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REGULAR PAPER

Feeding of *Arapaima* sp.: integrating stomach contents and local ecological knowledge

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Abstract

The giant arapaima (*Arapaima* sp.) has been described as a fish of change in Amazonia because of its important role in the conservation of floodplains, food security and income generation for rural communities. Nonetheless, despite the cultural, ecological and economic importance of arapaima, data on diet are scarce. Aiming to expand knowledge about arapaima diet in western Amazonia, scientific knowledge was integrated with the knowledge of local dwellers. During the low-water period (September 2018) and the falling-water period (June 2019), arapaima stomachs were collected from 11 floodplain lakes in the middle Juruá River. All fishes were measured [TL (total length)] and sexed. Food items from each stomach were categorized as fishes, invertebrates, plants and bone remains and weighed. Also, in the latter period, experienced local fishers were interviewed about arapaima feeding. This integrated approach revealed that young arapaima eat fish and invertebrates but adult arapaima eat fish of a wide range of species, which were mainly of low and intermediate trophic positions. This study reports the first case of cannibalism for arapaima and also shows that during the low-water period, many individuals had empty stomachs or only some small fish-bone remains and/or plant material. Arapaima sex and TL had no influence on the absence of prey in stomach contents. Overall, it can be concluded that local people had consistent ethnobiological knowledge of arapaima feeding ecology that could be useful within management projects in the region.

KEYWORDS

Amazon, diet, ethnobiology, ichthyology, predator

1 | INTRODUCTION

Arapaima sp., also known as pirarucu or paiche, is the largest freshwater scaled fish in the world. It can weigh up to 200 kg and reach up to *ca*. 3 m in total length (TL; Nelson, 1994). It is endemic to the Amazon basin, inhabiting mainly floodplain lakes and flooded forests. During rising and high-water levels, arapaima move from lakes to flooded-forest habitats, exploiting spatially and temporally heterogeneous resources of the floodplain, which presumably improves growth and reproduction (Castello, 2008; Campos-Silva *et al*., 2019). Five species of the genus have been proposed (Castello & Stewart, 2010; Stewart, 2013a, 2013b), but there is still no consensus on its taxonomy (Farias *et al*., 2019). Arapaima is also traditionally and commercially fished in the Amazon basin because of the quality of its meat, being highly overexploited over most of its geographical range and currently facing local extinction in many localities (Castello *et al*., 2015). Despite its importance, arapaima is listed as data deficient by the IUCN (2020) and included in Appendix II of the

Convention on International Trade in Endangered Species of Wild Fauna and Flora.

Because of population declines of the species in some natural environments, arapaima fishing is prohibited in some regions of the Amazon, such as most of the state of Amazonas, Brazil. Nonetheless, community-based management (CBM) programmes have been established to recover and maintain arapaima stocks and improve local people's income (Castello *et al*., 2009). These initiatives have been successfully recovering wild populations of arapaima, combining biodiversity conservation with social development (Campos-Silva *et al*., 2017, 2019; Campos-Silva & Peres, 2016; Castello *et al*., 2009; Freitas *et al*., 2020; Petersen *et al*., 2016). The CBM of arapaima is largely based on harvest zoning systems, in which lakes are classified into three management categories: (a) open-access lakes, where commercial fishing activities are allowed with no restrictions; (b) subsistence-use lakes, where fishing is allowed to supply local subsistence needs; and (c) protected lakes, where fishing is banned except for a brief arapaima harvest period each year. In the protected lakes, population monitoring is undertaken through annual population counts carried out by local inhabitants. Based on this information, environmental authorities allow the removal of 30% of the adult population during the yearly harvesting period. In the Juruá River, a major tributary of the Amazon River, the CBM of arapaima has induced the recovery of wild populations, with increases of more than 420% within 11 years (Campos-Silva *et al*., 2019). This is an example of a win–win programme, allowing stock recovery and providing food and income for riverine people (Campos-Silva & Peres, 2016).

Despite the cultural, ecological and economic importance of arapaima, data on diet, which may provide information to improve conservation and management plans for the species, are still scarce. Some authors consider adult arapaima as apex predators that occupy relatively high positions on the food chain (Carvalho *et al*., 2018). Others have concluded that arapaima are omnivorous, typically secondary consumers, feeding relatively low or in the middle of the food web (Watson *et al*., 2013). Queiroz (2000) concluded that arapaima diet is composed mainly of fishes and characterized the species as mainly piscivorous though the smallest individuals also complement their diet with invertebrates.

Many studies have demonstrated the value and usefulness of fishers' ecological knowledge to research and management (Braga & Rebêlo, 2017; da Silva *et al*., 2019; Nunes *et al*., 2019), showing agreement between information derived from interviews and what was found with scientific methods. In a study from Africa's Lake Tanganyika, Bulengela *et al*. (2019) concluded that fishers' local knowledge of ecological conditions, fish availability and fishing pressures could benefit fisheries management. Braga and Rebêlo (2017) also found that fishers from the lower Juruá River presented an extensive and detailed knowledge of the reproductive behaviour of the region's fish species. Sometimes, because of difficulties in finding and accessing academic literature, local knowledge can be the only available data and can indicate directions to decisions-makers. Researchers can also gain considerable insight from interviews with experienced fishers (Silvano & Valbo-Jørgensen, 2008).

Taking this aspect into account, to increase knowledge on the trophic ecology of arapaima in the Juruá River, stomach-content analyses and interviews were conducted with experienced fishers involved in the arapaima CBM programme. The knowledge of local dwellers is a promising strategy to assess arapaima feeding ecology due to their generations of empirical observations. In other regions, combining distinct knowledge sources has proven useful in developing a complete understanding of ecological phenomena (*e.g*., Abu *et al*., 2019; Jackson *et al*., 2014; Mantyka-Pringle *et al*., 2017). A multi-pronged approach to knowledge generation could therefore improve the understanding of arapaima feeding in the floodplain lake management system in western Amazonia and offer an example for such knowledge synthesis elsewhere.

2 | MATERIALS AND METHODS

2.1 | Data collection

Data were collected from 11 lakes along the middle section of the Juruá River (Figure 1), a tributary of the Amazon River, including two protected areas (Reserva de Desenvolvimento Sustentável Uacari and Reserva Extrativista do Médio Juruá). The middle Juruá River region is influenced by pronounced and predictable hydrology, with the period of high-water levels from January to June and that of low-water levels from August to November (Hawes & Peres, 2016).

During the low-water period in September 2018, arapaima stomachs from individuals caught by fishers were collected using gillnets as part of the CBM programme. Stomachs were also collected in June 2019 to include samples from the season when water levels are falling. These latter individuals were captured by fishers using a traditional harpoon method. All fishes were measured from the tip of the snout to its tail (TL in centimetres) and sexed. The stomachs were stored on ice in the field. At a field station, food items from each stomach were separated as fish, invertebrates, plants and bone remains and weighed using a digital scale. Samples were frozen at −20°C in the field, and later, animal prey were identified to the lowest possible taxonomic level with the aid of a fish taxonomist. Then the proportion of each item in each stomach was calculated according to the item's weight.

During the falling-water period, in June 2019, interviews were also conducted with experienced fishers who were over 21 years old and involved in the CBM programme. Interviews were conducted through informal conversations using simple and commonly used vocabulary, where the same specific questions present in a semi-structured questionnaire were always included (Supporting Information Table S1). Broadly, the authors of this study were interested in knowing the experience and perceptions about arapaima feeding as a function of body size, season and lake management status. Before the interview, consent was obtained from each participant to be interviewed.

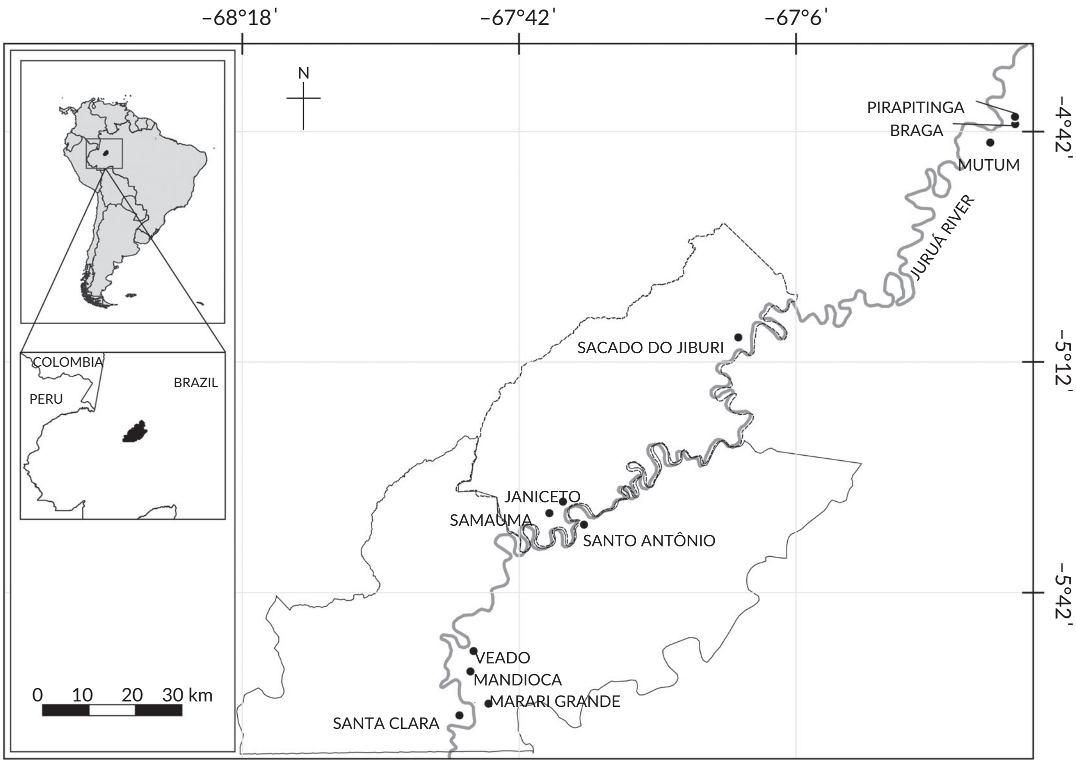

FIGURE 1 Location of the 11 lakes where stomach contents were collected along the middle Juruá River (Amazonas, Brazil), including two protected areas (Reserva de Desenvolvimento Sustentável Uacari and Reserva Extrativista do Médio Juruá) (● Sampled lakes, ▭ RDS Uacari and ⬚ RESEX Médio Juruá)

Data collection was authorized by the Sistema de Autorização e Informação em Biodiversidade (SISBIO – 62427-1), by the Departamento de Mudanças Climáticas e Gestão de Unidades de Conservação (DEMUC – 41/2018) of the Secretaria Estadual de Meio Ambiente do Amazonas (SEMA) and by the Ethics Committee of the Instituto Nacional de Pesquisas da Amazônia (INPA), permit numbers 040/2018 and 3.474.092.

2.2 | Data analysis

Data obtained from stomach contents and interviews were analysed separately and then compared, as they are complementary sources of information. An attempt was made to identify and classify the common names of fish cited in the interviews according to the scientific names from specific literature for the region's fauna (Santos *et al*., 2006; Silvano *et al*., 2001). As some stomachs were empty a generalized linear model was performed to determine if arapaima size or sex influenced the presence or absence of prey in stomach contents. The model formula was as follows: stomach (with or without prey) total length + sex, family = "binomial." Given that the presence or absence of stomach contents is a categorical variable, a binomial distribution was used in the model. Because differences in prey items associated with ontogeny were expected (Oliveira *et al*., 2004; Queiroz, 2000; Wu & Culver, 2011), arapaima TL (predictor variable) was regressed against prey trophic level and prey maximum length (response variables). Trophic level and maximum length of fish prey were recorded at the species level and obtained from Fishbase (www.fishbase.org). For shrimp, only the maximum length was obtained (Moraes-Riodades & Valenti, 2002). All analyses were performed using R 3.6.2 (R Core Team, 2019), and the package ggplot2 was used for drawing the figures (Wickham, 2016).

3 | RESULTS

3.1 | Stomach contents

A total of 113 stomachs were collected during the CBM harvesting activities in September 2018 (low-water period) and 5 stomachs in the falling-water period (June, 2019). The TL of sampled arapaima varied from 60 to 245 cm (Supporting Information Table S2). Thirty-one stomachs (26%) were empty, and all of these were from the low-water period. The mean TLs of arapaima with and without prey in stomachs were, respectively, 171 and 175 cm, and neither TL ($P = 0.69$) nor sex ($P = 0.40$ male and 0.76 female) influenced the presence or absence of prey in the stomachs. Overall, 41 stomachs (35%) had animal prey, but only in 35 could the prey be identified (Supporting Information - Table S2). The remaining 46 stomachs (39%) contained only plant material (pieces of leaves, branches and seeds) and/or fish-bone remains (Supporting Information Table S2). Plant material was found in 79 stomachs (Supporting Information Table S2).

Vertebrates were the most common prey (Supporting Information Table S3) and were represented only by fish from the orders Characiformes (47%), Siluriformes (30%), Osteoglossiformes (7%), Perciformes (3%) and Gymnotiformes (3%). Invertebrates were represented by the orders Decapoda (3%), Ephemeroptera (3%) and Hemiptera (3%) (Supporting Information Table S3). The smaller arapaima had higher proportions of invertebrates in their stomachs than adults, whose diets were composed almost entirely of fish (Figure 2). Invertebrates were found only in arapaima <160 cm TL (Supporting Information Table S2).

The most common prey type in the samples consisted of fish from the genus *Pimelodus* (six stomachs) (Supporting Information Table S2). In one case, a young arapaima individual weighing 650 g and measuring *ca*. 60 cm TL was found in the stomach of a large male (208 cm TL) captured in Santo Antônio Lake (5° 33′ 9.06″ S, 67° 33′ 33.43″ W). The size of the arapaima eaten indicates that it was at least 10 months old (Lima *et al*., 2017). A positive relationship between maximum length of ingested prey and arapaima TL was observed (prey maximum length = −20.66 + 0.40 × arapaima TL, $F_{1,16}$ = 6.85, r^2 = 0.30, P = 0.02; Figure 3a), but the cannibalistic event was excluded because the maximum length of the arapaima was much larger than that of the individual that consumed it. Some taxa such as *Macrobrachium amazonicum* were found in multiple small individuals, and others such as *Osteoglossum bicirrhosum* occurred only in the stomachs of large individuals. No relationship was found between prey trophic level and arapaima TL ($F_{1,12}$ < 0.01, r^2 < 0.01, P = 0.96; Figure 3b).

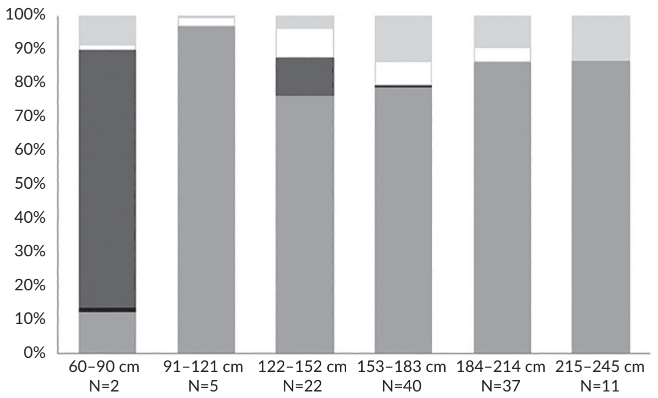

FIGURE 2 Proportional contribution by mass (g) of prey types present in arapaima stomach contents by arapaima size category (30 cm difference in each size category). Prey types include bone remains, fish, insects, plant materials and shrimp (▩Fish, ■ Insects, ■ Shrimp, □ Plant materials and □ Bone remains)

3.2 | Interviews

Sixteen fishers aged 21–64 from eight communities and actively involved in arapaima-fishing activities were interviewed (Supporting Information Table S4). These interviews produced a list of prey commonly found in arapaima stomachs, represented by 21 types of fishes (Figure 4), shrimps and crabs. Interviewed participants also mentioned the presence of mud and plant material, such as fruits and grass. For *ca*. 40% of those interviewed, "cascuda" (*Psectrogaster rutiloides*, *Psectrogaster amazonica*) is the preferred prey of arapaima, followed by "acará" (*Apistogramma* spp., *Heros appendiculatus*, *Mesonauta insignis* – 12.5%) and "mocinha" (*Potamorhina altamazonica* – 12.5%). Cascuda was also mentioned as being the species most commonly found in arapaima stomach contents (37.5%) (Supporting Information Table S4).

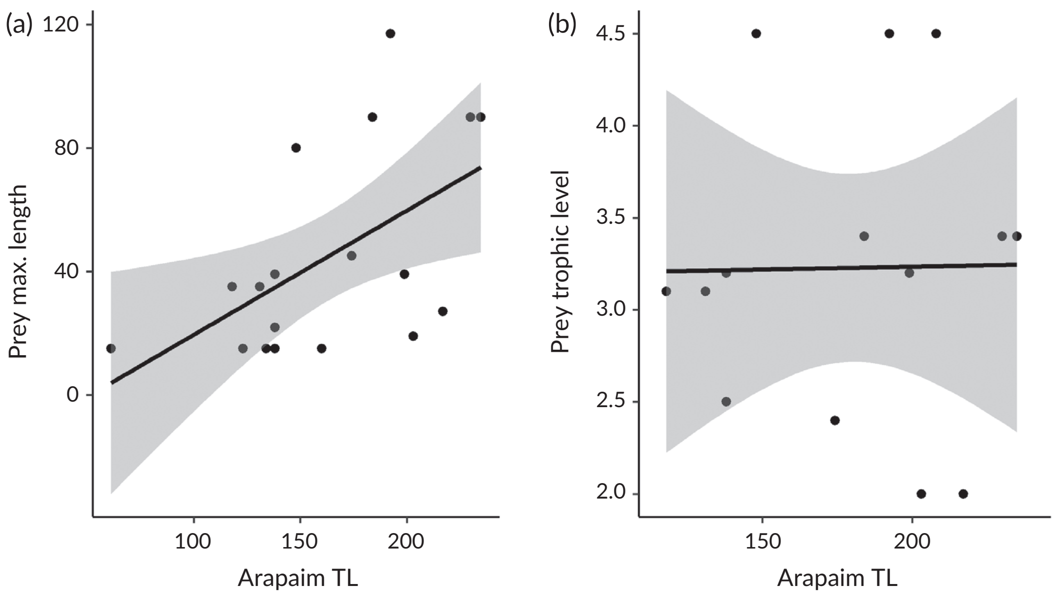

FIGURE 3 (a) Relationship between arapaima total length (TL) and maximum length of prey ingested and identified to species level. (b) Relationships between arapaima TL and fish prey trophic level identified to species level

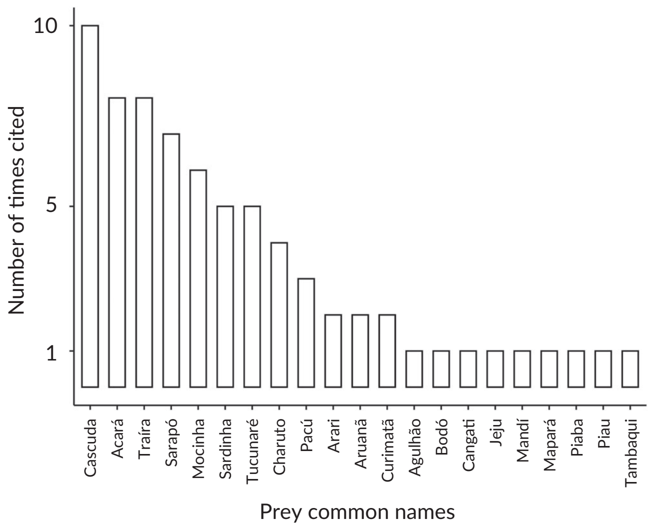

FIGURE 4 Popular names of fishes and number of times cited by interviewed fishers

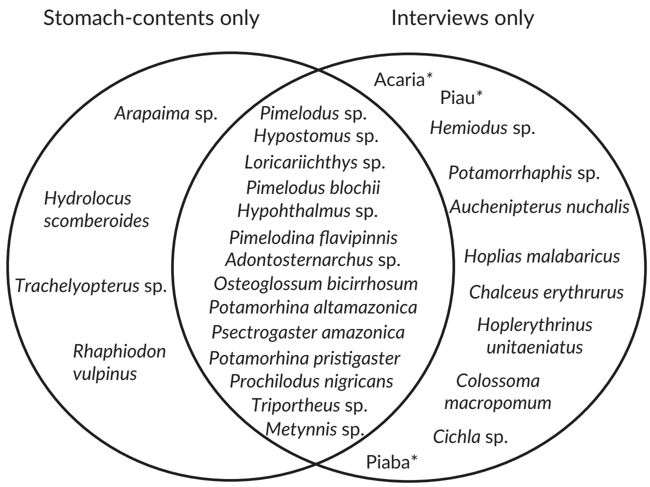

FIGURE 5 Venn diagram showing the number of genera or species in arapaima stomach contents but not in interviews (left), the number of species cited in the interviews but not observed in stomach contents (right) and the number of genera or species observed in both (centre). *Popular name that can be many species

According to all interviewees, there were no feeding differences between managed (protected or subsistence-use lakes) and unmanaged lakes (open-access lakes) (Supporting Information - Table S4). When asked about the differences in arapaima feeding between low- and high-water periods, 56% of those interviewed said that arapaima eat the same types of prey throughout the year. Some fishers said that arapaima eat more during the high-water period (12.5%) and that "traíra" (*Hoplias malabaricus*) is the prey most eaten in the high-water season (25%). "Cascuda" and "mocinha" were cited more often (25%) as the most consumed prey during the low-water period (Supporting Information Table S4). Fishers were also asked if young arapaima ate the same type of prey as adult arapaima. Most interviewed (81%) said that young and adult arapaima eat the same prey types. Nonetheless, some interviewees commented that younger individuals eat more shrimps and crickets and adults eat fish (Supporting Information Table S4). One of the interviewees said that the only difference among age classes is that adult arapaima can eat the prey of larger size than young individuals. When asked if adult arapaima eat smaller arapaima (cannibalism), 31% of those interviewed said "yes" and 25% said that they had seen it firsthand (Supporting Information Table S4).

The relative contribution from each source of information (stomach-content analyses and local knowledge) is illustrated in Figure 5, considering the popular names of fish cited by local stakeholders and the fish identified to genus or species level in arapaima stomach contents, totalling 29 types of fish ingested by arapaima.

4 | DISCUSSION

The different knowledge sources used in this study, understanding of local fishers and stomach-content analysis, provided complementary information about arapaima feeding. In general, there was agreement that young arapaima have a generalist feeding habit, eating fish and invertebrates, but adult arapaima had eaten fish almost exclusively in the samples, including the possibility of cannibalism. With increases in body length, arapaima are able to feed on prey of larger sizes but also continue to eat small prey, but this increase in prey size is not associated with an increase in prey trophic level. During the low-water season, many arapaima had empty stomachs or stomachs with just some small bone remains and plant material, suggesting that the species may undergo periods of fasting like other large predatory fishes (Arrington *et al*., 2002).

Comparisons between fish species found in stomach contents and those mentioned by interviewees are difficult in this species-rich ecosystem, especially because many popular names may represent more than one species. For example, "bodó" or "cascudo" is a popular name for different species of Siluriformes. Despite these challenges, it can be concluded that most fish species identified in stomach contents were also cited by interviewees, including "aruanã" (*O. bicirrhosum*), "bodó" (*Hypostomus* sp., *Loricariichthys* sp.), "cascuda" (*P. amazonica*), "curimatã" (*Prochilodus nigricans*), "mandí" (*Pimelodina flavipinnis*, *Pimelodus blochii*), "mapará" (*Hypophthalmus* sp.), "mocinha/branquinha" (*P. altamazonica*, *Potamorhina pristigaster*), "pacú" (*Metynnis* sp.), "sarapó" (*Adontosternarchus* sp.) and "sardinha" (*Triportheus* sp.). This list of 14 taxa in common was greater than the sum of species observed in only one information source, which suggests a general agreement between the two methods. On the contrary, species such as *Rhaphiodon vulpinus* and *Hydrolycus scomberoides*, both popularly known as "cachorra," were not mentioned by the interviewees but were identified in arapaima stomach contents. Other species not found in stomach contents were cited by interviewees, greatly contributing to the knowledge of arapaima feeding. These included "acará" (can be many species of cichlids: *Astronotus crassipinnis*, *Chaetobranchus semifasciatus*, *Heros efasciatus* and

Satanoperca jurupari), "agulhão" (*Potamorrhaphis* sp.), "arari" (*Chalceus erythrurus*), "cangati" (*Auchenipterus nuchalis*), "charuto" (*Hemiodus* sp.), "jeju" (*Hoplerythrinus unitaeniatus*), "piaba" (can be many species belonging to the Characidae), "piau" (can be many species belonging to the Anostomidae: *Leporinus* spp., *Schizodon fasciatus*, *Abramites hypselonotus*), "tambaqui" (*Colossoma macropomum*), "traíra" (*H. malabaricus*) and "tucunaré" (*Cichla* sp.).

The current study contrasts to some degree with that of Queiroz (2000) conducted in Mamirauá Reserve (Brazil), in which "tamoatá" (*Hoplosternum thoracatum*) was the most important fish in the arapaima diet in all seasons, except during the high-water period when "branquinha" (*Potamorhina* sp.) was most consumed. Tamoatá was not found in stomach contents or mentioned in interviews, even though it is known to occur in the Juruá River. Instead, Curimatidae and Pimelodidae were the most common fish families in arapaima stomachs in the Juruá River. These families are mainly known in the region by common names, such as cascuda, branquinha or mocinha and mandí, and are abundant in shoals in lakes and lentic waters (Santos *et al*., 2006). These most common species are of low and intermediate trophic levels (*e.g*., *P. altamazonica*, *P. pristigaster*, *P. amazonica*, *P. blochi*, *P. flavipinnis* – respective trophic levels according to Fishbase: 2, 2.5, 2, 3.1 and 3.2), as are many of the individuals identified only to family or genera, such as Loricariidae that is composed mainly of detritivorous and herbivorous species.

The size of the arapaima appeared to influence the prey type ingested. Prey size eaten often increases with predator size (Mittelbach & Persson, 1998; Scharf *et al*., 2000), which implies higher trophic positions, but this is not expected in diverse tropical food webs (Layman *et al*., 2005) such as the Juruá River. The capacity to ingest larger prey increases as arapaima grow, but large individuals may still ingest small prey as well (Queiroz, 2000). Nonetheless, invertebrate prey were found only in smaller arapaima, and in general, the largest prey species, such as *H. scomberoides* (maximum length 117 cm – Fishbase), *Hypophthalmus* sp. (maximum length 57.5 cm – Fishbase) and *O. bicirrhosum* (maximum length 90 cm – Fishbase), were ingested only by larger arapaima. These species, although large bodied, show a large variation in trophic level based on information in Fishbase (4.5, 2.9 and 3.4, respectively). Despite the fact that mean prey size increased with arapaima ontogeny, there was no evidence of an increase in prey trophic level.

Lima and Batista (2012) conducted interviews with local arapaima fishers in the Mamirauá Reserve and, similar to the interviews in the current study, fishers said that arapaima had a diversified diet, with fish and shrimp as the principal prey. They did not mention the presence of other types of invertebrate prey, such as Ephemeroptera and Belostomatidae. This reason may be that these organisms are generally very small and difficult to identify in stomachs or that these invertebrates were found only in arapaima smaller than 160 cm and arapaima fishing during the CBM is allowed only for individuals >150 cm. This is also the reason for the small number of samples of younger arapaima in the data set.

Diet comparisons were not made between low- and falling-water periods because of the small number of arapaima sampled during the latter period. Nonetheless, according to the interviewees, there are few changes in prey types ingested during the high- and low-water seasons, but the food supply decreases during the dry season. During the low-water season, many fish species show marked decreases in feeding activity (Junk, 1985), and a large number of stomachs without prey were also observed in the low-water period that was not related to arapaima sex or TL. In contrast, all five fish sampled at falling-water periods had fish in their stomachs.

During the low-water season, empty stomachs or stomachs with only plant material (seeds, branches or leaves) were also common in floodplain lakes in the Purús River (Carvalho *et al*., 2018). Little or no connectivity between floodplains and the main river during the dry season can cause a reduction in prey availability. Also, it was observed that some arapaima regurgitated prey when they were captured (Jacobi *et al*. 2020, in review); nonetheless, it was not possible to quantify the frequency of this occurrence. It is still not clear why arapaima ingest plant material. Queiroz (2000) inferred that plant material found in arapaima stomachs was ingested accidentally during suction feeding on animal prey. Also, plant material has high cellulose content that can be slow to digest, so it can accumulate in the stomach.

In this study of 118 arapaima with stomach contents, only one incidence of cannibalism was observed. Although some interviewees said that they had seen one arapaima eating another, this is the only cannibalistic event scientifically documented for this species, highlighting the importance of local knowledge in affirming scientific observations and suggesting that cannibalism might be more common than previously thought. The overall incidence of these events in protected lakes where arapaima densities have been steadily increasing (Campos-Silva & Peres 2016) remains a subject worth studying.

In summary, an adult arapaima can best be classified as an opportunistic piscivore, which feeds on a wide range of fish species, being able to consume larger prey with the increase in body size. This generalist feeding behaviour suggests that management of particular prey species is not necessary in these lakes, but the maintenance of a diversity of prey including large-bodied species would be beneficial in sustaining a range of arapaima life stages. This information is important with regard to CBM of arapaima because there are some initiatives to manage other high-value fish species during the harvesting season, including tambaqui (*C. macropomum*) and pirapitinga (*Piaractus brachypomus*). Drawing on local knowledge, diet during the dry season may not be greatly different from that seen at other times of the year. Arapaima also has different predominant prey species in different areas, such as the lower Japurá River (Queiroz, 2000) and the middle Juruá River (this study). Therefore, diet studies need to be undertaken in each area of interest. The local fishers involved in the CBM programme of the middle Juruá River had consistent ethnobiological knowledge of arapaima feeding ecology. This experience could be used in future fisheries-management projects in the region and also, by expanding the inclusion of fishers' local knowledge, these knowledge holders will realize that their information is valued, motivating them to contribute to sustainable management practices.

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AUTHOR CONTRIBUTIONS

C.M.J. helped with planning, data collection, data analysis, and writing. F.V. helped with planning, data collection, writing and funding. J.V.C.-S. was involved in data analysis and writing. T.J. was involved in field assistance, data analysis and writing. W.E.M. helped with planning and writing the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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