (ICMBIO 2015).

The sampling in the present study was carried out at six sampling sites located in tributaries and in the main channel of the Doce River basin (Figure 1, Table 1). Of these, three sites were selected in regions directly affected by ore tailings from the rupture (RD1, RD2 and RD3). The other three, considered as control sites (C1, C2 and C3), are in tributaries that flow into the region of each of the affected sites. The distribution of sites was made to encompass the different regions of the basin: Upper Doce River (sites C1 and RD1), Middle Doce River (sites C2 and RD2) and Lower Doce River (C3 and RD3).

Site C1 is located on the Piranga River, the main source of the Doce River (Nascimento and Castro 2012). Site C2 is located on the Santo Antônio River, which is the river with the largest area of preserved forest in the basin (Alves and Valory 2018). Site C3 is located on the Manhuaçu River, which is 288 km long and predominantly coffee-growing (Barbosa et al. 2019). In relation to the affected sites on the Doce River, RD1 is situated in the reservoir of the Hidropower Plant (HPP) Risoleta Neves, where approximately 9.9 million m^3 of tailings were retained, thereby exacerbating the impacts on the fauna of this location (Bastos, 2021). Site RD2 is located near the city of Naque, Minas Gerais, where concentrations of arsenic, cadmium, manganese, nickel and selenium were found above those permitted by legislation (Gonçalves 2016). Site RD3 is located close to the city of Aimorés, where the lower Doce

River begins, and is influenced by sanitary waste from several cities, in addition to livestock and agricultural activities (Rodrigues 2022).

Fish sampling

Food resources and specimens of *K. moenkhausii* were collected at the six sampling sites for isotopic analysis between the months of August and September 2020. Specimens of *K. moenkhausii* were collected at each sampling site using sieves (80 cm in diameter, 1mm mesh) and trawl nets (3m long, with 5mm mesh). A standardized collection of 5 *K. moenkhausii* individuals was performed at each sampling site. Each captured individual had its entire digestive tract removed, was stored in plastic tubes, and kept on ice until processing in the laboratory, where the samples were lyophilized, ground, and homogenized using a mortar and pestle. Fish sampling, euthanasia and transport were authorized by the Biodiversity Authorization and Information System (SISBIO), Chico Mendes Institute for Biodiversity Conservation (ICMBio), Ministry of the Environment (MMA) (SISBIO authorization number 80532-1) and by the committee of ethics at the Federal University of Viçosa (number 7982018).

The collection of five samples (at each sampling site) of each of the following food resources was also standardized: (a) periphyton (biofilm); (b) filamentous algae; (c) suspended matter; (d) CPOM (coarse particulate organic matter); (e) macrophytes, (f) aquatic invertebrates (benthos) and (g) terrestrial invertebrates. The entire process of storing and processing resource samples occurred in accordance with a specific methodology, as described below. Periphyton (PE) was collected by scraping rocks with a small brush and stored with distilled water in plastic pots. Samples of coarse particulate organic matter (CPOM), filamentous algae (AL) and macrophytes (MA) were collected randomly from the bed of all sampling sites where they were found. Suspended matter (MS, i.e. seston) was obtained by fixing a phytoplankton net (45 μm mesh) in the water column for a period of 3 minutes. Aquatic/benthos invertebrates (BE) were sampled using Surber nets and sieves (80 cm diameter, 1 mm mesh) near the banks, in aquatic macrophytes, underground banks and in rapids. Terrestrial invertebrates (IT) were manually sampled at different sites in the riparian forest and river banks. After collection, all samples were stored in plastic bottles and kept on ice until frozen in freezers and processed in the laboratory.

Sample processing and isotopic analysis

Periphyton and suspended matter samples were filtered through quartz fiber filters (Whatman ® QMA quartz filters) using a filtration device coupled to a vacuum pump. They were then dried in an oven at 40 degrees Celsius until their weight stabilized. The remaining food resource samples, as well as the fish samples, were lyophilized for a minimum period of 24 hours before being ground and homogenized using a mortar and pestle, and subsequently stored in Eppendorf-type plastic tubes. Approximately 2 to 5mg of animal tissue samples and 10mg of basal resource samples were selected for isotopic analysis.

A total of 226 samples was sent for isotopic analysis, including 30 fish samples, 30 periphyton samples, 30 filamentous algae samples; 30 samples of suspended matter; 30 samples of CPOM (coarse particulate organic matter); 16 samples of macrophytes (the only resource not found in all sampling sites), 30 samples of aquatic invertebrates and 30 samples of terrestrial invertebrates.

Stable isotope analysis for carbon and nitrogen were carried out at the Center for Nuclear Energy in Agriculture (CENA), at the University of São Paulo. For this, a continuous flow mode mass spectrometer system (CF-IRMS) was used with the Carlo Erba element analyzer (CHN 1110, Milan, Italy), associated with the mass spectrometer (Thermo Scientific, Bremen, Germany). The results are expressed as the difference from international reference standards in delta notation (δ) in parts per thousand (%), and calculated using the following formula: $\delta X = [(R \text{ sample} / {}_{R} \text{ standard}) - 1] \times 10$, in which, X represents ^{13}C or ^{15}N and R represents the isotopic ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Peterson and Fry 1987).

Data analysis

For each sampled site, differences in the isotopic compositions of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of *K. moenkhausii* were tested between the control site and the respective affected site (C1*RD1, C2*RD2 and C3*RD3), using the T test. To evaluate whether the isotopic compositions of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of *K. moenkhausii* differed between the three control sites and between the three affected sites, analyses of variance (ANOVAs) were performed, once the assumptions of normality and/or homogeneity of variance were met (Shapiro-Wilk and Levene's test, respectively). When significant differences were observed ($p < 0.05$), pairwise comparisons were made using Tukey's post-hoc test to identify means that were significantly different from each other.

The *bi-plot* graphs were constructed using the isotopic compositions of the fish and resources (x-axis: $\delta^{13}C$ and y-axis: $\delta^{15}N$). In these graphs, the isotopic composition of each *K. moenkhausii* individual was represented by a single dot, while each resource was represented as mean and standard deviation.

The isotopic niches (trophic niches) occupied by *K. moenkhausii* at each sampling site were estimated using the SIBER package, to assess whether there are differences between the sites affected and not affected by the dam rupture. The standard ellipse area (SEA, expressed in ‰2) was calculated individually for each sampling site and represents the central isotopic niche space and a proxy for the richness and uniformity of resources consumed by the population (Bearhop et al. 2004).

The main carbon sources assimilated by *K. moenkhausii* at each of the sites were determined through Bayesian isotopic mixture models (Moore and Semmens 2008; Parnell et al. 2010), specifically using the MixSIAR package in R (Stock and Semmens 2016). The choice of food resources used in the partition analysis was carried out using information about the feeding habits of *K. moenkhausii* available in the literature, and through the evaluation of the *bi-plot* graph. Therefore, for this analysis, basal resources, periphyton and filamentous algae, and terrestrial and aquatic invertebrates were considered. The fractionation values used for consumers were 1.3 ± 0.3 ‰ for carbon and 2.9 ± 0.32 ‰ for nitrogen per trophic level (McCutchan et al. 2003).

Results

The isotopic composition of $\delta^{13}C$ in *K. moenkhausii* differed among the three sampled regions, both in the affected areas ($F = 5.76$, $p = 0.02$) and in the control areas ($F = 19.95$, $p < 0.001$). The pairwise comparisons further revealed that, across the three regions, there were no differences in the $\delta^{13}C$ of *K. moenkhausii* between the affected sites and their respective controls (C1*RD1: $t = -0.77$, $p = 0.48$; C2*RD2: $t = -2.02$, $p = 0.08$; C3*RD3: $t = 0.34$, $p = 0.74$) (Figure 2a). Regarding the isotopic composition of $\delta^{15}N$ of *K. moenkhausii*, these values also differed among the control sites ($F = 50.49$, $p < 0.001$), but were similar among the affected points ($F = 1.86$, $p = 0.20$). The pairwise comparison revealed that only the affected sites in the upper (C1*RD1: $t = 5.86$, $p = 0.03$) and mid-course (C2*RD2: $t = 7.93$, $p = 0.02$) differed from their controls, while those sites in the lower course exhibited a similar $\delta^{15}N$ signature (C3*RD3: $t = -0.10$, $p = 0.92$) (Figure 2b). Notably, there was a high variability in the signatures of individuals collected at the site closest to the rupture (RD1), resulting in a much broader isotopic niche compared to other locations (Figure 2c).

When evaluated in relation to resources, it is possible to observe that individuals from *Knodus moenkhausii* had, from all sampled sites, signatures closer to algae, periphyton, and aquatic and terrestrial invertebrates (Figure 3, Table S1). However, while in the control sites (C1, C2 and C3), invertebrates (mainly aquatic ones) represented more than 50% of the assimilation of *K. moenkhausii*, in the sites affected by the disruption (RD1, RD2 and RD3), the primary producers (filamentous algae and periphyton) were the most important resources (Table 2, Figure 4).

Discussion

We found that the trophic ecology of *K. moenkhausii* varied between affected and unaffected (control) sites along the Doce River basin. At the control sites, individuals of *K. moenkhausii* fed on more nutritious resources, such as invertebrates, while in the affected areas, they assimilated more algae and periphyton. The hypothesis that the species would present different trophic niches between sites affected and sites not affected by the rupture of the ore tailings dam, especially in the regions closest to the rupture, was corroborated only by the signature of $\delta^{15}N$. We also confirmed the importance of the geographic context in evaluating the species, since differences were observed between the ^{13}C and ^{15}N isotopic compositions of the control sites in the three regions (upper, middle and lower sections). However, while these differences were observed for $\delta^{13}C$ in the main stem sites, $\delta^{15}N$ values remained similar along the studied river sections. These results indicate that, in the context of the rupture of the tailings dam in Mariana, the $\delta^{15}N$ values not only better reflect changes in the affected sites compared to their controls but also a potential standardization of this parameter in the channel due to the endured impacts. Furthermore, the affected site closest to the rupture was where the greatest variation in the trophic ecology of *K. moenkhausii* was observed. At this site, individuals explored a broad trophic niche (intraspecific variation in diet), with filamentous algae being the most assimilated resource.

Our results pointed to a high level of similarity in the isotopic compositions of fish from the control sites with the closest affected sites C1*RD1, C2*RD2 and C3*RD3. However, the most enriched values of ^{15}N in fish from the Piranga River (C1) and the affected site immediately downstream, UHE Risoleta Neves (RD1), drew attention. Although high values of ^{15}N generally indicate higher trophic positions (Philippsen and Benedito 2013; Vanderklift and Ponsard 2003), we must consider that external factors may also be influencing, such as the enrichment of ^{15}N in food resources in response to excess nitrogen in water (de Carvalho, Alves, Flecker, et al. 2020). This enrichment can occur, for example, due to the use of fertilizers, which have the capacity to alter the ^{15}N available in the soil for plants, and which can occasionally have their residues carried into water courses (de Carvalho et al 2017). Near the Piranga River (C1), mining, agricultural, forestry and industrial activities take place, in addition to the release of sanitary sewage and the presence of erosion and silting processes in its bed (IGAM 2019). Therefore, this scenario may be responsible for the higher values of $\delta^{15}N$ at site C1, as well as at the river channel (RD1). This result also draws attention to the importance of maintaining the quality of tributaries, since they have a great influence on the water quality of the main channel (Metcalf and Harrison 2015).

In contrast, at site C2, *K. moenkhausii* presented the lowest values of $\delta^{15}N$ and $\delta^{13}C$, a result that may be related to the conservation status of the Santo Antônio River, which has the most preserved relative area in the basin (Alves & Valory, 2018). Furthermore, the Water Quality Index in this watercourse was considered "Good" in all studies carried out by IGAM from 2014 to 2018 (IGAM 2019), including a high diversity of algae, with the presence of species that indicate low anthropogenic impact (Pacheco et al. 2019). Additionally, endemic and endangered fish species are also found in this stretch, with indications that the drainage of the middle and upper Santo Antônio River is home to very representative populations of these species (Vieira, Pompeu, and Neto 2010). This makes the Santo Antônio River considered the most important tributary for the conservation of the Doce River. However, it is worth noting that the basin suffers some anthropogenic interferences, such as the influence of the

Salto Grande Hydroelectric Power Plant (UHE), located in the middle-upper stretch of the Santo Antônio River and in operation since 1956. While UHE has been able to impede the colonization of some exotic species, such as the dourado (*Salminus brasiliensis*), which now occurs in the rest of the basin, it also hampers the movement of fish from the upper part of the Santo Antônio River to the Doce River.

Individuals of *K. moenkhausii* from the lower part of the Doce River basin (C3 and RD3) also presented isotopic compositions very similar to each other, even presenting a large overlap of niches. At both sites, *K. moenkhausii* presented enriched $\delta^{13}C$ values compared to sites in the upper and middle portion of the basin. This result suggests that this species may be feeding on resources of C4 origin indirectly (through invertebrates, which were highly assimilated items at both sites), such as pasture grasses, which generally have enriched carbon values (Boesing et al. 2021). However, the primary producers were also important resources for *Knodus* at these sites, being filamentous algae most assimilated in the Manhuaçu River (C3), and periphyton at the affected site downstream (RD3). Both resources also presented enriched ^{13}C values, therefore being another explanation for the ^{13}C values of *K. moenkhausii,* since algae use different metabolic pathways during photosynthesis, and reflect the concentration of inorganic carbon dissolved in the water (Albrecht et al. 2021; Fry and Ewel 2003),

Regarding trophic niches, we saw that in most places *K. moenkhausii* had rather narrow niches, that is, they present little intraspecific variation in diet (Ceneviva-Bastos and Casatti 2007). The only exception was the site in the reservoir (RD1), which was responsible for retaining around 9.9 million m^3 of ore waste from the collapse of the Fundão dam (Bastos 2021). The largest trophic niche of *K. moenkhausii* in the HPP Risoleta Neves reservoir suggests a large intraspecific variation in the diet of *Knodus,* which may be related to the characteristics of the environment. At this site, although algae were the predominant item, the fish also fed on periphyton and aquatic invertebrates, confirming the dietary plasticity already documented for the species (de Carvalho et al. 2019; Ceneviva-Bastos, Taboga, and Casatti 2015). The change in *Knodus'* diet in the face of anthropogenic impacts has been reported elsewhere (de Carvalho et al. 2019), however little is known about how this species behaves in reservoirs. Our results suggest that changes to the riverbed, as in the case of the reservoir, alter the trophic ecology of *Knodus,* resulting in a more generalist behavior. Our results are also corroborated by other studies, which report the inclusion of large amounts of algae in the diet of other fish species from different trophic guilds in reservoirs (Delariva 2002; Hahn and Fugi 2007). On the other hand, at the control site upstream (C1) the opposite pattern was observed, with fish exploring a very small range of resources. This result may be related to a small variety and availability of resources in this location, or simply because the fish prefer to feed on that most abundant or attractive item, as has already been observed in other studies with this species (de Carvalho et al. 2019). The second hypothesis is reinforced, since at site C1 more than 50% of *Knodus'* diet was based on aquatic invertebrates.

Our results also indicated a more nutritious fish diet at the control sites, compared to the affected sites of the Doce River, due to the higher consumption of invertebrates in the unaffected sites. This result is similar to that described by de Carvalho et al. (2019), in which the consumption of benthic macroinvertebrates by *Knodus moenkhausii* was more expressive in streams with natural cover. Similarly, recent studies have also observed that a predatory fish species (*Genidens genidens*) presented a poor-quality diet in the Doce River estuary, in contrast to the diet described in other little-impacted Brazilian estuaries (Andrades et al. 2021). It is possible that in unaffected sites, the availability of aquatic and terrestrial invertebrates is greater. The composition of benthic macrofauna is influenced by sedimentary variables (Matthews-Cascon et al. 2018), and consequently, might have been affected by tailings from the Fundão dam. The presence of allochthonous items is also directly related to the type and degree of conservation of the forest found on the banks of rivers, which are important sources of plant and animal matter for aquatic ecosystems (Ribeiro et al., 2014).

Finally, it is important to highlight that there was a significant difference between the sampling sites located in the upper, middle and lower sections of the basin, which highlights the importance of considering the regional context. Differences in carbon sources across the river gradient were expected and can be explained by different theories (Vannote et al., 1980; Junk et al., 1989; Thorp and Delong, 1994). These theories indicate variations along the river in the importance of the initial processing of terrestrial organic matter, the relevance of connectivity and flows of carbon sources from adjacent flooded areas, as well as the combination of local autochthonous production and direct contributions from the riparian zone. Additionally, factors such as geology and local impacts can directly affect resource availability (Carvalho et al., 2015; 2020; 2023; Tejerina-Garro et al., 2005). About the nature of *Knodus moenkhausii*, this species satisfies most of the characteristics that qualify indicator organisms (Hutcheson et al., 2019; Holt and Miller, 2011): they are widespread and abundant, they withstand and have apparently responded to habitat change within a short-time frame, they are clearly measurable (in this case, through diet analysis), and are cross-referable to other indicators (like IBI for example). Certainly, comparative studies on other basins will provide a more definitive answer to that question.

Conclusion

Through this study it was possible to reaffirm the dietary plasticity of *Knodus moenkhausii,* which may be the reason for its wide distribution throughout the Doce River basin. Its ability to adapt in places with different characteristics, such as site RD1 (lotic environment), gives it great resistance, increasing its chances of establishment. This situation is not observed in all species, especially native ones, which end up being harmed by variations in food availability and the competitiveness that increases with the presence of introduced species (Lima and Chagas 2019). Furthermore, we observed that in degraded environments, the diet of individuals tends to be less nutritious in relation to control sites, which may reflect the degree of conservation of the studied areas, including the impact caused after the passage of ore tailings mud. In the case of future studies that aim to study the impacts on the ichthyofauna of the Doce River, our results make clear the need to have sites distributed throughout the basin, since the isotopic compositions of both fish and resources vary between the different upper, middle and lower regions of the basin.

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Figure Captions

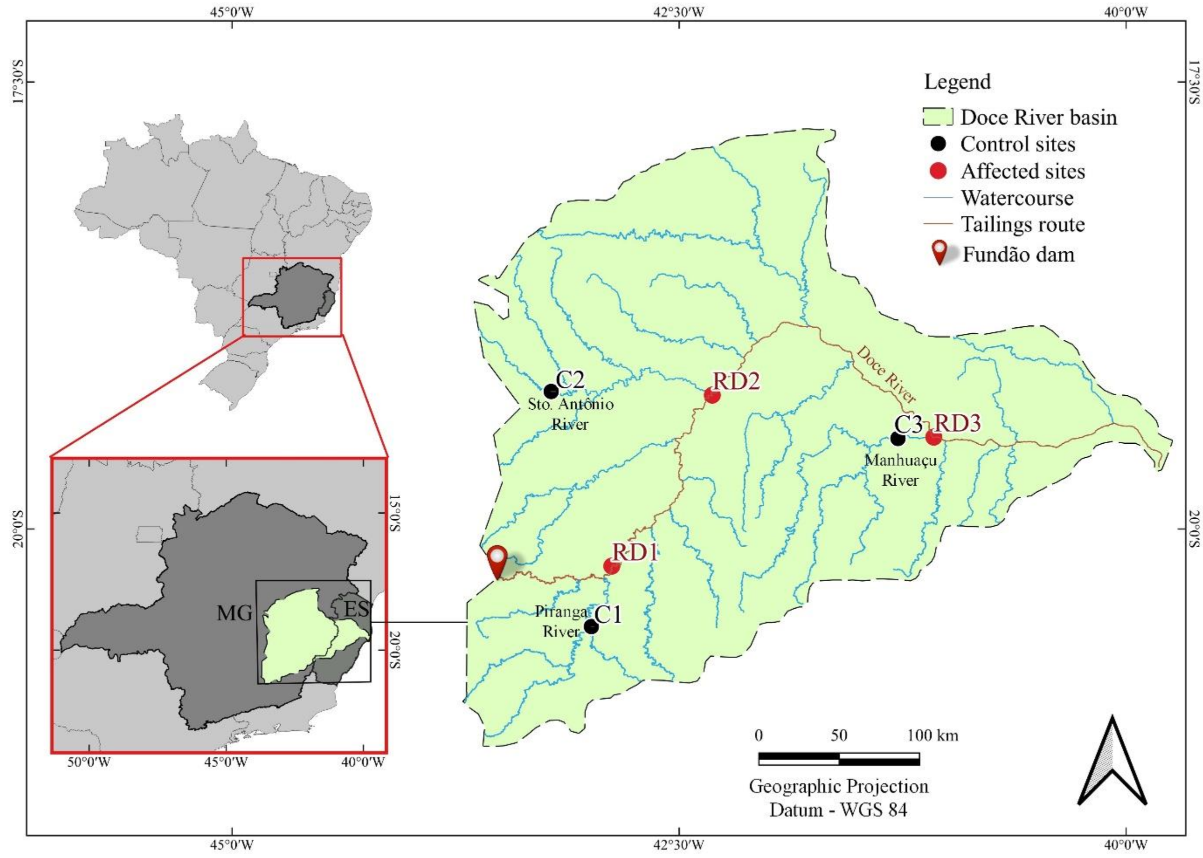

Fig. 1 Control sites (C1, C2 and C3) and sites affected by the collapse of the Fundão ore tailings dam (RD1, RD2 and RD3) sampled along the Doce River basin, Brazil

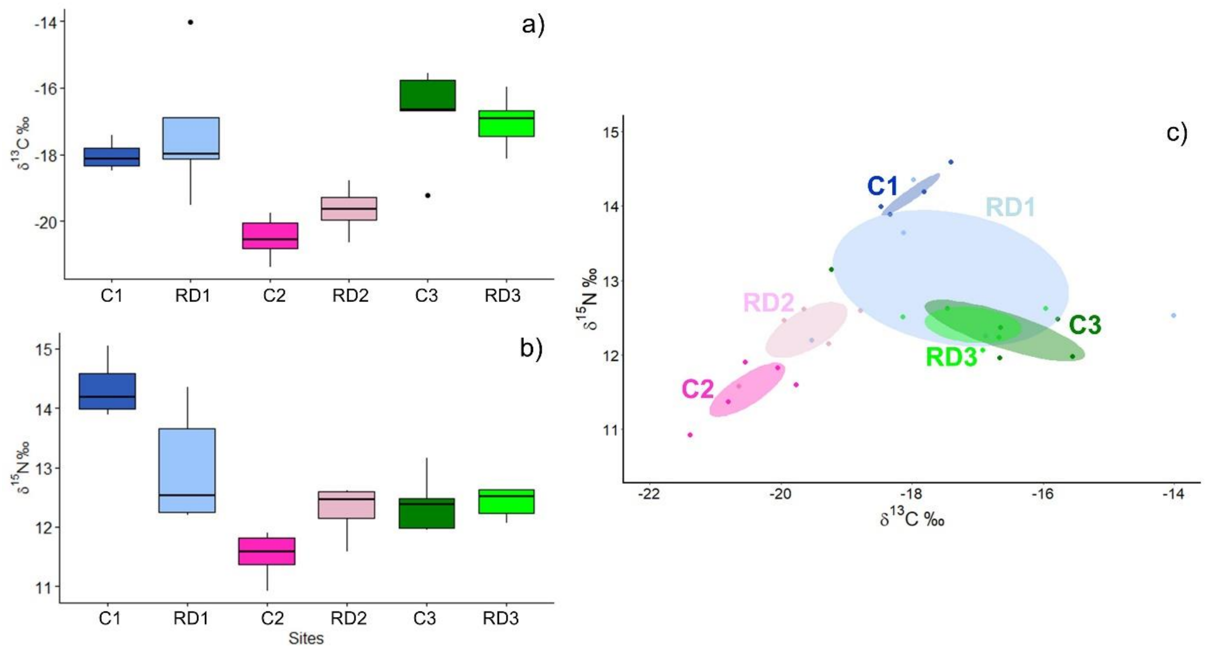

Fig. 2 Variation in the isotopic composition of a) carbon ($\delta^{13}C$ ‰), b) nitrogen ($\delta^{15}N$ ‰), and c) trophic niches (SEA) of *Knodus moenkhausii* in the control sites (C1, C2 and C3) and in the sites affected by the collapse of the Fundão dam (RD1, RD2 and RD3)

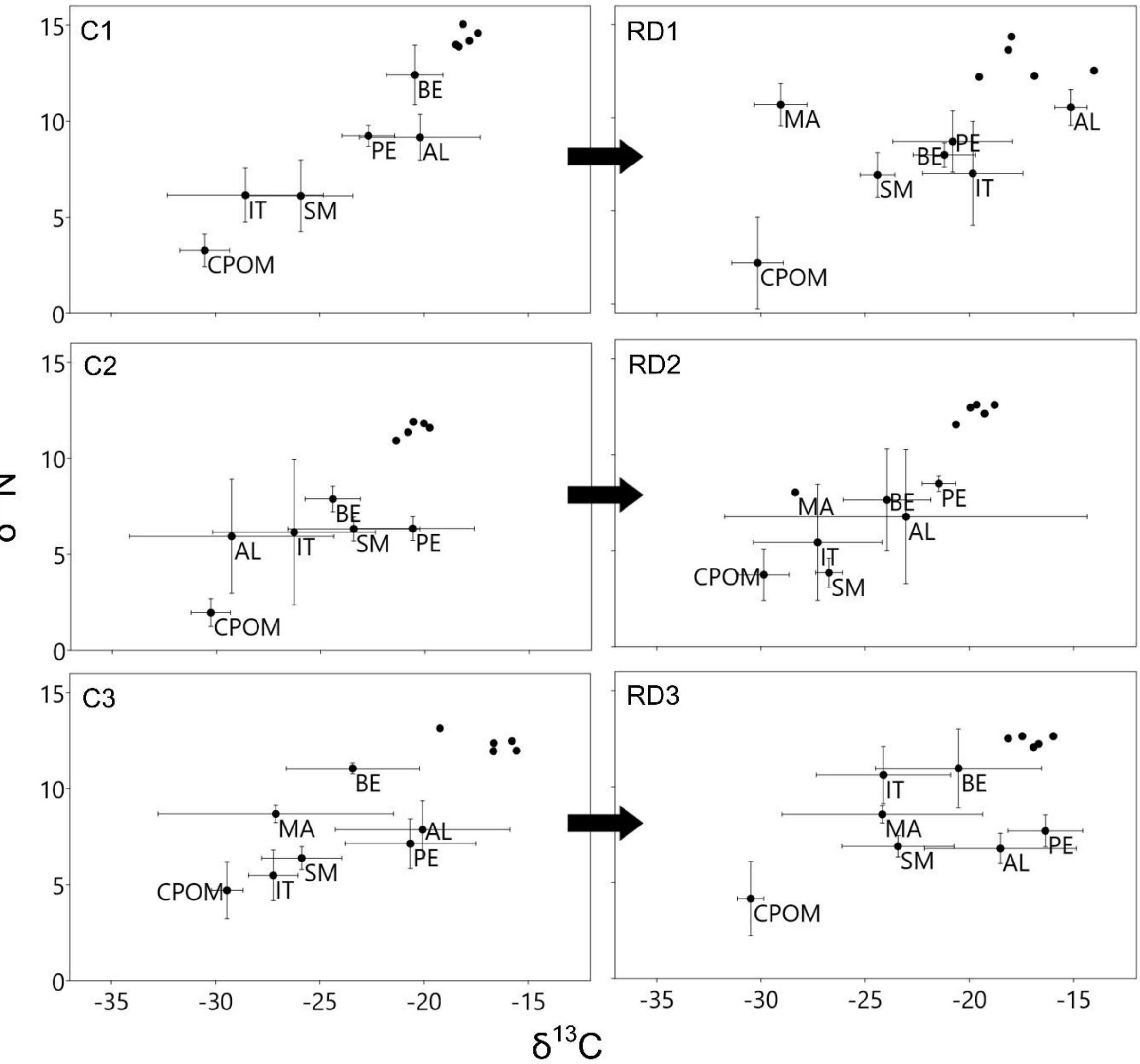

Fig. 3 *Bi-plot* graph representing the trophic structure of the control sites (C1, C2 and C3) and the affected sites (RD1, RD2 and RD3) by the collapse of the Fundão dam. Each dot represents an individual of *K. moenkhausii*. Food resources: PE = periphyton; AL= filamentous algae; IT = terrestrial invertebrates; BE = aquatic macroinvertebrates; MA = macrophytes; CPOM = coarse particulate organic matter; SM = suspended matter

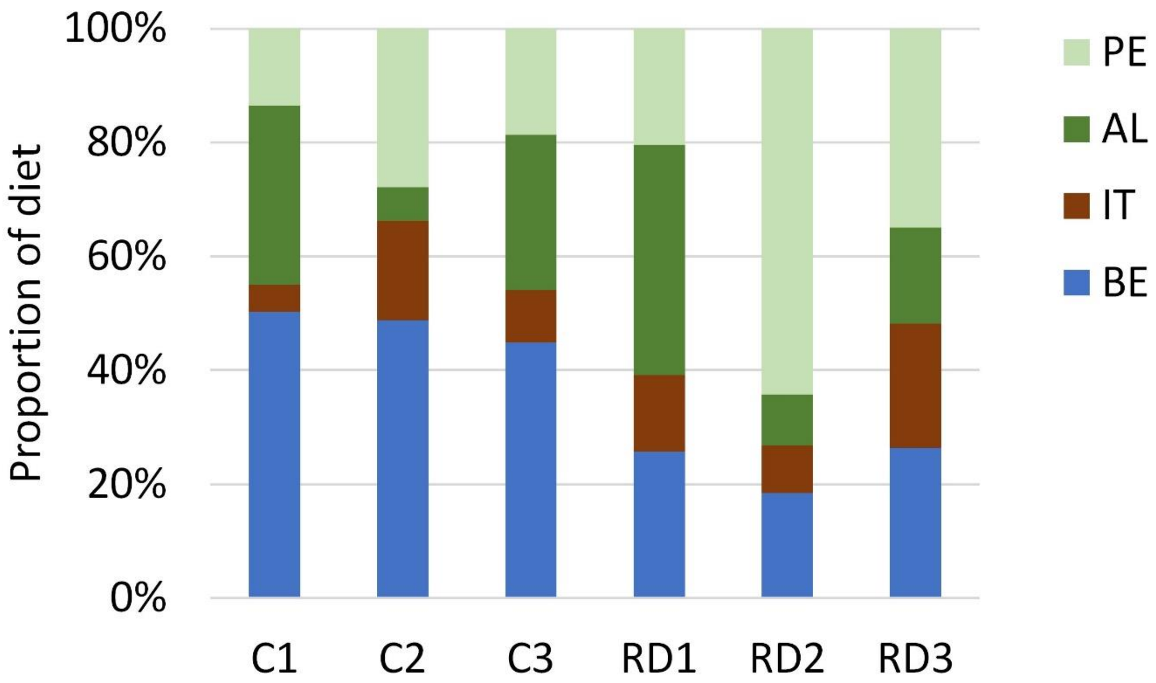

Fig. 4 Percentage of assimilation of food items by *Knodus moenkhausii* at control sites (C1, C2 and C3) and at sites affected by the collapse of the Fundão dam (RD1, RD2 and RD3). PE = periphyton; AL= filamentous algae; IT = terrestrial invertebrates; BE = aquatic macroinvertebrates

Tables

Table 1 Geographic coordinates of the sites sampled for stable isotopes along the Doce River basin. RD = Sites affected by the dam collapse (RD1, RD2, RD3); C = Control sites, not impacted by the dam collapse (C1, C2 and C3); Coord = coordinates

Site	Condition	Drainage/Reference	State	UTM	Coord. (E)	Coord. (N)
C1	Control	Piranga River (Guaraciaba)	MG	23K	709518	7726784
C2	Control	Rio Santo Antônio (S. Ant. downstream)	MG	23K	687610	7872625
C3	Control	Manhuaçu River (Aimorés)	MG	24K	261172	7842938
RD1	Affected	Doce River (UHE Risoleta Neves)	MG	23K	721890	7764082
RD2	Affected	Doce River (Naque)	MG	23K	782354	7869156
RD3	Affected	Doce River (Aimorés)	MG	24K	282205	7844032

Table 2 Partition of food resources assimilated by *Knodus moenkhausii* in the control sites (C1, C2 and C3) and in the sites affected by the collapse of the Fundão dam (RD1, RD2 and RD3). PE = periphyton; AL= filamentous algae; IT = terrestrial invertebrates; BE = aquatic macroinvertebrates. Most assimilated resources are represented in bold

Site	AL	PE	BE	IT	Primary producers	Invertebrates
C1	**0.314**	0.136	**0.502**	0.048	0.450	**0.550**
C2	0.059	**0.279**	**0.488**	0.174	0.338	**0.662**
C3	**0.272**	0.187	**0.448**	0.093	0.459	**0.541**
RD1	**0.404**	**0.204**	**0.257**	0.135	**0.608**	0.392
RD2	0.089	**0.643**	0.185	0.083	**0.732**	0.268
RD3	0.168	**0.350**	**0.264**	**0.219**	**0.518**	0.483

Supplementary material

Table S1 Mean and standard deviation of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions of *Knodus moenkhausii* and food resources collected at control sites (C1, C2 and C3) and at sites affected by the collapse of the Fundão dam (RD1, RD2 and RD3). SD = Standard variation

Sample	Site	$\delta^{13}C$		$\delta^{15}N$	
		Mean	SD	Mean	SD
Filamentous algae	C1	-20.19	2.90	9.16	1.20
	C2	-29.27	4.90	5.94	2.97
	C3	-20.07	4.19	7.87	1.50
	RD1	-15.12	0.78	10.56	0.96
	RD2	-23.04	8.70	6.78	3.49
	RD3	-18.51	3.65	6.78	0.79
Periphyton	C1	-22.67	1.26	9.24	0.55
	C2	-20.58	2.95	6.34	0.62
	C3	-20.65	3.13	7.14	1.29
	RD1	-20.80	2.88	8.73	1.65
	RD2	-21.47	0.80	8.50	0.41
	RD3	-16.35	1.80	7.70	0.83
Macrophytes	C3	-27.11	5.65	8.69	0.46
	RD1	-29.05	1.26	10.71	1.14
	RD2	-28.35		8.04	
	RD3	-24.18	4.81	8.56	0.46
CPOM	C1	-30.52	1.20	3.28	0.86
	C2	-30.27	0.95	1.96	0.73
	C3	-29.44	0.76	4.71	1.48
	RD1	-30.16	1.24	2.20	2.46
	RD2	-29.86	1.22	3.76	1.34
	RD3	-30.49	0.63	4.17	1.93
Terrestrial invertebrates	C1	-28.57	3.73	6.15	1.42
	C2	-26.28	3.91	6.15	3.78
	C3	-27.23	1.19	5.49	1.32
	RD1	-19.84	2.41	7.01	2.79
	RD2	-27.28	3.08	5.44	3.02
	RD3	-24.12	3.22	10.61	1.49
Aquatics invertebrates	C1	-20.44	1.36	12.41	1.55
	C2	-24.42	1.33	7.88	0.67
	C3	-23.41	3.19	11.05	0.29
	RD1	-21.20	1.50	8.00	0.65
	RD2	-23.96	2.10	7.65	2.65
	RD3	-20.52	3.98	10.95	2.06

Sample	Site	$\delta^{13}C$		$\delta^{15}N$	
		Mean	SD	Mean	SD
Suspended matter	C1	-25.91	2.51	6.12	1.86
	C2	-23.41	3.16	6.32	0.63
	C3	-25.86	1.92	6.39	0.60
	RD1	-24.41	0.83	6.93	1.19
	RD2	-26.73	0.64	3.86	0.75
	RD3	-23.43	2.69	6.90	0.56
Knodus moenkhausii	C1	-18.04	0.43	14.35	0.48
	C2	-20.51	0.63	11.52	0.40
	C3	-16.78	1.46	12.39	0.49
	RD1	-17.31	2.07	13.00	0.96
	RD2	-19.66	0.70	12.28	0.43
	RD3	-17.03	0.82	12.41	0.25