

Trophic Ecology of *Arapaima* sp. in a ria lake–river–floodplain transition zone of the Amazon

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Abstract

Neotropical floodplains are usually productive systems that are maintained by the nutrient, detritus and sediment inputs provided by the main river channel flood pulse. Ria lakes represent a special feature and habitat in the Amazonian floodplains, being characterised by a dendritic morphology and dependence on terrestrial inputs provided by an intricate stream network. Our objective was to evaluate the trophic ecology of the arapaima (*Arapaima* sp.). We combined stomach content analysis with measurements of carbon and nitrogen stable isotope values from dorsal muscle to infer the ontogenetic changes in trophic level and isotopic niche width in floodplain and ria lakes. *Arapaima* diet was dominated by fish from low trophic positions. While most of the stomachs sampled in the study ria lake were full, empty stomachs predominated in samples taken in the floodplain lakes. These differences indicate that ria lakes may provide better feeding grounds for arapaima during the dry season, presumably because ria lakes are interconnected with a large stream network and the main river channel year round. Nitrogen stable isotope results further indicated an ontogenetic dietary shift in arapaima, with piscivory increasing as a function of length in both environments. Carbon stable isotope analysis indicated that energy sources used by arapaima varied by environment, with arapaima using a greater diversity of food sources in ria lakes than in floodplain lakes. Information about the main carbon sources is useful for fishery management because stakeholders may choose to conserve key vegetal groups to ensure the productivity and diversity of aquatic ecosystems.

KEYWORDS

fisheries management, osteoglossidae, stable isotopes, threatened species, tropical fishes

1 | INTRODUCTION

The predictable and seasonal rise and drawdown of river waters in the Amazon basin, termed the flood pulse, create riparian areas that alternate between terrestrial and aquatic phases (i.e. floodplain). During the flooding, nutrients from the main river channel and the recently inundated “terrestrial” zone become available for aquatic primary producers, thereby increasing ecosystem productivity (Bayley, 1995; Jepsen & Winemiller, 2002; Junk, Piedade, Wittmann, Schöngart, &

Parolin, 2010). A variety of terrestrial and aquatic plants are adapted to these dynamic conditions, contributing to the observed high turnover rates (Junk, Bayley, & Sparks, 1989; Martinelli, Devol, Victoria, & Richey, 1991). Most of the primary production in such systems is provided by C₄ aquatic grasses, although phytoplankton, periphyton and forest trees are also important (Martinelli et al., 1991). However, C₄ plants provide only 2%–17% of the carbon that is consumed in Amazonian food webs (Forsberg, Araujo-Lima, Martinelli, Victoria, & Bonassi, 1993). The contrast of high primary production and low

consumption by fishes points to highly selective feeding behaviour by the herbivorous and detritivorous fishes that predominantly consume phytoplankton, fruits and parts of inundated forest trees in preference to C_4 macrophytes (Araújo-Lima, Forsberg, Victoria, & Martinelli, 1986; Benedito-Cecílio, Araujo-lima, Forsberg, Bittencourt, & Martinelli, 2000; Forsberg et al., 1993).

To date, most of the Amazonian trophic ecology literature has focused on these river–floodplain habitats (Araújo-Lima et al., 1986; Bayley, 1995; Benedito-Cecílio et al., 2000; Forsberg et al., 1993; Junk et al., 1989; Martinelli et al., 1991). In contrast, the trophic ecology of Amazonian ria lakes' habitats has not been adequately studied even though they exhibit high fishery yields and serve as critical nursery and/or feeding habitats for many fishes (Nolan, Fabr e, & Batista, 2009). Ria lakes were formed by eustatic changes. They are the drowned mouths of tributaries surrounded by upland environments and only receive waters from the main river channel during the wet season (Henderson & Crampton, 1997). The dendritic morphology of ria lakes increases the perimeter of the terrestrial–aquatic interface, increasing the potential for allochthonous inputs to the water (e.g. terrestrial material; Henderson & Crampton, 1997; Irion, Junk, & Mello, 1997; Nolan et al., 2009). The nutrient-poor catchment of ria lakes typically yields waters with high oxygen levels in comparison with floodplain lakes (Henderson & Crampton, 1997). Ria lakes are also usually deeper than floodplain lakes and can provide appropriate refuge for fish during extreme droughts (Arantes, Castello, Cetra, & Schilling, 2013). Some ria lake areas may be more distant from the main river channel than floodplain lakes, making them harder to access for fishing (Araújo-Lima, Agostinho, & Fabr e, 1995). As a result, ria lakes provide fishes with important refugia for reproduction and feeding (Araújo-Lima et al., 1995). Although biodiversity in ria lakes is lower than that in floodplain lakes owing to the relative lack of detritivorous fishes, ria lakes may contain large fish populations and biomass due to their higher stability over the seasonal cycle (Henderson & Crampton, 1997).

As a direct consequence of the abundance of vegetable/plant and detrital matter inputs to tropical freshwater ecosystems, most tropical freshwater food webs are dominated by species with low positions in the food chain, such as detritivorous and omnivorous fish (Araújo-Lima et al., 1986; Bayley, 1973; Forsberg et al., 1993; Jepsen & Winemiller, 2002; Winemiller, 1995). While omnivory is believed to be an important adaptation for fishes to deal with seasonal variability in food composition (Winemiller, 1995), trophic position may vary with ontogenetic shifts in feeding behaviour and diet (Werner & Gilliam, 1984). Ontogenetic dietary changes arise from improvements in the visual acuity, swimming performance and gape size of fish and from the use of different habitats across the life cycle (Beamish, 1978; Karpouzi & Stergiou, 2003; Werner & Gilliam, 1984). As a result, an increase in body size is usually accompanied by an increase in the range of prey sizes and types consumed (Scharf, Juanes, & Rountree, 2000; Wilson, 1975).

A fish that uses both ria lake and floodplain environments is the arapaima (*Arapaima sp.1*). Arapaima is a large, fast-growing fish that reaches up to 3 m total length (TL) and 200 kg and is one of the most heavily exploited in the Amazon (Arantes, Castello, Stewart, Cetra, &

Queiroz, 2010; Queiroz, 2000). In the Central Amazon, arapaima may grow to 50 cm TL in 3 months (Castello, 2008) and 88 cm in a year (Arantes et al., 2010). Arapaima are threatened by overfishing, habitat degradation and bycatch (Castello, Arantes, McGrath, Stewart, & Sousa, 2015; Castello & Stewart, 2010) and have been listed by the International Union for Conservation of Nature (IUCN) on the Red List of Threatened Species and in Appendix II of the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora. Because of their large size and fast growth, arapaima may play an important role in regulating energy flows in Amazonian food webs. Initial feeding studies used captive specimens, which do not accurately inform about natural diets and feeding behaviour (Fontenele, 1948; Menezes, 1951; S anchez, 1961). Subsequent field-based stomach content studies have classified arapaima from the Solim oes River as a "carnivore specialist," noting that piscivorous fish constituted only a minor fraction of the diet and that plants were only ingested accidentally (Queiroz, 2000). However, combined stomach content and stable isotope analyses from the Essequibo basin, Guyana, have suggested that arapaima are secondary consumers, with an omnivorous diet (Watson, Stewart, & Teece, 2013). Although different in terms of ecological productivity, both studies worked with specimens sampled from river–floodplain systems. Given the apparent variation in feeding habits among populations, further research is required to characterise arapaima feeding in a broader range of habitats, including ria lakes.

Here, we evaluate the trophic ecology of arapaima sampled from two different habitats: floodplains and ria lakes. We combined stomach content analysis with measurements of carbon and nitrogen stable isotopes obtained from dorsal muscle samples to compare the feeding ecology of arapaima between the different environments. Specifically, we test the following hypotheses: (i) the trophic position of arapaima as measured by $\delta^{15}N$ varies similarly with ontogeny in both habitats and (ii) arapaima inhabiting ria lakes will have larger isotopic niche due to the greater diversity of carbon sources available in ria lakes. The first hypothesis is based on the commonly observed ontogenetic change in feeding behaviour in many freshwater and marine fishes, where the range of prey sizes eaten expands with increasing predator body size (Scharf et al., 2000) and there is an associated increase in trophic level with body size (Jennings, Pinnegar, Polunin, & Warr, 2002). The second hypothesis is based on the larger terrestrial–aquatic perimeter in ria lakes and known relationships between differences in lake morphology and sediment particle influx (Weyhenmeyer & Bloesch, 2001), which suggests an increased likelihood of allochthonous material inputs from the environment to dendritic lakes.

2 | MATERIAL AND METHODS

2.1 | Study area

The study was conducted at the Piaga u-Purus Reserve, which is located in the lower Purus River, Central Amazon, 223 km southwest from the city of Manaus in the state of Amazonas, Brazil (Figure 1). About 45% of the reserve is located in floodplain environments, which include the main river channel, connecting channels, floodplain lakes

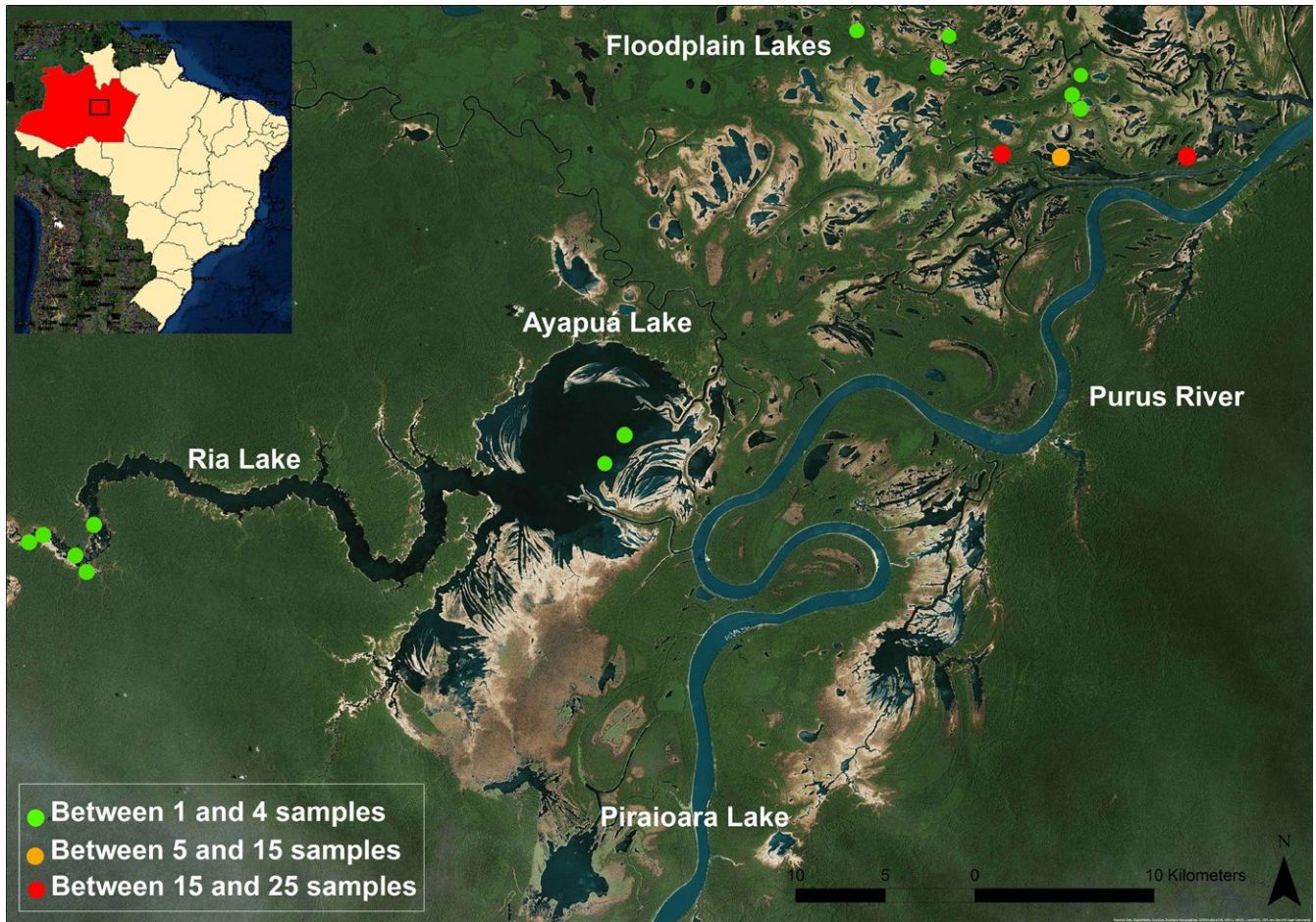


FIGURE 1 Satellite image of the northern area of the reserve during the dry season, depicting the ria and floodplain lakes of the lower Purus River. Inset map in the upper left highlights in red the Amazonas state. Dots denote arapaima sampling locations and intensity, with green dots representing between one and four samples, orange dots representing between five and 15 samples and red dots representing between 15 and 25 samples collected at a given location

and the flooded forest. The Purus River has high nutrient and suspended sediment concentrations (Junk, Soares, & Carvalho, 1983), is highly productive and is the main source of fishes found in the markets of Manaus (Batista & Petrere, 2003). Within the Purus River basin, floodplain lakes usually occur in a horseshoe shape (Figure 1; Nolan et al., 2009). The lakes vary in pH (5.0–7.2), conductivity (9–45 μ S/cm), transparency and water colour and remain isolated from other water bodies during the dry season.

At the edge of the floodplain, ria lakes are embedded in upland environments with well-developed riparian vegetation (Antunes et al., 2011). Ria lakes stay interconnected with the Purus River tributaries and main river channel all year round and are usually cooler (26.5 vs 30.5°C in this study) than floodplain lakes (Gourou, 1950; Irion et al., 1997). During the wet season, the study ria lake is connected to Ayapuá Lake which connects to a floodplain system to the south (Figure 1).

2.2 | Sampling

Data for trophic ecology studies are traditionally generated from stomach content analysis, which can provide high-resolution temporal

information about the food items consumed (Almeida, 1984; Santos, 1981; Soares, 1979). Such studies provide only a “snapshot” of the most recent feeding activity (hours to days) of the organism (Pinnegar & Polunin, 1999) and can underestimate the relative importance of soft-bodied prey items that digest easily (McCarthy, Fraser, Waldron, & Adams, 2004). Thus, without continuous sampling over long periods, stomach content techniques do not provide accurate information about diet variation and individual specialisation, especially for species with seasonally variable diets (Peterson & Fry, 1987). A complementary method, with an established history of use in ecological studies, is stable isotope analysis (e.g. Fry, 2006), which is able to characterise temporally assimilated diets (Kling, Fry, & O'Brien, 1992). In particular, nitrogen isotopes ($\delta^{15}\text{N}$) and carbon isotopes ($\delta^{13}\text{C}$) can be used to characterise trophic position variation and ontogenetic dietary shifts (Fry, 2006).

For this study, arapaima were sampled in November 2013 (end of dry season) in the Ayapuá, Itapuru and Caua/Cuiana lake systems of the Piagaçu-Purus Reserve. Adults were collected in eleven floodplain lakes (Itapuru and Caua/Cuiana) during the arapaima fishery that occurs when the lakes are isolated from the connecting and main river

channels. Supplementary samples from the floodplain were collected during the monitoring of other fishery activities in the connecting channels, where arapaima juveniles were occasionally caught as by-catch. Fish from the study ria lake were collected at a distance of approximately 50 km from the floodplain lakes. All individuals were measured to the nearest centimetre from the tip of the lower jaw to the tip of the caudal fin (total length or TL). For analysis, individuals were separated into three size classes: juveniles (<1 m TL); subadults (1–1.5 m TL) and adults (>1.5 m TL). The last division was determined using the minimum size of capture of 1.5 m, which roughly corresponds to the literature-established length at first maturation (1.57 m; Arantes et al., 2010).

A total of 68 arapaima stomachs were collected and analysed: 13 from fish captured in the study ria lake (two subadults and 11 adults) and 55 from fish captured in floodplain lakes (nine juveniles, seven subadults and 39 adults). To classify the level of recent feeding activity, stomachs were categorised on the basis of fullness as empty, almost empty (only partial food remains), half full or completely full. Prey items were identified to the lowest possible taxonomic level and classified according to trophic guilds described in the literature (Dos Santos, Ferreira, & Zuanon, 2006). Detritivorous fishes feed mainly on organic material attached to soft or consolidated substrates. Omnivorous/invertivorous fishes include those with significant amounts of plant and animal content in their stomachs and/or individuals that specialise in consuming invertebrates. Piscivorous fish feed exclusively on other fish, tearing pieces of flesh from prey or swallowing whole fish.

Samples from arapaima dorsal muscle tissue and minimally digested fish found in the foregut were rinsed and dried at 50°C for stable isotope analysis. Stomach contents have been suggested as a useful source of prey isotope signatures in trophic studies (Grey, Thackeray, Jones, & Shine, 2002; Tieszen, Boutton, Tesdahl, & Slade, 1983). Although biases may occur due to the faster digestion of small prey, provided prey are obtained from the foregut, minimally digested and suitably rinsed before analysis, they may be reliably used for stable isotope studies (Guelinckx, Dehairs, & Ollevier, 2008). Dorsal muscle samples for stable isotope analysis were obtained from 60 of 68 arapaima sampled for stomach contents. Tissue samples of eight arapaima from the floodplain lakes could not be obtained, and floodplain lake stable isotope samples were supplemented with ten muscle samples collected opportunistically from arapaima captured at other sites throughout the floodplain lakes and connecting channels.

2.3 | Laboratory analysis

Stable isotope analyses (SIA) were completed at the Environmental Isotope Laboratory, University of Waterloo, using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyser (CHNS-O EA1108, Carlo Erba, Milan, Italy). Analytical precision was $\pm 0.1\%$ and $\pm 0.2\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively and was determined by repeated analysis of duplicates (one in ten). All resulting measurements were taken using standard delta (δ) notation as parts per thousand differences (‰) with respect to the international

reference standards, carbonate rock from the Peedee Belemnite formation for $\delta^{13}\text{C}$ (Craig, 1957) and nitrogen gas in the atmosphere for $\delta^{15}\text{N}$ (Mariotti, 1983). Analytical accuracy was validated against internal laboratory standards cross-calibrated against the International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen.

2.4 | Data analysis

All statistical analyses were carried out using the software R (R Core Team 2014). Statistical significance in all testing was set at $\alpha = 0.05$. Fisher's exact test was used to evaluate differences in the recent feeding status of arapaima (empty or almost empty stomachs vs. half full or full stomachs) between environments (e.g. Zar, 2010). To test the ontogenetic dietary shift hypothesis in arapaima, we used linear regression to estimate the significance of correlations between nitrogen stable isotope and total length measures, with environment-specific relationships compared by means of an ANCOVA (Zar, 2010).

The package Stable Isotope Analysis in R (SIAR, Parnell, Inger, Bearhop, & Jackson, 2008; Jackson, Inger, Parnell, & Bearhop, 2011) was used to evaluate isotopic niche width hypothesis (measured as the standard ellipse area in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space) for adult arapaima only as the number of juveniles sampled in the study ria lake was too low to obtain statistically valid estimates (e.g. Jackson et al., 2011). The standard ellipse area encompasses 40% of the isotope data points and represents approximately 1 standard deviation of the data (Batschelet, 1981). Here, we presented standard ellipse area values adjusted for small sample sizes (<30) to obtain a measure which corrects for possible underestimation of the ellipse area as a result of small sample sizes (Jackson et al., 2011). For analytical purposes, isotopic enrichment from prey to predator was assumed to equate with values routinely used in the literature (e.g. Post, 2002). Thus, enrichment for $\delta^{15}\text{N} = 3.4\%$ (one standard deviation = 1%) and for $\delta^{13}\text{C} = 0.4\%$ (one standard deviation = 1.3%). The same analytical package was used for isotopic biplots to compare the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of juvenile and adult arapaima, and prey items. For each group, the range represents two standard deviations of the mean value.

3 | RESULTS

Fish found in arapaima stomachs were mostly omnivorous/invertivorous (46%) and detritivorous (41%, Table 1). The occurrence of piscivorous prey in arapaima stomachs was low (13%). From a total of 15 fish genera identified in the stomachs, seven occurred exclusively in samples from the study ria lake habitat, five occurred exclusively in samples from the floodplain lakes and only three occurred in samples from both types of lake. Although many stomachs contained traces of plant material (seeds, branches or leaves), only one arapaima contained a sufficient amount of leaves and branches (e.g. dry weight > 0.3 mg) for stable isotope analysis.

Recent feeding activity varied according to lake type (Fisher's exact $p < .001$), with adults from the study ria lake being more likely to have fed recently (20% empty stomachs) than adults from floodplain

TABLE 1 Prey items identified in the stomachs of arapaima sampled in ria and floodplain lake habitats of the Piagaçu-Purus Reserve. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ average values for prey are given when N (number) > 1

Habitat/Species	N (Prey)	$\delta^{13}\text{C}$ (Prey)	$\delta^{15}\text{N}$ (Prey)	N (Arapaima sp.)	$\delta^{13}\text{C}$ (Arapaima sp.)	$\delta^{15}\text{N}$ (Arapaima sp.)	Trophic Group (Prey)
Ria Lake							
Subadults:							
Hydrolycus spp.	1	-36.54	7.66	1	-31.66	9.79	P
Adults:							
Anodus elongatus	2	-34.70	9.30	1	-33.69	9.51	I
Characidae	1	-34.64	9.02	1	-33.69	9.51	O
Cichlasoma amazonarum	2	-33.78	11.34	2	-31.69	10.30	O
Hydrolycus spp.	2	-36.67	7.91	1	-31.70	9.97	P
Pimelodus spp.	2	-33.68	9.61	2	-31.01	10.22	O
Pterodoras granulosus	3	-29.81	10.11	2	-31.19	9.86	O
Semaprochilodus spp.	1	-35.45	11.19	1	-30.89	9.90	D
Tetragonopterus spp.	1	-28.09	9.00	1	-30.93	9.81	I
Hoplias spp.	2	-33.05	11.30	2	-31.23	9.86	P
Floodplain Lakes							
Juveniles:							
Boulengerella spp.	1	-34.50	10.84	1	-34.03	8.82	P
Cichlasoma amazonarum	1	-36.52	7.13	1	-33.47	8.85	O
Leoporinus spp.	1	-30.54	8.81	1	-34.63	9.21	O
Hoplosternum littorale	3	-35.63	7.30	3	-33.75	8.98	O
Triportheus spp.	2	-37.13	7.00	2	-33.75	8.95	O
Subadults:							
Pterygoplichthys spp.	1	-33.38	7.29	1	-31.72	9.51	O
Plant Material	1	-31.33	4.33	1	-32.69	9.76	
Adults:							
Acestrorhynchus spp.	1	-33.61	11.43	1	-32.48	10.02	P
Pimelodus spp.	1	-32.60	10.92	1	-33.09	10.12	O
Pterodoras granulosus	1	-34.00	8.86	2	-32.48	10.02	O
Pterygoplichthys spp.	1	-32.33	9.63	1	-31.69	11.10	O
Triportheus spp.	3	-32.55	10.19	2	-32.41	10.66	O
Hoplosternum littorale	1	-35.16	7.32	1	-32.60	9.89	O

Arapaima $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ average values are given every case that more than one arapaima consumed a respective prey species. Trophic guilds were defined as I, invertivorous; P, piscivorous; O, omnivorous; D, detritivorous following Dos Santos et al. (2006).

lakes (80% empty stomachs). No difference was found in the recent feeding activity of subadults (Fisher's exact $p = .222$).

The variability in nitrogen isotope signature for juveniles (8.82‰–9.20‰) was smaller than that for subadults (8.51‰–10.64‰) and adults (9.30‰–11.30‰). Length (TL) and $\delta^{15}\text{N}$ were positively related (Figure 2) for both environments, indicating ontogenetic shifts in the trophic position of arapaima in the study ria lake ($r^2 = .368$, $p < .050$) and floodplain lakes ($r^2 = .612$, $p < .010$). Slopes and intercepts from both regressions did not differ significantly (ANCOVA: slope $p = .687$, intercept $p = .158$), indicating that the rate at which the ontogenetic dietary shift occurred was similar for both environments. Length (TL) and $\delta^{13}\text{C}$ (Figure 3) were positively related in river–floodplain systems ($r^2 = .380$, $p < .010$), but not in the study ria lake ($r^2 = .023$, $p = .652$).

The values for standard ellipse areas adjusted for small sample sizes were virtually identical for study ria lake (0.99‰²) and floodplain (1.00‰²) individuals, with the Bayesian approach used in SIAR indicating an overlap of 46% between the ellipse areas—the range in the $\delta^{13}\text{C}$ axis was higher for the study ria lake ellipse (3.37 vs 2.57‰) and significantly different between environments ($F_{34,10} = 3.509$, $p = .007$), whereas the variation in the $\delta^{15}\text{N}$ axis was greater for the floodplain ellipse (1.12 vs 1.99‰) but not significantly different ($F_{34,10} = 2.584$, $p = .130$) between environments.(Figure 4)

Comparison of the nitrogen stable isotope signatures of arapaima prey showed significant differences in the trophic position of prey consumed by juveniles and adults (t test: $p < .001$) with the mean $\delta^{15}\text{N}$ value for adult prey items being 2.4‰ higher than that for juvenile

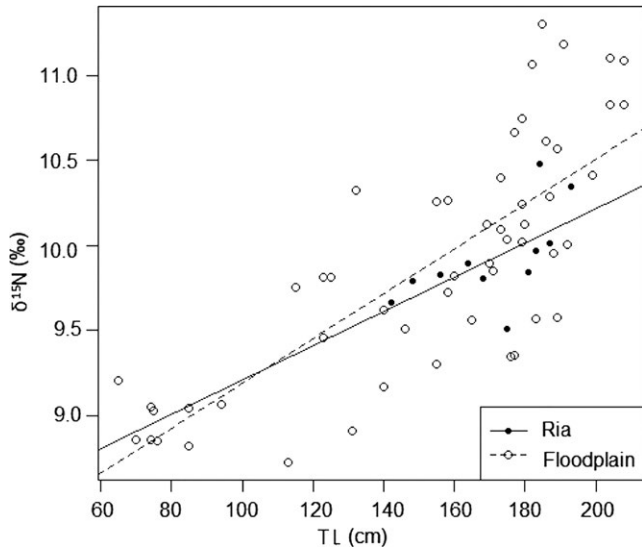


FIGURE 2 Nitrogen stable isotope ($\delta^{15}\text{N}$, ‰) and size (TL, cm) linear regressions for arapaima sampled in ria lakes and river-floodplain systems

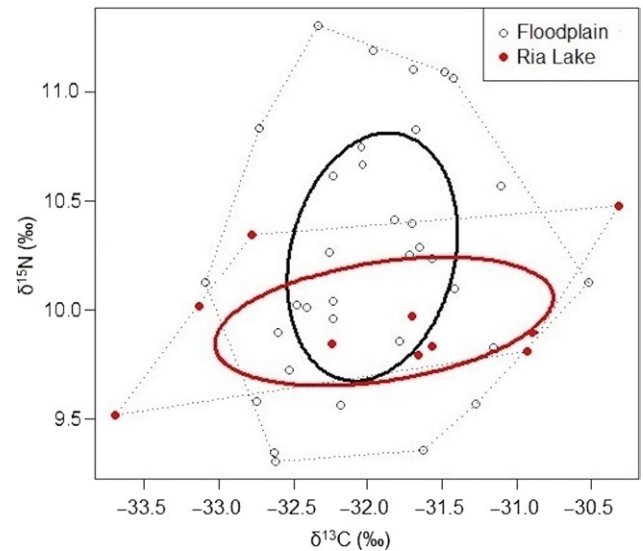


FIGURE 4 Standard ellipse areas estimated from the carbon and nitrogen stable isotopes (‰) for adult arapaima collected in floodplain (black) and ria lakes (red)

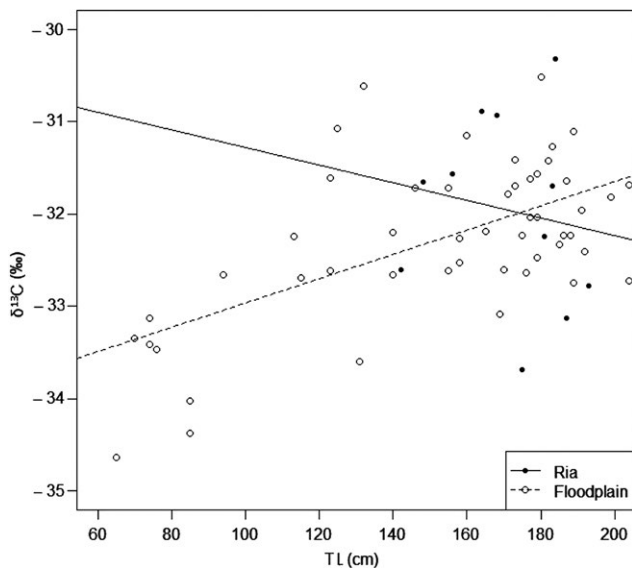


FIGURE 3 Carbon stable isotope ($\delta^{13}\text{C}$, ‰) and size (TL, cm) linear regressions for arapaima sampled in ria lakes and river-floodplain systems

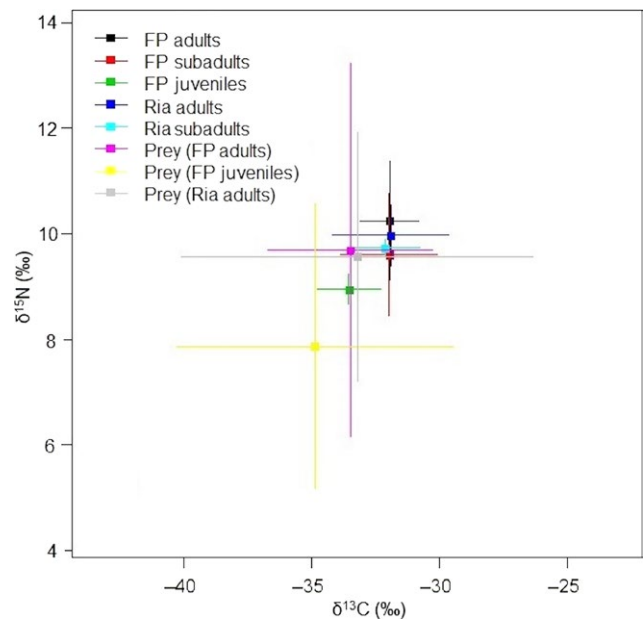


FIGURE 5 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) biplot of arapaima and prey items by size (juveniles, subadults and adults) sampled

prey items. The carbon isotope signature of prey found in juvenile samples was similarly lower than that in adult arapaima prey (t test: $p < .030$), with mean separation between prey groups equal to 1.9‰. The ranges for both carbon and nitrogen isotopes were larger for the prey items than for arapaima (Figure 5).

4 | DISCUSSION

Analysis of arapaima stomach contents and dorsal muscle samples using stable isotope analysis corroborated the ontogenetic dietary

shift hypothesis, with arapaima from both ria lake and floodplain lake study sites evidencing an increase in $\delta^{15}\text{N}$ as a function of length. The rate at which the ontogenetic shift occurred was similar in both studied habitats. Data on prey items ingested by arapaima, however, confirmed some differences in the diversity of food resources found in the two habitats, with arapaima consuming a broader and greater diversity of food sources in the study ria lake than in floodplain lakes. Ria lake connectivity appears to increase food availability in this environment—at least at the end of the dry season—as reflected in a lower incidence of empty stomachs among fish captured in that environment.

Despite the relatively low sample size in our study, there were significant differences between the size (age) classes studied, with adult arapaima utilising a broader range of prey resources than juveniles (Figures 2 and 3). These findings contrast with previous research that has indicated that among immature arapaima the diversity of food decreased with size (Queiroz, 2000) and that smaller juveniles displayed the greatest trophic plasticity (De Oliveira, Poletto, & Venere, 2005). Our results indicated that juvenile arapaima feed mainly on prey from lower trophic levels, while adults are able to feed across the entire trophic spectrum. As shown in the biplot of isotope values (Figure 5), our results also point to limited overlap between the trophic position of the smallest and largest arapaima size classes, suggestive of some form of feeding niche segregation. Ontogenetic variation in type and size of prey items is usually a reflection of the predator gape and body size, improvement in swimming performance, digestive capacity and visual acuity, in addition to variation in the feeding grounds used by juvenile and adult individuals (Hart, 1997; Karpouzi & Stergiou, 2003). The increased variability in the use of prey resources with size has been observed for several other marine and freshwater fishes (Karpouzi & Stergiou, 2003; Lukoschek & McCormick, 2001; Mittelbach, Osenberg, & Leibold, 1988; Winemiller, 1989). While some have noted that ontogenetic changes in relative prey sizes eaten can be statistically undetectable because of subtle changes in predator foraging abilities (Scharf et al., 2000) that do not appear to be the case with arapaima where larger size confers clear forage and resource acquisition advantages.

While earlier studies have classified arapaima as carnivorous (Fontenele, 1948; Menezes, 1951; Queiroz, 2000), Watson et al. (2013) noted that arapaima in Guyana were omnivorous, leading the authors to classify the genus as a secondary consumer. The demonstrated change in $\delta^{15}\text{N}$ during ontogeny, however, suggests that arapaima shift from secondary towards tertiary consumers as they grow, at least over the course of the dry season period for which we had data. As omnivorous species dominate tropical aquatic food webs and quaternary consumers are rare (Winemiller 1991; Cohen, 1994), adult arapaima should be considered as being relatively high in the food webs within which they operate. Indeed, as adults, arapaima may be apex predators and have significant structuring effects on lake food webs in the Central Amazon. Moreover, as arapaima from differing habitats were observed to feed with relatively low niche overlap as evidenced by the low standardised ellipse area overlaps, they have apparent high dietary flexibility.

Stomach content data from this study did support previous findings that piscivorous species constitute only a minor fraction of arapaima diets (Queiroz, 2000; Watson et al., 2013). Detritivorous and omnivorous organisms occurred in higher frequency in stomach samples, indicating that arapaima feed mainly on species with a low position in the food web. Although it is also known that juvenile arapaima may feed abundantly on crustaceans, molluscs and insects (Queiroz, 2000), the absence of such groups in our stomach content data may result from the restriction of sampling to the dry season. The contribution of crustaceans and insects to arapaima diet occurs mainly during rising water levels and peak flood periods (Mérona & Rankin-de-Mérona, 2004; Queiroz, 2000). As the water advances to the riparian areas, prey fish density is reduced, as are the prey-predator encounter rates

(Winemiller & Jepsen, 1998). As a consequence, arapaima may be less selective during high-water flood periods.

The occurrence of seasonal variation in the intensity of arapaima feeding remains a subject of debate: Queiroz (2000) indicated that arapaima feed mainly during the dry and rising water periods. During the drought, many isolated lakes become hypoxic, resulting in high fish mortalities (Castello, 2008; Junk et al., 1983; Welcomme, 1979). Arapaima, however, thrive and feed actively in these environments because of their adaptation for aerial respiration (Castello, 2008; Lowe-McConnell, 1987). Junk (1985b) showed that arapaima lipid content showed very low seasonal variation. Similarly, Castello (2008) indicated that the main prey families that comprise arapaima diet inhabit the floodplains year round and are constantly available as food sources. Our results suggest that during the drought, some floodplain lakes may be a poor feeding ground for arapaima compared to ria lakes. After an approximate period of 2 months, during which floodplain lakes remain isolated from the connecting and main river channels, 75% of the adults inhabiting floodplain lakes were found to have empty stomachs. In contrast, feeding activity in the study ria lake was intense during the same season as evidenced by the prevalence of full stomachs found during sampling. Although the warmer waters of floodplain lakes could increase digestion rates and thereby affect the frequency of empty stomachs, a 4°C difference between habitat types is unlikely to account for the notable between-habitat differences in empty stomachs observed here. The connectivity of ria lake environments to tributary stream networks and the main river channels may provide a better explanation of higher prey availability in ria lakes at the end of the dry season (Freitas, Siqueira-Souza, Florentino, & Hurd, 2013; Nolan et al., 2009). For example, Arantes et al. (2013) found that floodplain lakes with more connectivity have a higher arapaima density than lakes with low connectivity, suggesting a greater availability of food resources in the better-connected lake habitats. Therefore, the ria lake may provide better conditions as an appropriate refuge for fish during extreme drought events for both prey and predators. The dendritic morphology of ria lake environments and the large terrestrial-aquatic interface perimeter may result in increased nutrient inputs and enhancement of lake productivity (Nolan et al., 2009). Although predation and predator-prey encounter rates are affected by water transparency (Turesson & Brönmark, 2007), one of the studied floodplain lake with a transparency that exceeded the study ria lake (150 cm vs. 80 cm) only yielded adult arapaima with empty stomachs. While we interpret the data to indicate higher productivity and prey availability in the study ria lake, it remains possible that the chosen floodplain lakes had abnormally low prey availability, particularly at the end of the dry season when prey resources would be expected to be depleted.

In the present study, we were not able to assign characteristic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to primary producers, which limited our ability to estimate arapaima trophic position relative to the base of the food web and to determine which were the most important primary producers in the aquatic food web for arapaima. Previous studies in similar floodplain environments assigned average values of -12‰ for C_4 aquatic macrophytes and -27‰ and -33‰ for forest trees and phytoplankton respectively (Benedito-Cecílio et al., 2000; Forsberg et al., 1993;

Martinelli et al., 1991). Therefore, the mean values of $\delta^{13}\text{C}$ for arapaima juveniles (-33.6‰) and adults (-31.9‰) point to C_3 primary producers as contributing more significantly to arapaima carbon sources—at least during the low-water period (Araújo-Lima et al., 1986; Forsberg et al., 1993; Junk, 1985a; Martinelli et al., 1991;). The dynamics of seasonal patterns of carbon reliance may be altered by seasonal variations in floodplain and ria lakes. Particularly during the flooding and wet periods, lake systems are provided with nutrients, detritus and sediment inputs that significantly increase productivity (Winemiller et al., 2014). The greater connectivity of Amazonian habitats during the wet season supports greater diversity of carbon sources that will potentially be reflected in the isotopic signatures of species throughout the food web. Therefore, it is also expected an increase in the isotopic niche width of consumers during the wet season.

Trophic ecology has important implications for the sustainable management of arapaima and other species in conservation units in the Amazon basin, especially when one considers current deforestation trends in Amazonian freshwater ecosystems (Castello et al., 2013). The reduction in C_3 input from tree/shrub/leaves due to deforestation may negatively affect arapaima populations by reducing the availability of food sources, making them more vulnerable to ecosystem shifts due to their partial reliance on carbon fixed by forest trees and phytoplankton. And while this study has shed some light on the variation in arapaima feeding and isotopic relationships, considerably more needs to be conducted to understand the trophic ecology of this iconic Amazonian species.

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NOTE

¹ Taxonomic status of the studied population remains uncertain (Castello & Stewart, 2010; Stewart, 2013).

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