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Fishers' knowledge on abundance and trophic interactions of the freshwater fish *Plagioscion squamosissimus* (Perciformes: Sciaenidae) in two Amazonian rivers

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Small-scale fisheries provide income and food security to local peoples around the world. In the Brazilian Amazon, the pescada (*Plagioscion squamosissimus*) is among the fishes that contributes most to catches in small-scale fisheries. Our main goal was to evaluate the abundance, size, relevance to small-scale fisheries and trophic ecology of *P. squamosissimus* in the Tapajós and Tocantins rivers, in the Brazilian Amazon. We combined data from fishers' local ecological knowledge (LEK) and fish sampling. We expected that fishers in the Tapajós River, less altered by anthropic changes, would cite a higher abundance, larger size and more prey and predators of *P. squamosissimus*. We interviewed 61 and 33 fishers and sampled fish in nine and five sites in the Tapajós and Tocantins rivers, respectively. The comparison between fishers' citations and fish sampled indicated a higher relevance of *P. squamosissimus* to fishers in the Tapajós River, where this fish had an average larger size and where the fishers mentioned more food items. This pattern could be partially related to the history of anthropogenic changes in the Tocantins River. These results indicated that *P. squamosissimus* is a generalist fish, which could be resilient to fishing and environmental pressures.

Keywords: Environmental impacts, Human ecology, Small-scale fisheries, Tapajós River, Tocantins River.

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A pesca de pequena escala fornece renda e segurança alimentar para as populações locais em todo o mundo. Na Amazônia brasileira, a pescada (*Plagioscion squamosissimus*) está entre os peixes que mais contribuem para as capturas em pescarias de pequena escala. Nosso objetivo principal foi avaliar a abundância, tamanho, relevância para a pesca artesanal e ecologia trófica de *P. squamosissimus* nos rios Tapajós e Tocantins, na Amazônia brasileira. Combinamos dados do conhecimento ecológico local dos pescadores (CEL) e amostragem de peixes. Esperávamos que os pescadores do rio Tapajós, menos alterado por mudanças antrópicas, citassem maior abundância, maior tamanho e mais presas e predadores de *P. squamosissimus*. Entrevistamos 61 e 33 pescadores e amostramos peixes em nove e cinco locais nos rios Tapajós e Tocantins, respectivamente. A comparação entre as citações dos pescadores e os peixes amostrados indicou uma maior relevância de *P. squamosissimus* para os pescadores do rio Tapajós, onde este peixe teve um tamanho médio maior e onde os pescadores mencionaram mais itens alimentares. Esse padrão pode estar parcialmente relacionado ao histórico de mudanças antrópicas no rio Tocantins. Esses resultados indicaram que *P. squamosissimus* é um peixe generalista, que pode ser resiliente à pesca e às pressões ambientais.

Palavras-chave: Ecologia humana, Impactos ambientais, Pesca de pequena escala, Rio Tapajós, Rio Tocantins.

INTRODUCTION

Tropical freshwater environments have high species diversity with many interactions, hence providing important ecosystem services (Castello *et al*., 2013; Pelicice *et al*., 2022). These ecosystem services (Holmlund, Hammer, 1999), include the transfer of organic matter and nutrients by detritivorous fish (Flecker, 1996; Kominoski, Rosemond, 2012), dispersal of seeds by frugivorous fish (Hawes, Peres, 2014) and top-down control of prey populations by predators (Estes *et al*., 2011). Understanding of the trophic ecology of freshwater species can provide insights on these species interaction and consequences of interspecific interactions at the community and ecosystem levels (Holmlund, Hammer, 1999; Estes *et al*., 2011; Pendleton *et al*., 2014). Moreover, some fisheries harvest top predators, which could lead to the overexploitation and decline of important species for the maintenance of trophic chains and ecosystem functions, which could have potentially devastating impacts to the people who rely on them for food security (Pauly *et al*., 1998; Estes *et al*., 2011).

Local ecological knowledge (LEK) is useful to infer the ecological interactions of organisms that are regularly used by human populations (Huntington, 2000). Fishers' LEK has provided invaluable information about fish ecology, including abundance, behavior, reproduction, as well as temporal trends on abundance and composition of species harvested in coastal and freshwater ecosystems (Arantes *et al*., 2007; Silvano, Valbo-Jørgensen, 2008; Braga, Rebêlo, 2017; Hallwass *et al*., 2020a). Fishers' LEK can also indicate fish diets and even fish trophic levels (Silvano, Begossi, 2002, 2012,

2016; Batista, Lima, 2010; Ramires *et al*., 2015; Braga, Rebêlo, 2017; Pereyra *et al*., 2021). Furthermore, fishers' LEK can be a source of new biological hypotheses and management actions, especially when financial resources are sparse and fisheries are widespread (Huntington, 2000; Johannes *et al*., 2000; Silvano, Valbo-Jørgensen, 2008; Doria *et al*., 2014; Campos-Silva, Peres, 2016; Pereira *et al*., 2021).

The Amazon Basin is one of the most important aquatic ecosystems in the world with the highest diversity of fishes (Tedesco *et al*., 2017; Jézéquel *et al*., 2020). However, the Brazilian Amazon basin has experienced anthropic pressures, such as intensive fishing of some target species, the building of dams to provide hydropower, mining, deforestation and pollution (Castello *et al*., 2013; Winemiller *et al*., 2016; Keppeler *et al*., 2018). These anthropogenic changes can negatively affect aquatic ecosystems, imposing threats to the structure of food chains, water quality, hydrological characteristics and nutrient cycling (Estes *et al*., 2011; Castello *et al*., 2013; Santos *et al*., 2020; Swanson *et al*., 2021).

The Tapajós and Tocantins are important clear water rivers in the Brazilian Amazon, but these two rivers have distinct histories of environmental impacts and anthropic changes. The Tocantins is amongst the largely human-altered rivers in the Brazilian Amazon (Barthem *et al*., 2005). In this river, seven dams have been built including the large dam and reservoir of Tucuruí, filled in 1984 known to have negatively affected fish and fisheries (Fearnside, 1999, 2001; Hallwass *et al*., 2013a). The region in the middle Tocantins River is currently threatened by two large-scale development projects: the hydropower dam of Marabá and the waterway of Araguaia-Tocantins. These development projects may exacerbate negative impacts affecting fish and fishers in the region (Akama, 2017; Daga *et al*., 2019; Pelicice *et al*., 2021; Chamon *et al*., 2022).

The Tapajós River is less altered, by having several protected areas and indigenous lands, and being still free of dams along its main course (Hallwass *et al*., 2020a,b; Nagl *et al*., 2021). However, there are dams already built or planned in the tributaries of the Tapajós River (Athayde *et al*., 2019). Furthermore, plans to build dams in this river, may negatively affect the fish communities and fisheries (Fearnside, 2015; Runde *et al*., 2020). One of these planned dams is São Luiz do Tapajós that, if implemented, will be the fourth largest dam in Brazil (Hess, Fenrich, 2017). This dam could affect fishes and fisheries across approximately 275 km of river downstream from the dam area (Runde *et al*., 2020). The upper reaches of the Tapajós River have been also affected by gold mining, which threatens fish and riverine people through mercury contamination (Nevado *et al*., 2010; Lino *et al*., 2019; Vasconcellos *et al*., 2021).

The *Plagioscion squamosissimus* (Heckel, 1840) (Sciaenidae) with the common name of pescada, is important for freshwater fisheries in Brazil, especially in the Amazon, where this non-migratory fish is caught year-round (Cetra, Petrere, 2001; Parente, Batista, 2005; Hallwass *et al*., 2011; Hallwass, Silvano, 2016). This species inhabits regions of lakes and lagoons, in both benthic and pelagic habitats (Juras *et al*., 2005; Casatti, 2013). The *P. squamosissimus* has a continuous reproductive cycle with seasonal peaks, and its size at first maturity ranges from 20.5 to 32.5 cm in native habitats (Queiroz-Sousa *et al*., 2018). Studies on the feeding habits of this species suggest they are opportunistic carnivorous, eating shrimps, zooplankton and fish (Bennemann *et al*., 2006; Hahn *et al*., 2008). However, most studies on the diet of *P. squamosissimus* were carried out in reservoirs in other Brazilian river basins where this fish species has been introduced (Silvano, Begossi, 2001, 2002; Bennemann *et al*., 2006; Agostinho *et al*., 2007; Hahn

et al., 2008; Santos *et al*., 2018). Fewer studies on the diet of this fish species have been conducted in the Brazilian Amazon (Mérona, Rankin-de-Mérona, 2004; Dary *et al*., 2017). Notwithstanding the importance of fishes for the income and food security of Amazonian people (Hallwass, Silvano, 2016); few studies have used fish sampling and fisheries landings data to compare environmental availability and harvests of fish (Silvano, 2020; Nagl *et al*., 2021).

Our main goal is to evaluate the abundance, size, relevance to small-scale fisheries and trophic ecology of *P. squamosissimus* in two Brazilian Amazon rivers. To achieve this main goal, we adopt an interdisciplinary approach based on fishers' LEK (interviews) and fish sampling. We investigate the ecological interactions between *P. squamosissimus* and its prey and predators through trophic networks based on information from fishers' LEK (Silvano, Begossi, 2002, 2012; Pereyra *et al*., 2021). We compare fish sampling data and interviews with fishers to estimate the relative abundance and relevance to fisheries of *P. squamosissimus* in the two studied rivers. Based on the history of anthropic changes in each studied river, our overall hypothesis is that the less altered Tapajós River will show higher abundance, larger size, and more complex feeding interactions (more prey and predators cited by fishers) of *P. squamosissimus* compared to the more impacted Tocantins River.

MATERIAL AND METHODS

Study area. This study was conducted in the middle course of the Tapajós and Tocantins rivers, in the Brazilian Amazon (Fig. 1). These rivers have clear waters with low levels of sediments and low nutrient concentration (Albert, Reis, 2011; Reis *et al*., 2016). These clear water rivers differ from the more productive and nutrient-rich muddy white-water rivers, such as the lower Amazon River. The Tapajós River, which is formed by the Teles Pires and Juruena rivers, flows into the lower Amazon River near the city of Santarém (ICMBio, 2009). The Tapajós has an extension of 1,992 km and drains an area of nearly 460,200 km^2, accounting for about 6% of the freshwater discharge into the Amazon River (Latrubesse *et al*., 2005). We conducted this research (fish samples and interviews with fishers) in September 2018, in a river section considered here and in previous studies (Runde *et al*., 2020) as the middle Tapajós, between the municipalities of Aveiro and Itaituba (Fig. 1). A stretch of rapids occurs in this region near the communities of São Luiz do Tapajós and Pimental, where the construction of the São Luiz do Tapajós dam is planned (Hess, Fenrich, 2017; Runde *et al*., 2020). All the riverine communities addressed in this study are potentially vulnerable to the negative impacts of the São Luiz do Tapajós dam. A previous study indicates potential declines on the abundance of fish caught by fishers, resulting from possible changes in the hydrological regimes (Runde *et al*., 2020). In the middle Tapajós, fisheries are the most important source of income and animal protein for riverine fishers, who exploit mainly the channel of the river and its islands (Runde *et al*., 2020).

The Tocantins and Araguaia rivers form the Tocantins-Araguaia basin and both are clear water rivers formed by the Almas and Maranhão rivers on a plateau at 1,000 m of altitude. The Tocantins River is 1,960 km long and drains an area of 767,000 km^2, covered by vegetation from the Amazon, Brazilian savannah (Cerrado) and a transition

between these ecosystems (Ribeiro *et al*., 1995). We conducted this research in the middle course of the Tocantins River in October 2018, between the municipalities of Itupiranga and Marabá, including some samples in the Araguaia River, near its confluence with the Tocantins (Fig. 1). There are two hydroelectric projects planned in this region: The Marabá Hydroelectric Project will form a reservoir in the region between the Espírito Santo and Apinajés communities, and the Santa Isabel Hydroelectric Project has a planned reservoir in the region of the Santa Cruz community, in the Araguaia River. In addition, the Vila Tauri community is located ~50 km upstream from the dam of the Tucuruí reservoir. There is also the Araguaia–Tocantins Waterway Project with a planned stretch from Bógea Island to the Lourenção Rock, in the region of the Vila Tauri community. This region has rocks and rapids (known as 'pedral' in Portuguese) and is an important breeding ground and exclusive habitat for several fish species. The pedral is also the main place where artisanal fishing is carried out, representing the highest fishing yield for the riverside communities (Da Cunha, 2019). The waterway of Araguaia–Tocantins will destroy the rocky rapids in this part of the river (Akama, 2017).

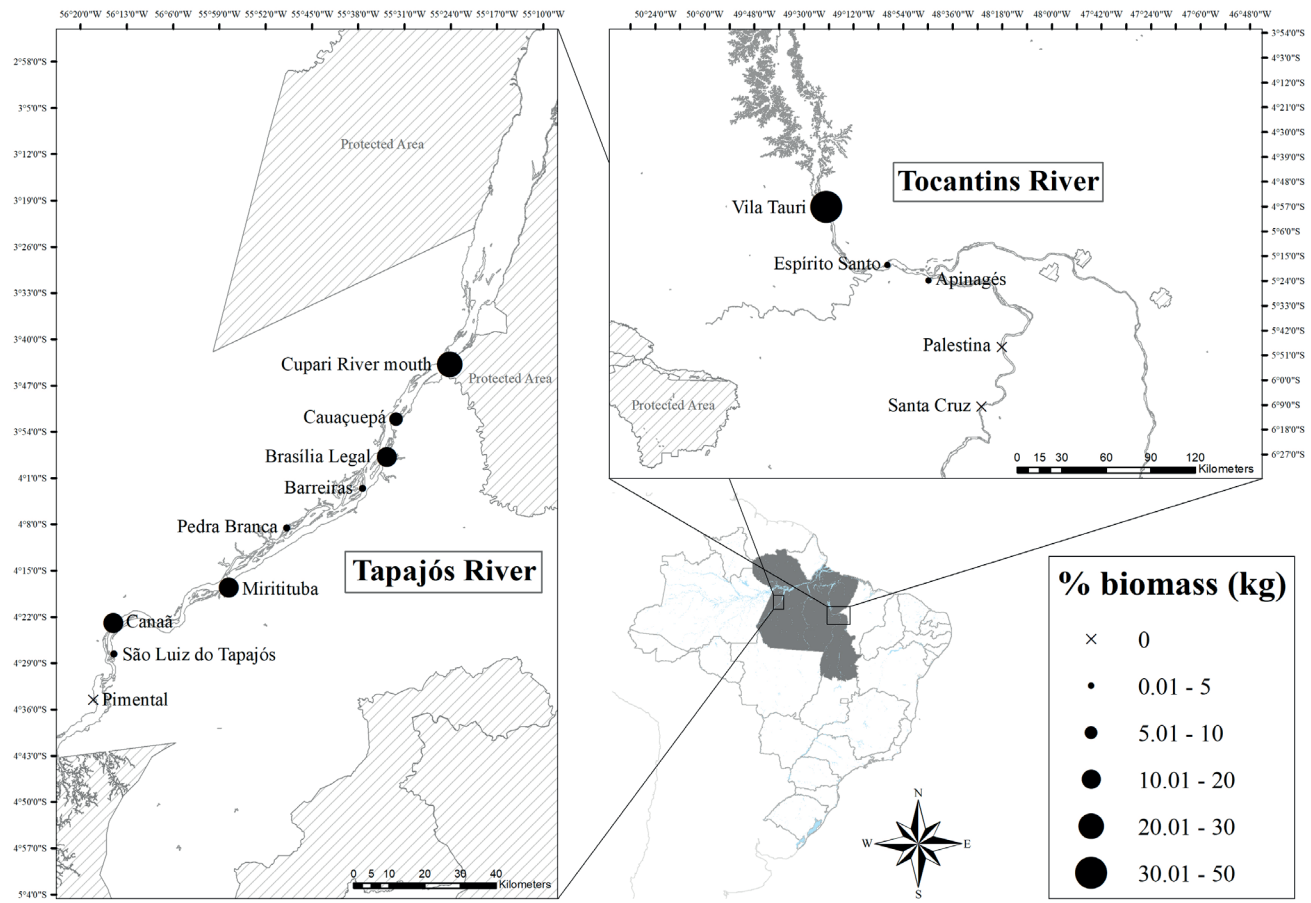

FIGURE 1 | Map of the studied region in the middle course of the Tapajós, Tocantins-Araguaia rivers, in the Brazilian Amazon, showing the fishing communities and distribution of biomass of *Plagioscion squamosissimus* (black circle) sampled where the research (fish sampling and interviews) was conducted.

People living in the studied fishing communities in both rivers are riverine people, whose livelihoods are based mainly on fishing and small-scale agriculture. Fishing is conducted mostly by using small canoes, and varied fishing gear, but mostly gillnets and hook and line, and fish are either consumed or locally sold (Hallwass *et al*., 2011; 2020a,b; Keppeler *et al*., 2020; Runde *et al*., 2020).

Fish sampling. We sampled fish during the low water season in both rivers (September in the Tapajós, October in the Tocantins) in nine sites in the Tapajós and five sites in the Tocantins (Fig. 1). These included two sites in the Tapajós and one site in the Tocantins where we sampled fish, but could not conduct interviews with fishers. We sampled fish during 24 h, one sample per site, using two sets of gillnets, each set with seven nets of distinct mesh sizes (15, 25, 35, 50, 60, 70, and 80 mm between adjacent knots) and 420 m² of area. We checked the nets at regular intervals at every six hours to collect fish. We set the gillnets in the river, but usually in sites with calm waters closer to river margins and sometimes in adjacent lakes connected to the river in the Tapajós. In both rivers, some sampling sites were located near river rapids, which is a characteristic habitat of these rivers. We opportunistically chosen sampling sites with the help of fishers who know the region, as not all sites were suitable for fishing with gillnets. We identified fish to species and recorded the length (standard length, in cm) and weight of all sampled fish, including *P. squamosissimus.* Some fish caught alive were released after they were measured, while others were euthanized through immersion in water containing anesthetic (clove oil), being then preserved in formalin and stored in the laboratory. The sampled fish were deposited in the ichthyological collection of the Ichthyology Laboratory of the Grupo de Ecologia Aquática (GEA.ICT) of the Universidade Federal do Pará, Belém, Pará, Brazil. List of catalog numbers of voucher specimens: GEA.ICT 12107 to 12163.

Interviews with fishers. We interviewed 61 fishers in seven fishing communities in the Tapajós River: Barreiras, Brasília legal, Canaã, Cauaçuepa, Miriticuba, Pedra Branca, and São Luiz do Tapajós (Fig. 1). These interviews were made in March 2018 as part of a broader study about the fisheries in the Tapajós River (Runde *et al*., 2020). We included these interviews here to check the most used fish according to fishers and hence the relevance of *P. squamosissimus* to these small-scale fisheries (Silvano, Hallwass, 2020). Additionally, we interviewed 67 fishers in the Tapajós River in September 2018 in these same communities (Fig. 1), to get detailed data about fishers' LEK on the diet of *P. squamosissimus*. In the Tocantins River, we gathered data on both the relevance for fisheries and the diet of *P. squamosissimus* through interviews with 33 fishers in four fishing communities: Apinagés, Espírito Santo, Santa Cruz, and Vila Tauri (Fig. 1).

We first contacted community leaders, explained the study, and requested permission to conduct research in the community. We then asked the leaders to indicate experienced fishers, who would fit the criteria to be included in our research: older than 18 years, dedicated to fishing as one of their main economic activities and to be living in the community or study region for at least 10 years. After locating and interviewing the first fishers indicated by leaders, we found and selected other fishers to be interviewed through the 'snowball' sampling method. In this method, each interviewed fisher indicated others who would fit the criteria and could be included

in the research, following the approach of previous studies on fishers' LEK (Hallwass *et al*., 2013a; Runde *et al*., 2020). Before the interview, we explained the study to each fisher and asked his or her consent to be interviewed. The interviews were based on a standard and structured questionnaire. This questionnaire included questions about the most relevant fish caught, asking each fisher to mention up to five fish species, in addition to questions on the trophic ecology of *P. squamosissimus*, such as food items consumed and its predators.

Analyses. We estimated the relative abundance or availability of *P. squamosissimus* in the environment by calculating the percent of the biomass of this species sampled relative to the total fish biomass sampled, at each sampling site (fishing community). Sampling sites were considered replicates in the analyses. We conducted t-tests to compare the average age and experience (number of years fishing) of fishers between the two rivers. We estimated the relative importance of *P. squamosissimus* to local fisheries in each studied fishing community by calculating the percent of citations of this fish relative to the total citations of all fish by the interviewed fishers (Runde *et al*., 2020). We then compared the average percentages of relative abundance and importance to fisheries of this fish between the two studied rivers through t-tests. We also compared the average percentages of relative abundance and relative importance to fisheries in each river through paired t-tests, considering only those fishing communities (7 in Tapajós and 4 in the Tocantins) for which we had both fish sampling and interviews data. We calculated the percent of citations of prey and predators of *P. squamosissimus* by the interviewed fishers in each river to construct the diagrams of feeding interactions.

We conducted t-tests to compare the mean number of prey items and predators of *P. squamosissimus* cited by each fisher between the two studied rivers. We also conducted t-tests to compare the average size of sampled individuals of *P. squamosissimus* between the two rivers. We organized the size data of sampled individuals of *P. squamosissimus* in 5 cm size classes and compared the size distributions between the two rivers through a two-sample Kolmogorov-Smirnov test.

We checked the normality of data through the tests of Shapiro-Wilk or Lillefords (depending on sample size) and log-transformed data if not normally distributed. We used the non-parametric Mann-Whitney test to compare medians if the data did not achieve normal distribution, even after being transformed. Statistical analyses were done using the Bioestat software (Ayres, 2007) and R (R Development Core Team, 2010).

RESULTS

Abundance, size and relevance to fisheries. We sampled 108 individuals and 22.5 kg of *P. squamosissimus* from a total of 228.6 kg and 3,455 individuals of fish sampled in the Tapajós River. In the Tocantins River, we sampled 121 individuals and 28.7 kg of *P. squamosissimus*, from a total of 109.4 kg and 1,639 individuals of fish sampled. Overall, the *P. squamosissimus* accounted for 9.9% and 26% of the total biomass of fish sampled in the Tapajós and Tocantins rivers, respectively. The average relative abundance of *P. squamosissimus* did not differ between the two studied rivers ($t = -0.76$, $df = 12$, $p = 0.45$) (Fig. **S1**).

We interviewed 161 fishers along the two studied rivers. The average age and fishing experience (lifetime dedicated to fishing) of the fishers were, respectively, 56.5 (± 14 SD) and 34.8 (±17.6 SD) years in the Tocantins River (n = 33). In the Tapajós River (n = 128), average age and fishing experience were, respectively, 47.9 ± (12 SD) and 28 (± 12.5 SD) years. Fishers age ($t = -3.5$, $df = 160$, $p = 0.00042$) and fishing experience ($t = -2.5$, $df = 160$, $p = 0.01$) differed between the rivers, as fishers were older and more experienced in the Tocantins River.

The interviewed fishers in the Tapajós River cited 62 times the *P. squamosissimus* as one of the main fish caught, corresponding to 12.6% of the total fish citations (n = 490), whereas in the Tocantins River this fish was cited by fishers 7 times, corresponding to 4.6% of the total fish citations (n = 150). Although the *P. squamosissimus* was, on average, almost twice more cited by fishers in the Tapajós River compared to the Tocantins River, the average relative importance of this fish to the small-scale fisheries, here measured as a percentage of citations in each community, did not differ statistically between the two rivers ($t = 1.7$, $df = 9$, $p = 0.14$) (Fig. 2).

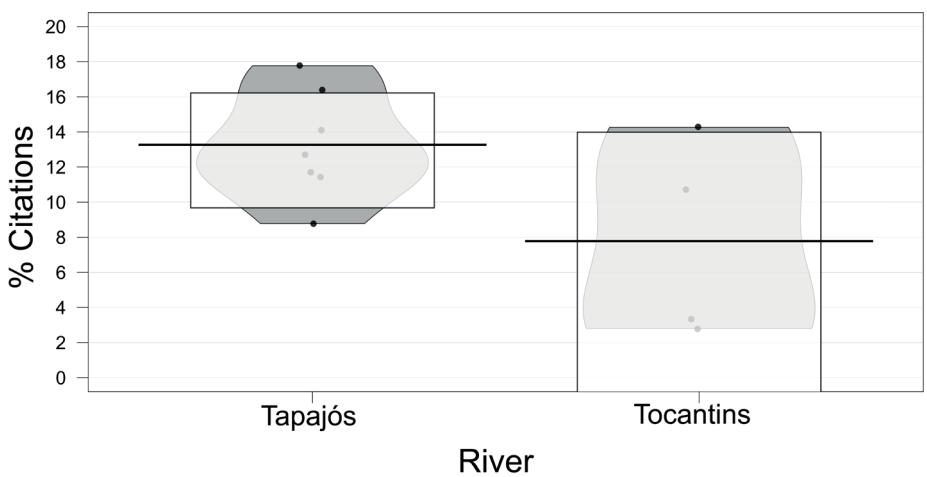

FIGURE 2 | Comparison of mean relative relevance to fisheries (% of citations in interviews) of *Plagioscion squamosissimus* according to the interviewed fishers in the Tapajós (n = 7) and Tocantins (n = 4) rivers. Mean (dark horizontal line), data distribution (bean gray area), data (points), confidence interval (rectangle). Points indicate the fishing communities, considered as replicates in this analysis.

The mean relative relevance of *P. squamosissimus* to fisheries (fishers' citations) was higher than its mean relative abundance in the environment according to fish samples in the Tapajós River ($t = -3.4$, $df = 6$, $p = 0.01$) (Fig. 3). Conversely, in the Tocantins River the mean relevance to fisheries of this fish (7.8 ± 5.6 %) did not differ ($t = -0.43$, $df = 3$, $p = 0.7$) from its mean relative abundance (12.2 ± 22.3 %) (Fig. **S2**).

The average size of *P. squamosissimus* sampled was larger in the Tapajós than in the Tocantins ($U = 4621.5$, $p = 0.0002$) (Fig. 4). The frequency distributions of *P. squamosissimus* among size classes did not differ between the two studied rivers (Kolmogorov-Smirnov Chi-square = 6.2, $p > 0.05$), as most of the sampled individuals were 21 to 25 cm in both rivers (Fig. **S3**).

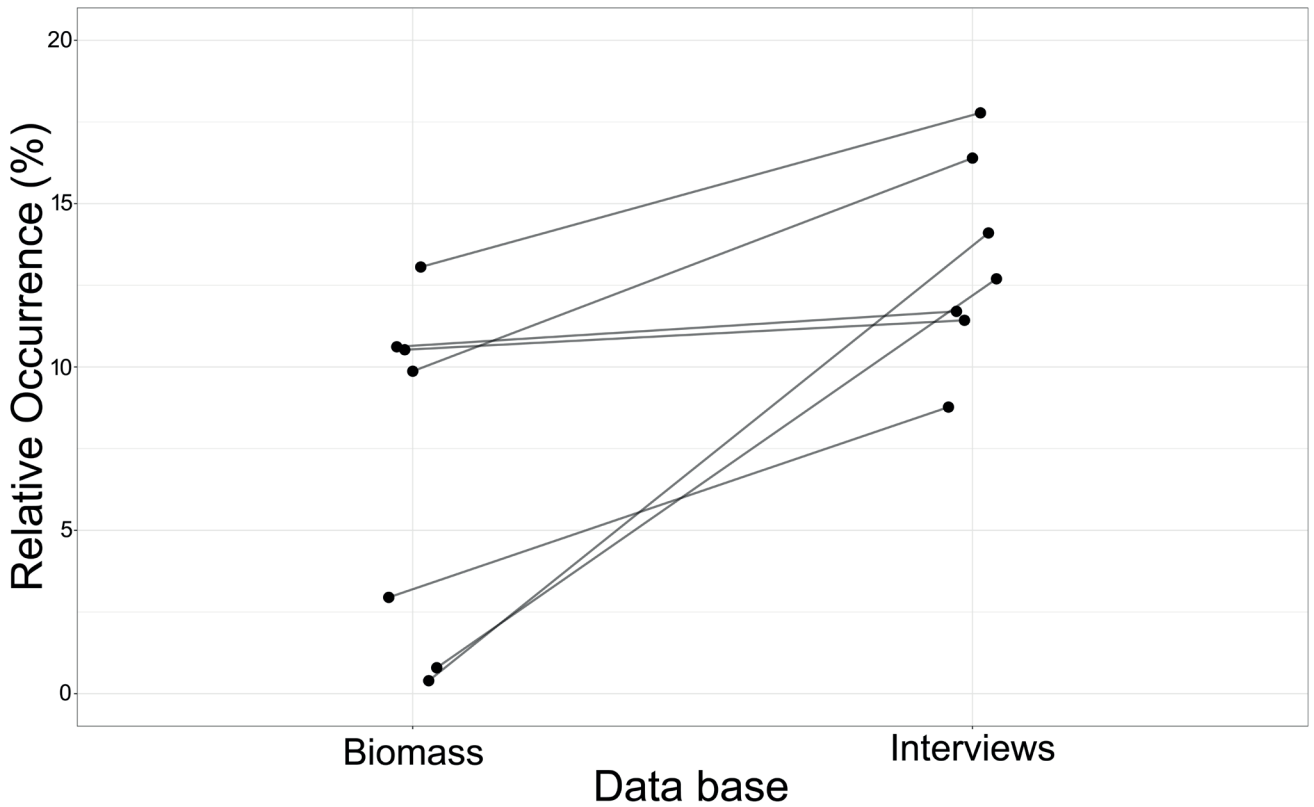

FIGURE 3 | Paired comparison between the relative abundance (% of biomass in kg) in samples and relative importance for fisheries (% of citations in interviews) of *Plagioscion squamosissimus* in the Tapajós River. Dots indicate the sampling sites for biomass and fishing communities for interviews.

Fishers' LEK on trophic ecology. The fishers cited a total of 20 food items as being consumed by *P. squamosissimus* in both rivers (Tab. **S4**). The most cited preys were fish (mostly three species), besides crustaceans (shrimps) and insects (Fig. 5; Tab. **S4**). The interviewed fishers also mentioned 18 groups of predators of *P. squamosissimus* in both rivers, including aquatic mammals (river dolphin, otter, and giant river otter), birds, alligator and other fish, such as tucunaré, dourada and jaú. The interviewed fishers also mentioned the occurrence of cannibalism by individuals of the same species (Fig. 5; Tab. **S5**).

On average, each interviewed fisher cited more prey items of *P. squamosissimus* in the Tapajós than in the Tocantins (U = 691, p = 0.003) (Fig. 6). The average number of predators of *P. squamosissimus* mentioned by each interviewed fisher did not differ between the two rivers (t = -1.93, df = 97, p = 0.056) (Fig. **S6**).

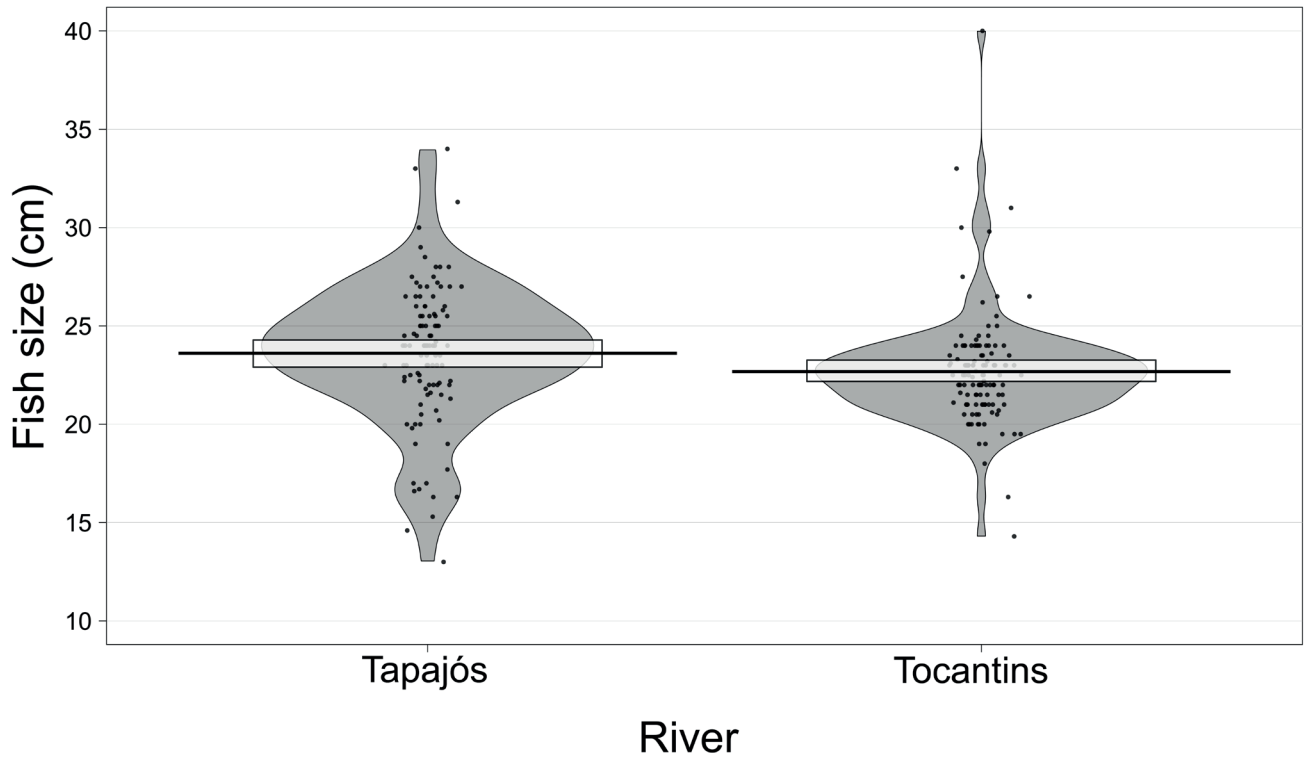

FIGURE 4 | Mean size (standard length in cm) of *Plagioscion squamosissimus* sampled in the Tapajós and Tocantins rivers. Mean (dark horizontal line), data distribution (bean gray area), data (points), confidence interval (rectangle). The median sizes of *P. squamosissimus* were 23.6 cm in the Tapajós and 22.7 cm in the Tocantins.

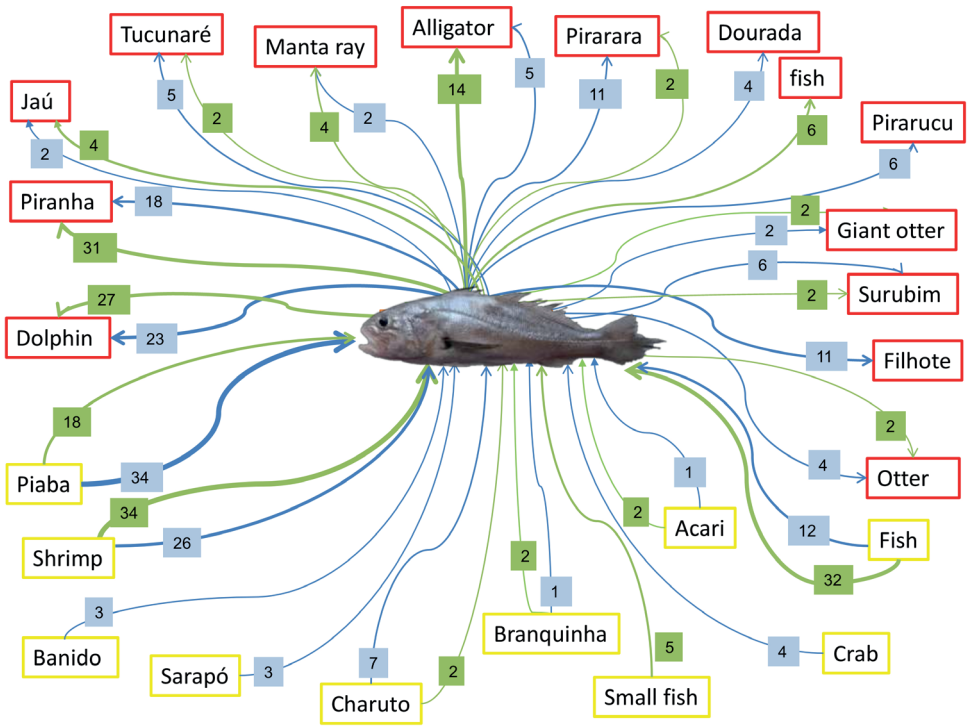

FIGURE 5 | Diagram depicting the main trophic interactions (simplified food web) of *Plagioscion squamosissimus* based on fishers' LEK (interviews) indicating the 10 most cited prey (yellow) and the 14 most cited predators (red), in the Tapajós (blue) and Tocantins (green). Numbers inside squares are the percent of citations of prey and predators of *P. squamosissimus* by the interviewed fishers. We obtained 150 citations of prey and 129 citations of predators by the interviewed fishers in the Tapajós River and 56 citations of prey and 50 citations of predators in the Tocantins River. Line thicknesses indicate the number of citations by the fishers interviewed.

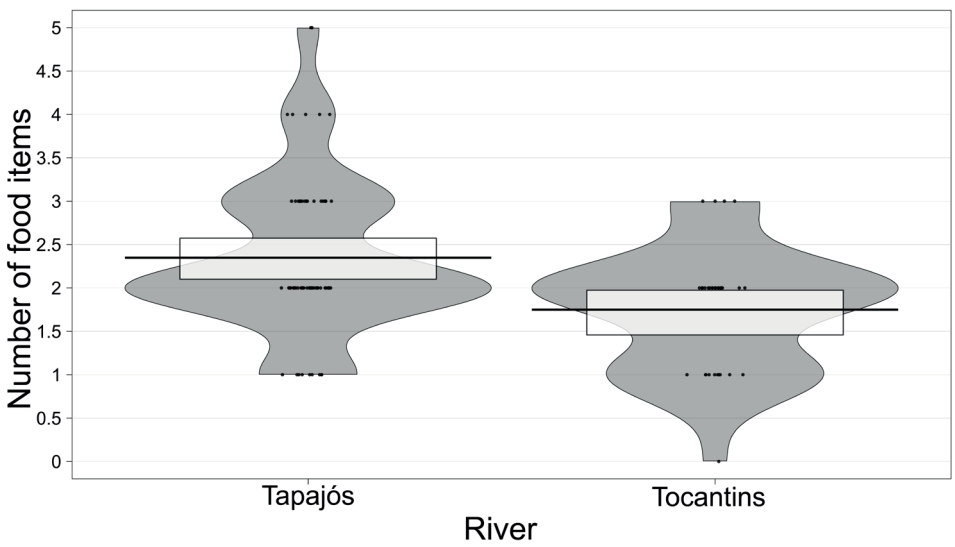

FIGURE 6 | The mean number of prey items of *Plagioscion squamosissimus* is cited by the interviewed fishers in the Tapajós and Tocantins rivers. Mean (dark vertical line), data distribution (bean gray area), data (points) correspond to individual fishers, confidence interval (rectangle). The median was 2 for both rivers.

DISCUSSION

Abundance and fishing of *Plagioscion squamosissimus*. Considering that the Tocantins River has been under greater pressures from anthropogenic stressors when compared to the less altered Tapajós River, our overall hypothesis was only partially confirmed. The relative abundance of *P. squamosissimus* did not differ between the two rivers, nor did its sampled population size distribution, but the average size of sampled fish was larger in the Tapajós River.

The fact that *P. squamosissimus* was commonly found in the two studied rivers is likely due to the generalist and opportunistic feeding habits of this fish species (Bennemann *et al*., 2006; Hahn *et al*., 2008). However, this can be viewed as a partial explanation, since there could be other evolutionary and ecological factors driving fish species distribution patterns. This behavior may confer resilience and adaptive capacity for this fish to cope with varied environmental conditions, including fishing pressure or habitat alteration (Silvano, Begossi, 2001; Hallwass *et al*., 2013a). Indeed, *P. squamosissimus* is sedentary, occurs mainly in lentic habitats and can change its diet to consume more abundant food items (Bennemann *et al*., 2006; Hahn *et al*., 2008; Casatti, 2013; Costa, Angelini, 2020). This plasticity probably contributes to the high catches of this fish in Amazonian fisheries, especially in clear water rivers (Hallwass, Silvano, 2016; Mesquita *et al*., 2019). Moreover, *P. squamosissimus* may be resilient to the impoundment of Amazonian rivers. This fish species catches have increased over time in small-scale fisheries of the lower Tocantins River after the Tucuruí dam construction upstream (Hallwass *et al*., 2013a). This fish is also among the most caught in the Xingu River, where the exploitation rates are below the maximum sustainable level (Mesquita *et al*., 2019). *Plagioscion squamosissimus* has been successfully introduced in several reservoirs in other Brazilian regions, where this fish has usually increased in abundance and is among the most harvested species (Silvano, Begossi, 2001; Bennemann *et al*., 2006; Agostinho *et al*., 2007; Hahn *et al*., 2008; Santos *et al*., 2018).

The relevance for fisheries, here measured by fishers' citations, did not differ statistically between the two rivers. Nevertheless, comparisons between fishers' citations and fish sampled (relative abundance) indicated a proportionally higher relevance of *P. squamosissimus* to fishers in the Tapajós River, as observed in a previous study (Runde *et al*., 2020). Furthermore, this fish species is the one most caught by fishers in the lower Tapajós (from 2016 to 2017) and in the lower Tocantins rivers (from 2006 to 2008), in addition to be the second most caught in the middle Tocantins River in 1997 (Cetra, Petrere, 2001; Hallwass *et al*., 2011, 2020b). Studies based on fishers' LEK show an increase in the relative importance of *P. squamosissimus* for artisanal fishers along the last 20 to 40 years in the lower Tapajós (Hallwass *et al*., 2020a) and in the lower Tocantins River (Hallwass *et al*., 2013a).

The relative abundance and importance to fisheries of *P. squamosissimus* observed in the studied rivers indicate that this fish species has potential to become even more important to local fishers. *P. squamosissimus* has less commercial value than other harvested species, such as the tucunaré (*Cichla* spp.) or large catfishes (Silvano, Hallwass, 2020). However, *P. squamosissimus* could be an alternative or complement to harvests of larger and more commercially valuable fish, which became increasingly scarce due to the increased fishing pressure in the Brazilian Amazon (Castello *et al*., 2013; Keppeler *et*

al., 2018; Hallwass *et al*., 2020a). Furthermore, the sedentary nature of this fish species and its widespread distribution can provide more predictable and available catches. This fish species could be caught year-round, even during times when preferred migratory fish are unavailable, or during the high-water season, when fish get more dispersed and hence more difficult to catch (Hallwass *et al*., 2013b; Keppeler *et al*., 2020). We lack detailed fisheries data of *P. squamosissimus* in the studied regions in the Tapajós and Tocantins rivers. Nonetheless, this fish is commonly found in fish samples, and it is amongst the most caught species. This fact, in addition to an increased trend in catches of *P. squamosissimus* in some Amazonian rivers (Hallwass *et al*. 2011, 2013b, 2020a,b; Hallwass, Silvano, 2016; Mesquita *et al*., 2019), suggest that this fish could be resilient to current rates of fishing pressure. Similarly, a study combining fish sampling and recording of fish landings shows that *P. squamosissimus* was abundant but seldom fished in the Negro River, in the Brazilian Amazon (Silvano, 2020). Nevertheless, fishers less cited the *P. squamosissimus*, so possibly less used, in the Tocantins River, which may be due to cultural or market preferences.

The length at first maturity of *P. squamosissimus* is approximately 20.7 cm (Froese, Pauly, 2022). Therefore, most of the individuals sampled in the two studied rivers would be adults larger than 21 cm and we found even larger fish, up to 40 cm, in our samples (Fig. **S3**). This further suggests that this species is not overfished in the studied rivers, as observed in the Xingu River (Mesquita *et al*., 2019). Nevertheless, the size at first maturity of *P. squamosissimus* can vary according to environmental conditions. There are records of first maturation with 20.5 to 32.5 cm in natural environments (Queiroz-Sousa *et al*., 2018). Furthermore, most of the available data on the size at first maturity of *P. squamosissimus* comes from studies carried out in reservoirs, where this species was introduced (Canelós, Benedito-Cecilio, 2002; Rocha *et al*., 2006; Queiroz-Sousa *et al*., 2018). Therefore, studies on this species reproduction in natural environments such as the Tapajós River are necessary to support management measures.

The proposal of recent laws by the Brazilian government would allow aquaculture of non-native species in the Brazilian Amazon, which raise conservation concerns. This aquaculture may cause environmental impacts, such as changes in the water quality, dissemination of diseases, and invasion of exotic species (Padial *et al*., 2017; Catelani *et al*., 2021). The *P. squamosissimus* should receive more attention by fisheries managers and policymakers, as a reliable alternative to maintain productive capture fisheries. This can reduce or eliminate the need to implement uncertain and potentially impacting aquaculture enterprises (Padial *et al*., 2017; Pelicice *et al*., 2017).

Assessing the fishery status and potential resilience of fish is important to evaluate the risk posed by ongoing anthropogenic changes. The resilient *P. squamosissimus* could be a viable option for food security of the riverine population in the face of anthropogenic changes affecting Amazonian rivers (Castello *et al*., 2013; Winemiller *et al*., 2016; Keppeler *et al*., 2018). This fish species could thus be a promising fishing resource to alleviate poverty, increase food security and promote economic development among Amazonian riverine communities. This fishing resource can be especially needed in less productive, more altered and less known clear water rivers.

Fishers' knowledge and trophic ecology. The interviewed fishers in the Tapajós cited more food items for *P. squamosissimus* compared to older and more experienced fishers in the Tocantins River. This was also observed in a previous study on fishers'

LEK about the diet of six fish species in these two rivers (Pereyra *et al*., 2021). These results suggested more complex feeding interactions of *P. squamosissimus* in the more pristine Tapajós River, as expected based on our hypothesis. Overall, the food items consumed by the *P. squamosissimus* according to the interviewed fishers in this study were similar to the food items recorded for this fish in the biological literature (Mérona, Rankin-de-Mérona, 2004; Dary *et al*., 2017). The information from fishers' knowledge thus agreed with biological studies based on stomach content analyses, according to which *P. squamosissimus* is a carnivorous fish, eating mainly fish and crustaceans (Stefani, Rocha, 2009; Santos *et al*., 2018). Some of the interviewed fishers also mentioned the occurrence of cannibalism in this fish species. This corroborates evidence in the biological literature that this fish can eats juveniles of the same species (Braga, 1997). Moreover, a recent study shows that both fishers' LEK and isotope analyses produce similar and consistent results to indicate trophic levels of fish species in the Amazon, including the *P. squamosissimus* (Pereyra *et al*., 2021). Previous studies have shown that fishers usually provide accurate data on the diet of piscivorous fish and such data from fishers' LEK agrees with biological studies (Begossi, Silvano, 2008; Silvano, Begossi, 2010; Pereyra *et al*., 2021). Fishers may gather this detailed knowledge while eviscerating fish or using bait (Silvano, Begossi, 2002). Biological studies based on stomach content analyses of fish may present some difficulties to identify and quantify the food items. For example, many individuals of piscivorous fish may show empty stomachs (Arrington *et al*., 2002), or some food items may be too digested, precluding identification (Stapp, 2002). In such a context, fishers' LEK may be an alternative or complementary source of detailed data about prey items consumed by carnivorous or piscivorous fish, such as *P. squamosissimus*.

Fishers' LEK indicated several animals that prey on *P. squamosissimus*, including some large fish and aquatic mammals. These large predators, such as the red river dolphin (*Inia geoffrensis*), tucuxi river dolphin (*Sotalia fluviatilis*), giant river otter (*Pteronura brasiliensis*) and the river otter (*Lontra longicaudis*), may be elusive, difficult to survey and may be threatened in the Amazon basin. Some of these species are endemic to specific regions, such as the river dolphin (*Inia araguaiaensis*) in the Tocantins-Araguaia River basin (Hrbek *et al*., 2014; ICMBio, 2019). These results agree with studies on diet of the river dolphins *Sotalia fluviatilis* (Beltrán-Pedreros, Araújo Pantoja, 2006) and *Inia geoffrensis* (Echeverria *et al*., 2022). On the other hand, *P. squamosissimus* has not been recorded as part of the diets of river otters *Pteronura brasiliensis* and *Lontra longicaudis* (Carter, Rosas, 1997; Cabral *et al*., 2010; Moraes *et al*., 2021). In such context, fishers' LEK can provide a new ecological hypothesis to be investigated (Silvano, Valbo-Jørgensen, 2008), regarding the consumption of the studied fish by these aquatic mammals. We could not find scientific literature about other predators of this fish species. Therefore, studies on fishers' LEK can help to better understand the ecological dynamics of the food webs, besides the diet of aquatic mammals, which may be difficult to sample (Ramires *et al*., 2015; Manzan, Lopes, 2016). The main fish guild that increased in abundance after the damming in the Tocantins River were the piscivores, such as *P. squamosissimus*, whereas other guilds decreased (Mérona *et al*., 2001). This may indicate a change in the abundance of predators of *P. squamosissimus* associated to dams. However, a previous study in the same communities addressed here, show that the number of fish predators mentioned by fishers for six fish species did not differ between the Tapajós and Tocantins rivers, even considering that Tocantins has been more altered by dams (Pereyra *et al*.,

2021). Although fishers cited more food items in the Tapajós, a larger number of items were cited for the more specialist frugivorous fishes (Pereyra *et al*., 2021). We sampled only some of the habitats included in the range of this fish species during one period of the year (dry season). We do not explicitly questioned fishers about seasonality of the diet of this fish. Therefore, more refined studies could bring even more information about this fish species.

The results of this study indicated that *P. squamosissimus* is a generalist carnivorous, which, given its relative abundance, may play a relevant ecological role through feeding interactions with prey and predators. This fish species is also important to fisheries in the two studied Amazonian rivers and elsewhere in the Amazon. This fish species may contribute to guarantee food security and income in altered river basins, by possibly alleviating the fishing pressure directed to other preferred fish. We thus recommend that fisheries managers and policymakers consider the promising role of this fish species as a fishing resource that could be a viable option for sustainable freshwater fisheries. Our results also show contributions of fishers' LEK to gather biological data, and improve understanding of fish trophic ecology, while also aiding to assessments of environmental impacts.

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AUTHORS' CONTRIBUTION

Márcia Caroline Friedl Dutra: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing-original draft.

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Gustavo Hallwass: Investigation, Methodology, Writing-review and editing.

Mark Poesch: Formal analysis, Funding acquisition, Writing-review and editing.

Renato Azevedo Matias Silvano: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing-review and editing.

ETHICAL STATEMENT

The ethics committee on animal research of the Universidade Federal do Rio Grande do Sul approved this study and its sampling methodology (CEUA: 34186). The ethics committee on research approved this study with people from the UFRGS (CAAE: 82355618.0.0000.5347). The researcher RAMS has a permanent license for collecting fish from Sistema de Autorização e Informação em Biodiversidade (SISBio 39549–5).

COMPETING INTERESTS

The author declares no competing interests.

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