



Feeding strategies differentiate four detritivorous curimatids in the Amazon

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Abstract. Differences in food intake and morphological attributes may facilitate the coexistence of detritivorous fish. The present study investigated the possible differences in the feeding strategies of four species of curimatids that inhabit the floodplain of the central Amazon. For this, we determined the diet, daily food cycle, and whether characteristics of the intestine were related to the length of the fish and the amount of detritus consumed. The detritivory was confirmed, and we observed a difference in the foraging time between species. We found differences in the length and weight of the intestine and the relationship of these variables with the length of the fish and the amount of detritus consumed. Our study suggests that despite belonging to the same family and food group, curimatids have characteristics that allow them to consume the detritus in different ways.

1 Introduction

One of the ecological questions still unanswered about aquatic environments concerns the factors that determine species richness in detritivorous communities (Moore et al., 2004). How is it possible for the detritus to sustain a high quantity and diversity of fish in neotropical environments?

In the Amazon basin, one of the most representative detritivore groups is from the Curimatidae family, accounting for approximately half of the total fish biomass in South American rivers (Bowen, 1983; Lowe-McConnell, 1999; Vari and Röpke, 2013). This family has approximately 70 species. The species of the genera *Psectrogaster* and *Potamorhina* are the most abundant and widely distributed (Albert and Reis, 2011; Vari and Röpke, 2013; Van der Sleen and Albert, 2018). However, coexistence mechanisms are still poorly understood for this group. The species, in general, share the same environment and co-occur throughout the year, regardless of the hydrological cycle (Batista et al., 1998; Correia et al., 2015; Röpke et al., 2016). Besides, studies of feeding ecology have not encountered significant differences in the diets of these species, which are invariably dominated

by detritus (Pereira and Resende, 1998; Vaz et al., 1999; Aranguren, 2002; Giora and Fialho, 2003; Alvarenga et al., 2006; Mérona et al., 2008).

Detritus is a highly available food resource, not limited to seasonal and spatial factors, and due to its structural characteristics, it may have been in the environment for millennia (Moore et al., 2004). It is defined as partially decomposed organic matter from plant and animal tissues, in addition to microorganisms and minerals (Gneri and Angeluscu, 1951; Gerking, 1994; Moore et al., 2004; Santana et al., 2015; Farrell et al., 2018; Zimmer, 2019). However, the chemistry of water and the spatial and seasonal availability of sources that form detritus is what will define its final composition (Bowen, 1983; Goulding et al., 1988).

The composition of the detritus (origin, quantity, and quality) can affect the feeding rate, population density, and trophic niche of detritivores (Rossi et al., 2015). However, niche overlap appears to be common for this food group. The fact that many species consume detritus and occupy the same environment, with an apparent lack of competition, seems to be promoted precisely by the abundance of the total resource

and its high availability (Gerking, 1994; Pianka, 2000; Sidlauskas, 2007). However, the coexistence of detritivores can also be favored by differences in the use of this resource. The possible variety of detritus composition allows detritivores to specialize in food aggregates with different combinations of substrates (Delariva and Agostinho, 2001; Oliveira and Isaac, 2013; Rossi et al. 2015; Bayley et al., 2018). In addition, differences in detritus consumption can also occur in ontogenetic development (*Semaprochilodus* spp., Winemiller and Jepsen, 2004; *Sarotherodon mossambicus*, Bowen, 1979), during the reproductive period (*Curimatella lepidura*, Alvarenga et al., 2006), associated with foraging space or seasonality (*Loricarichthys platymetopon*, Lopes et al., 2009; *Hypostomus* spp., Oliveira and Isaac, 2013; *Prochilodus* spp., Bowen, 1983), by competition (*Hypostomus* spp., Oliveira and Isaac, 2013), or due to other physiological and/or ecological demands (Loricariidae, Lujan et al., 2011).

Independent of these conditions, all detritivorous fish have adaptations in the digestive process to extract large amounts of nutrients, since the detritus provides less energy and protein than other types of food (Sazima and Caramaschi, 1989; Bowen et al., 1995; Yossa-Pérdomo and Araújo-Lima, 1996; Castro and Vari, 2004; German and Bitong, 2009; Faria and Benedito, 2011). To enable a high rate of absorption and assimilation of nutrients, the digestive tract of these species is characterized by an extremely long intestine when compared to other feeding categories (Zihler, 1982; Smith, 1989; Kramer and Bryant 1995a; Karachle and Stergiou, 2010; Becker et al., 2010; Griffen and Mosblack, 2011; German et al., 2015). This characteristic, although general, can vary from 3 to 10 times the body size among detritivorous species (Moraes et al., 1997; Giora and Fialho, 2003; Alvarenga et al., 2006; German, 2009; Silva, 2016).

The differences found in the digestive tract, the type of detritus consumed, and foraging location is what defines the feeding strategy of each species. And this set of factors is closely aligned with feeding habits and phylogeny (Hidalgo et al., 1999; Guisande et al., 2012). Comparisons of the feeding strategies of closely related and sympatric species are still lacking, as is the case with curimatids. These species could present similar morphological characteristics, and they may nevertheless respond to the environment in different ways. They may present subtle shifts in certain traits, in particular those related to metabolism and digestive morphology (Ward-Campbell et al., 2005; Hilton et al., 2008; Mérona et al., 2008; Wagner et al., 2009; Griffen and Mosblack, 2011; Porreca et al., 2017). Thus, we investigated variations in the feeding strategy, specifically the relationship between morphological attributes and intake of detritus, of four abundant curimatid species in an aquatic environment in the central Amazon basin. Therefore, our objectives are to (1) confirm that the species investigated are detritivorous, (2) analyze variations in the daily food cycle, and (3) correlate morphological structures with feeding. We hypothesize that these variations in feeding strategy (even if subtle) could differen-

tiate the consumption of detritus by the four species and facilitate their occurrence in the same ecological niche in Amazonian freshwater ecosystems.

2 Materials and methods

2.1 Fish sampling

The curimatid species selected for the present study are the most abundant and frequently found in the Catalão region, a seasonally flooded area on the opposite margin of the Negro River from the city of Manaus (3°08'–3°14' S and 59°53'–59°58' W). The four species were *Potamorhina altamazonica* (Cope, 1878), *Potamorhina latior* (Spix and Agassiz, 1829), *Psectrogaster amazonica* (Eigenmann and Eigenmann, 1889), and *Psectrogaster rutiloides* (Kner, 1858). We obtained the specimens analyzed in the present study from the Catalão/INPA Project (INPA – CEUA Ethics Committee, protocol 051/2015; IBAMA collecting license no. 52392-2). This project was initiated in 1999 and involves the collection of standardized monthly samples of specimens using a set of gill nets (mesh sizes ranging from 30 to 120 mm), which are positioned in the water for 24 h, with the fish being removed every 6 h (6, 12, 18, and 24 h). The specimens were taken to the Laboratory of Fish Population Dynamics (LDPP) at INPA in Manaus for identification, biometrics, and biological analyses.

2.2 Diet and the daily feeding cycle

We determined the composition of the diets of the specimens collected between June 2010 and July 2011 by two methods: (i) the frequency of occurrence (the percentage of the number of stomachs containing food that included the item) and (ii) the relative volume, based on a visual estimate of the percentage of the volume of each stomach taken up by the item (Hyslop, 1980). These values were multiplied by the estimated repletion of each stomach (0%, 10%, 25%, 50%, 75%, or 100%) to correct for errors resulting from the analysis of stomachs with different degrees of repletion (see Goulding et al., 1988; Ferreira, 1993). The values obtained by the two methods described above (frequency of occurrence and relative volume) were used to calculate the alimentary index (IA_i) proposed by Kawakami and Vazzoler (1980): $IA_i = F_i \times V_i / \sum(F_i \times V_i)$, where IA_i is the food index of item i , F_i the frequency of occurrence of item i , and V_i the relative volume of item i .

We used the data collected between January 2013 and June 2018 to determine the daily feeding cycle. The time at which the specimen was retrieved from the net (i.e., 06:00, 12:00, 18:00, or 24:00 UTC–4) was considered to be a sampling point representative of the food ingested by the fish during the preceding 6 h. In this case, the stomach contents of a specimen collected at 06:00 UTC–4 were assumed to represent the food ingested between 24:00 and 06:00 UTC–4,

while those of the specimens collected at 12:00 UTC–4 were considered to represent the food ingested between 06:00 and 12:00 UTC–4, those collected at 18:00 UTC–4 represent food ingested between 12:00 and 18:00 UTC–4, and those collected at 24:00 UTC–4 represent food ingested between 18:00 and 24:00 UTC–4. To control for the effect of the weight of the fish on the weight of its digestive tract, we calculated the digestive somatic index (DSI), given by $DSI = (\text{weight of digestive tract of the specimen} / \text{total weight of the specimen}) \times 100$.

2.3 Characterization of the digestive tract and morphological attributes

Here, we analyzed fish specimens collected between January 2018 and October 2019. We first measured the total length (TL) and standard length (SL) of each specimen in millimeters and its total weight (TW) in grams. We then obtained the weight of the intestine (with contents) and the total length of the intestine. We calculated the digestive somatic index ($DSI = [\text{weight of digestive tract weight} / \text{total weight of specimen}] \times 100$) as a measure of food consumed by each species.

2.4 Data analyses

We applied four statistical procedures to assess the differences among species in regarding morphological attributes and detritus intake. All analyses were performed with “log:log₁₀”-transformed data due to the allometric relationship between the variables (Ricker, 1973; Wagner et al., 2009; Zandonà et al., 2015). First, we applied analysis of variance to test for the differences of morphological attributes among species. A one-way analysis was applied to each attribute: TL, TW, intestine length (IL), and intestine weight (IW).

The second analytical approach tested the difference in the relationships between morphological attributes (intestine length and weight) and the standard body length (SL) among the four species. We applied an analysis of covariance (ANCOVA) model for IL and IW whose SL, species identity, and the interaction of SL and species identity were the predictor variables.

The third analysis focused on the inference of the possible relationship between the amount of food ingested (DSI) and the structures of the digestive tract across the four species. The DSI was modeled based on the length and weight of the intestine as well as the interaction among these two variables. We set species identity as a factor to test whether estimates differ between species, and the log₁₀-transformed standard length was included as a co-variate to control the differences in individual body sizes.

Then in the four analytical steps, we run a regression model for each morphological attribute (TL, TW, IL, IW, DSI) against the standard body size ignoring species identity

and retained the residuals. To visualize the difference among species, we conducted a canonical variate analysis (CVA) with those extracted residuals from each morphological regression using the Morpho package. We also calculated and included a confidence ellipse (0.95) for each species, and the *envfit* function from the vegan package was used to fit morphological attributes onto the CVA ordination. To confirm the significant difference between species identity, we used the first canonical axis (summarizing 89 % of the total variation) as a dependent variable against the species identity in an ANOVA and a posteriori Tukey’s test. All statistical tests were run in the R platform (R Core Team, 2020).

3 Results

3.1 Diet and daily feeding cycle

We analyzed the stomach contents of 488 specimens of *P. latior*, 37 of *P. altamazonica*, 794 of *P. rutiloides*, and 33 of *P. amazonica*. We identified a variety of items including detritus (degraded organic matter), fragments of plant material, chlorophyte and cyanophyte algae, testate amoebae, ostracods, snails, cladocerans, and copepods. Overall, the intake of detritus exceeded 99 % of the frequency of occurrence (Table S1 in the Supplement). There were also no macroscopic differences in the detritus ingested by the species (Fig. S1 in the Supplement).

The daily feeding cycle was determined from the capture times of 127 specimens of *P. latior*, 114 *P. altamazonica*, 386 *P. rutiloides*, and 59 *P. amazonica*. The times indicated that all species were diurnal, feeding preferentially between 06:00 and 18:00 UTC–4, although with some intraspecific variation (Fig. 1). *Potamorhina latior* and *P. rutiloides* presented the highest digestive somatic index (DSI) between 12:00 and 18:00 UTC–4, whereas feeding in *P. altamazonica* peaked at 18:00 UTC–4. By contrast, the DSI of *P. amazonica* did not vary over the diurnal period. None of the analyzed specimens had an empty stomach or intestine, with DSI values invariably higher than 3 in the 06:00–18:00 UTC–4 period.

3.2 Characterization of the digestive tract and morphological attributes

The morphology of the digestive tract is similar in all four species (Figs. S2 and S3). The esophagus is a small tubular organ with a thin muscular wall, which thickens slightly where it joins the anterior portion of the stomach. The stomach is small, of fundic type, with a thin mucous layer covered by a thick muscular layer in the cardiac, fundic, and pyloric portions. The species of the genus *Psectrogaster* have a smaller, more rounded stomach (Fig. S3c), while in the *Potamorhina* species, this organ is larger and more elongated (Fig. S2c). In all four species, the intestine is extremely elongated and folded under the stomach, occupying most of the

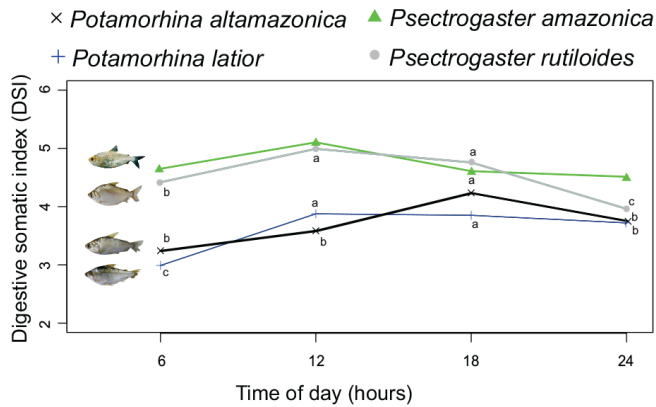


Figure 1. Circadian variation of the digestive somatic index (DSI) of four species of Curimatidae. Comparison between times by analysis of variance with statistical differences presented by different lowercase letters.

coelomic cavity (Figs. S2b and S3b). In *P. latior* and *P. altamazonica*, the diameter of the proximal portion of the intestine is enhanced, whereas in *P. rutiloides* and *P. amazonica* the intestine does not vary in width.

Morphological attributes varied among species. On average, *P. altamazonica* was the longest and heaviest intestine, and *P. latior* had the shortest intestine. *Psectrogaster rutiloides* had the lowest mean intestine weight, and *Psectrogaster amazonica* was the smallest species (Table 1).

Intestine length varied significantly among species ($p < 0.001$), and *P. altamazonica* presented the longest intestine followed by *P. amazonica*, *P. rutiloides*, and *P. latior* (Table 1). Regression analysis ($F_{7-183} = 74.54$, $p < 0.001$) showed that *P. altamazonica* ($p = 0.003$) and *P. latior* ($p = 0.029$) have significant variations in IL values. The relationship between intestine length and standard length was significant and positive for *P. altamazonica* ($b = 0.83$, $p < 0.001$), marginally significant for *P. latior* ($b = 0.46$, $p = 0.06$), and not significant for *P. amazonica* ($b = 0.83$, $p = 0.08$) and *P. rutiloides* ($b = -0.15$, $p = 0.59$).

Intestine weight varied significantly among the analyzed species ($p < 0.001$). *Potamorhina altamazonica* and *P. rutiloides* showed statistical differences between them ($p < 0.001$) and between *P. amazonica* ($p < 0.001$) and *P. latior* ($p < 0.001$). Regression analysis ($F_{7-183} = 87.12$, $p < 0.001$) showed that *P. altamazonica* ($p = 0.001$) and *P. latior* ($p < 0.001$) have significant variations in IW values. The relationship between intestine weight and standard length was significantly positive for *P. altamazonica* ($b = 1.60$, $p < 0.001$) and *P. latior* ($b = 0.65$, $p = 0.03$), negative for *P. rutiloides* ($b = -1.17$, $p < 0.001$), and not significant for *P. amazonica* ($b = -0.47$, $p = 0.41$) (Fig. 2b).

The relationship between the amount of food ingested (DSI) with the length (IL) and intestine weight (IW) was different among species ($r^2_c = 0.91$). *Potamorhina latior* showed variation in DSI values ($b = 0.008$ and $p = 0.002$).

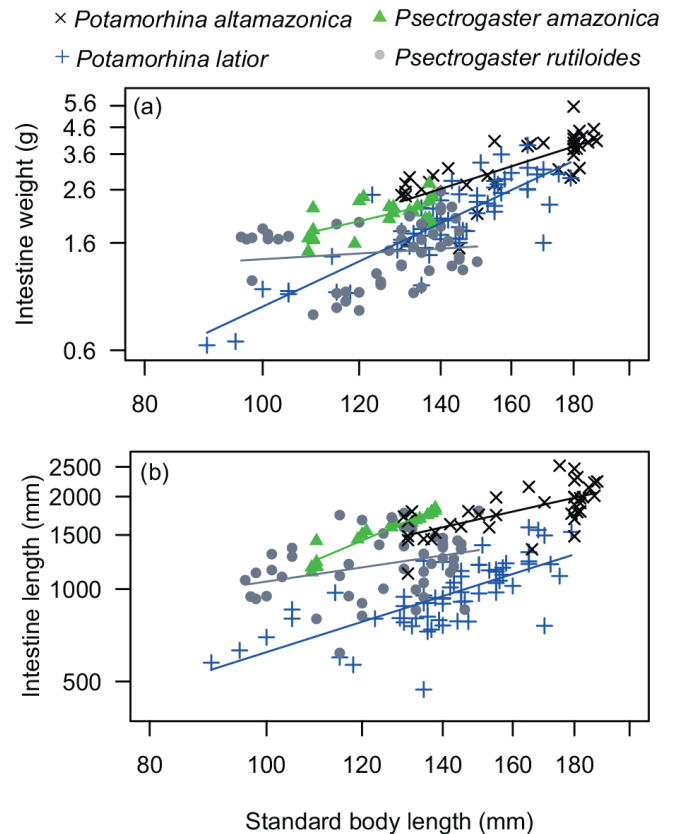


Figure 2. ANCOVA regression plots (a) between SL (standard body length) and IW (intestine weight) and (b) between SL and IL (intestine length) of the four analyzed species of Curimatidae. Note that the variables were \log_{10} -transformed.

The intestine weight showed a significant relationship with DSI ($p = 0.04$) (Table 2).

The canonical analysis (CAV) with the morphological attribute (TL, TW, IL, IW, and DSI) residuals showed 96 % of explained variation over the first two canonical axes. The first axis shows a significant difference between the four species (ANOVA, $F_{3-169} = 190.7$, $p < 0.01$, Fig. 3). Overall, the four species are distinguished from one another, except *P. altamazonica* and *P. rutiloides* (Tukey's test; $p > 0.05$). The ellipses of three species overlap, except *P. latior*, which shows an ellipsis in the opposite direction in the ordination space. *Psectrogaster rutiloides* presented individuals positively related to TW, IL, and IW. *Potamorhina altamazonica* and *P. amazonica* presented individuals positively related to a higher TW and IL, while *P. latior* was negatively associated with IL presenting lower values in the first CAV axis (Table S2).

4 Discussion

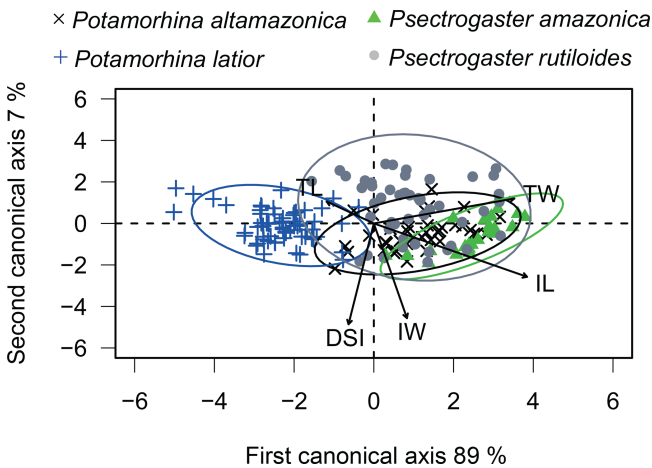
We confirmed the occurrence of detritivory in all four species analyzed in the present study. The absence of macroscopic

Table 1. Total length (TL), standard length (SL), total weight (TW), intestine weight (IW), and total intestine length (IL). Values are mean \pm SEM. Comparison between species by analysis of variance with statistical differences presented by different lowercase letters.

	TL (mm)	SL (mm)	TW (g)	IW (g)	IL (mm)
<i>Potamorhina altamazonica</i> (n = 45)	188 \pm 6 ^a	165 \pm 3 ^a	111 \pm 4 ^a	3.5 \pm 0.1 ^a	1843 \pm 38 ^a
<i>Potamorhina latior</i> (n = 67)	174 \pm 3 ^a	140 \pm 2 ^a	56 \pm 2 ^a	2.1 \pm 0.1 ^a	968 \pm 25 ^d
<i>Psectrogaster amazonica</i> (n = 28)	148 \pm 3 ^c	118 \pm 3 ^d	62 \pm 4 ^a	2.1 \pm 0.04 ^a	1454 \pm 46 ^a
<i>Psectrogaster rutiloides</i> (n = 57)	153 \pm 2 ^c	126 \pm 2 ^c	56 \pm 2 ^a	1.5 \pm 0.04 ^c	1236 \pm 33 ^c
	<i>F</i> = 47.9 <i>p</i> < 0.001	<i>F</i> = 42.64 <i>p</i> < 0.001	<i>F</i> = 59.73 <i>p</i> < 0.001	<i>F</i> = 79.52 <i>p</i> < 0.001	<i>F</i> = 90.95 <i>p</i> < 0.001

Table 2. Results from the model between the amount of food ingested (DSI) and structures of the digestive tract from each species. The interaction between intestinal length (IL) and weight (IW) is included. Species identity was as a co-factor to test whether estimates differ between species, and the standard length (SL) was included as a random variable to control the differences in individual body sizes. All variables were log₁₀-transformed. Bold values indicate significant variables in the model.

Dependent variable	β	SE	<i>t</i>	<i>p</i>	<i>r</i> ²
<i>Potamorhina altamazonica</i>	0.03	0.29	0.12	0.90	0.91
<i>Potamorhina latior</i>	0.08	0.27	3.10	0.002	
<i>Psectrogaster amazonica</i>	0.01	0.02	0.56	0.57	
<i>Psectrogaster rutiloides</i>	-0.02	0.26	-1.03	0.30	
Intestine weight	1.60	0.79	2.01	0.04	
Intestine length	0.09	0.10	0.92	0.35	
Intestine weight \times intestine length	-0.32	0.26	-1.22	0.22	

**Figure 3.** Plot of the first two canonical axes, calculated from the size-corrected morphological attributes (TW – total weight, TL – total length, IW – intestine weight, IL – intestine length, and DSI – digestive somatic index) of the four species.

differences in the food consumed may support our hypothesis that variations in the feeding strategy differentiate the consumption of detritus and facilitate the occurrence of curimatids in the same ecological niche. The species constantly forage during the day, where there is an overlap of the peak foraging time, between 06:00 and 12:00 UTC–4, for the two

species of *Psectrogaster* and *P. latior*. Similar patterns have been recorded for other curimatids and detritivores, which indicates that the overlapping of periods or forage sites may not inhibit their coexistence (Sazima and Caramaschi, 1989; Fugi et al., 1996; Oliveira and Isaac, 2013). Coexistence may be associated with the high availability of detritus (Moore et al., 2004; Zimmer, 2019): when food is unlimited, it is not a controlling factor in the abundance and distribution of fish, since there is no competition between species that feed on the same resource (Lowe-McConnell, 1999; Pianka, 2000). In this case, the space or time of foraging may be more limiting than the availability of food (Lowe-McConnell, 1999). Thus, *P. altamazonica* seeks alternative foraging times, reflecting a strategy to avoid competition for preferred foraging areas.

Although availability of detritus was not a limiting factor differences in the morphology of digestive attributes could be related to different feeding strategies (Karasov and Martinez Del Rio, 2007; German, 2011; Porreca et al., 2017). The digestive tract is formed by a small and muscular stomach and a very elongated intestine. This trait is common among curimatids and prochilodontids with similar feeding strategies (Al-Hussaini, 1949; Bowen, 1988; Yossa-Pérdomo and Araújo-Lima, 1996; Moraes et al., 1997; Silva, 2016). The small and muscular stomach, combined with the friction generated by the mineral component of the detritus, reduces the size of the particles, facilitating the action of digestive

enzymes found in the intestine. The elongated intestine is folded extensively to fit inside the celomic cavity, resulting in a long intestinal passage time (Bowen, 1983; Smith, 1989; Bone and Moore, 2008; Griffen and Mosblack, 2011). This keeps the ingested detritus in contact with digestive enzymes for an extended period, ensuring the maximum possible extraction of nutrients (German, 2009; German and Bitong, 2009).

The similarity in the digestive tract is easily supported by the phylogenetic proximity and feeding strategies of the four species. These factors influence and determine the shape of the digestive tract (Hidalgo et al., 1999; Farrel et al., 2011; Guisande et al., 2012). However, our study found significant differences between the length and weight of the intestine as well as the amount of food consumed by the curimatids, which may be facilitating the coexistence of these fish. The length of the intestine varied significantly between the species studied. The longer the intestine, the greater the absorption surface, and the longer the time for enzymatic activity (Zihler, 1982; German, 2011). Therefore, the variation in the length of the intestine suggests differences in digestive physiology and in the time of assimilation of the detritus. Thus, the fact that *P. latior* has a shorter intestine reflects a strategy that consists of less time spent absorbing nutrients and/or consuming easily digestible items.

The relationship between gut length and the standard length was also contrasting between species. For *P. altamazonica*, the larger the individual, the longer the intestine; however for *P. latior* and *P. amazonica*, this relationship is not significant, and, for *P. rutiloides*, even negative, although not significant. Although the IL *versus* SL relationship is not clear to the curimatids in this study, it was recognized in other detritivores (Fugi et al., 2001, $b = 0.961$; Angeluscu and Gneri, 1949, *apud* Kramer and Bryant, 1995b, $b = 1.06$). Therefore, consuming comparable food items may not be the only factor that determines this relationship. For example, Kramer and Bryant (1995b) found that herbivorous species showed wide variation in the slope of the IL \times SL ratio ($b = 1.36\text{--}2.11$) and concluded that this is due to different ways of digesting the same food item. Thus, factors other than diet can influence this relationship and should be investigated such as the physiological and ecological processes (Kramer and Bryant, 1995b; Mérona et al., 2008; Zandonà et al. 2015).

Intestinal weight also varied between species, with *P. rutiloides* being the species with the lowest value. The amount of food present in the digestive tract during each feeding may or may not be related to the length of the intestine (Starck, 2003; Barboza et al., 2010; German, 2011). However, only *P. altamazonica* obtained a positive association with high values of weight and length of the intestine. For the other species, this was not observed. Thus, in addition to length, other characteristics of the intestine (weight, number of folds and microvilli, etc.) must be considered to determine the intestinal capacity to accommodate food. There was also no

pattern for species in the IW *versus* SL ratio. *Psectrogaster amazonica* did not present a clear pattern; for *P. altamazonica* and *P. latior*, the larger the size of the fish, the heavier the intestine, indicating that larger individuals can consume and/or store more food. *Psectrogaster rutiloides* showed a negative relationship, indicating that larger individuals do not ingest/store more detritus. This negative relationship in *P. rutiloides* may also be related to the consumption of a different type of detritus or greater potential for the assimilation of nutrients in larger individuals. Farago (2018, unpublished data) showed that this species may be able to digest lipids up to 20 times more efficiently than other curimatids. In either case, *P. rutiloides* would have a strategy capable of extracting more energy from a smaller amount of detritus stored in the intestine.

The influence of the type and amount of food in the trophic niche of detritivores has been observed in other cases, and this seems to allow species in this group to specialize in discrete combinations of detritivorous compounds (Delariva and Agostinho, 2001; Constantini and Rossi, 2010; Oliveira and Isaac, 2013; Rossi et al., 2015; Santos et al., 2020). The species showed an association of their intestinal weight with the amount of food ingested (DSI). In curimatids, higher consumption of detritus tends to reflect in a heavier intestine. *Potamorhina latior* was the only species to have a significant and slightly positive relationship with the DSI, suggesting that it can compensate for its shorter intestine with higher consumption of detritus. This strategy would increase the amount of food items that pass through the digestive tract, allowing greater assimilation of nutrients (German, 2011).

Our results from the morphological attributes confirm the distinction between the curimatids. Even there is an overlapping between species, the intestine length (IL) was the main attribute that differentiated them. As this characteristic is directly related to digestive efficiency (Karasov and Martinez del Rio, 2007; Karachle and Stergiou, 2010; Griffen and Mosblack, 2011; German, 2011), it can be a relevant point to determine the different feeding strategies of species. The shorter intestine of *P. latior* suggests that the detritus consumed by this species needs less contact with digestive enzymes and, perhaps, less intestinal transit time (Smith, 1989; Karasov and Martinez del Rio, 2007; German, 2011). Despite the species of Curimatidae showing similar morphological adaptations to a diet restricted to detritus (Vari, 1989; Guisande et al., 2012; Melo et al., 2018), differences like this demonstrate that the evolutionary path to detritivory may not be the same for these fishes.

Data availability. The data are available from the authors by personal request.

Supplement. The supplement related to this article is available online at: <https://doi.org/10.5194/we-20-133-2020-supplement>.

Author contributions. TF, SA, GdS, AV, and EF designed the study. TF and JO collected the specimens in the field. TF and GB conducted the analyses. All the authors contributed, reviewed, and approved the final version of the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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