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Original article

Divergence in energy sources for *Prochilodus lineatus* (Characiformes: Prochilodontidae) in Neotropical floodplains

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The stable carbon isotopic variability and the contributions of autochthonous (sediment microbial biomass, phytoplankton, and periphyton) and allochthonous (soil microbial biomass) sources available to the detritivorous fish *Prochilodus lineatus* were investigated in three environments of the floodplain of the Upper Paraná River. The isotopic composition of carbon sources and fish varied significantly among the studied environments. The autochthonous resources, represented by the phytoplankton, were the most assimilated by the species, followed by periphyton and sediment microbial biomass. The species used the sources differently in each environment. This study suggests that the inherent characteristics of this area, as well as the size of the watershed, the dry season, anthropogenic actions, and phytoplankton productivity, favor the use of autochthonous resources by the species studied. Therefore, studies in the floodplain should employ an eco-hydrological approach that quantifies the magnitude of energy subsidies, as well as an access route to consumers, knowledge about the selectivity of detritivorous species and the effects of different land uses.

Keywords: Aquatic ecosystems, Carbon sources, Fish, Organic matter, Stable isotopes.

A variabilidade isotópica e as contribuições autóctones (biomassa microbiana do sedimento, fitoplâncton e perifíton) e alóctone (biomassa microbiana do solo) assim como as principais fontes de carbono para o peixe detritívoro *Prochilodus lineatus* foram investigadas em três diferentes ambientes, da planície de inundação do alto rio Paraná. A composição isotópica das fontes de carbono e dos consumidores variaram significativamente entre os ambientes estudados, e os recursos alóctones, representados pelo fitoplâncton, foram os mais utilizados pela espécie, seguido pelo perifíton e biomassa do sedimento microbiano. A espécie utilizou fontes de carbono distintas em cada ambiente. Este estudo sugere que características inerentes a cada ambiente, assim como o tamanho do ambiente, o período de seca, ações antropogênicas e produtividade do fitoplâncton favorecem o uso dos recursos alóctones pela espécie estudada. Portanto, estudos na planície de inundação devem empregar uma abordagem eco-hidrológicas que quantifique a magnitude dos subsídios energéticos, bem como as vias energéticas aos consumidores, o conhecimento acerca da seletividade das espécies de detritívoros e o efeito dos diferentes usos da terra.

Palavras-chave: Ecossistemas aquáticos, Fontes de carbono, Isótopos estáveis, Matéria orgânica, Peixes.

Introduction

Freshwater aquatic food chains are maintained by autochthonous sources of detritus, derived from phytoplankton, periphyton, sediment, macrophytes, and microorganisms, as well as by allochthonous sources (*i.e.*, material originating from terrestrial vegetation) (Cole *et al.*, 2011). Historically, it has been assumed that autochthonous carbon is responsible for the maintenance of aquatic consumers, especially carbon derived from the phytoplankton. However, the allochthonous subsidies may also be relevant as sources of energy for food chains (Reynolds, 2008; Kon *et al.*, 2012; Fuentes *et al.*, 2013; Oliveira *et al.*, 2014; Garcia *et al.*, 2017). Studies on feeding interactions have also reported the relevance of bacteria due to their importance in the transformation of matter and energy (Torsvik *et al.*, 1996), being responsible for much of the energy flow in ecosystems (Wagener *et al.*, 1998). Odum (1988) comments that dead organic matter is transferred to microorganisms and these (again) are consumed by detritivores and predators.

Thus, due to constant interaction between aquatic and terrestrial systems, these resources are essential in floodplains (Winemiller *et al.*, 2010). Many fish species of wetland areas have adaptive features that facilitate the exploitation of resources during seasonal flood pulses, allowing

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the use of these areas for reproduction, refuge, and feeding (Bisson *et al.*, 2009). These evolutionary adaptations are influenced by season and are reflected in the feeding and diet of fish species (Berra, 2007). Bozza, Hahn (2010) have reported changes in the diet and frequency of feeding in fish, caused by alterations in resources during periods of flooding in Upper Paraná River. Stephens, Krebs (1986) reported that fish optimize their nutrient acquisition, which influences the availability of food in the food choice by the consumer.

Detritivores consume a mixture of an amorphous material composed of terrestrial detritus, microorganisms, phytoplankton and periphyton (Smoot, Findlay, 2010a, 2010b), therefore playing a key role in the organization and maintenance of aquatic ecosystems (Hamilton *et al.*, 2004). In this case, the use of stable isotopes ($\delta^{13}C$) has been shown to be appropriate because it successfully identified the origin of energy for consumers. Some studies carried out in tropical environments have proposed that most of the energy comes from the allochthonous material because the forested area has considerable supplies of tree litter and riparian vegetation. In this case, autochthonous production is limited by shading, so that the detritivorous species depend predominantly on allochthonous energy sources (Benedito-Cecilio, Araujo-Lima, 2002; Ock, Takemon, 2013). However, this is not a consensus opinion. Several authors argue that the autochthonous resources, especially those from phytoplankton and periphyton communities, are also important to detritivores. These results were reported in several regions, including small shaded streams in Porto Rico (March, Pringle, 2003), Brazil (Brito *et al.*, 2006), and for tropical Asia (Mantel *et al.*, 2004), in arid regions (Bunn *et al.*, 2006), Australia (Medeiros, Arthington, 2011), the Orinoco (Lewis *et al.*, 2001), and in the floodplain of the Amazon River (Araujo-Lima *et al.*, 1986). Detritivorous species can use autochthonous resources as a source of energy. These species play a fundamental role in floodplains because a major part of the metabolic processes is supported by terrestrial detritus, which accounts for maintaining the detritivorous food chain (Santana *et al.*, 2015).

Among detritivorous species, the migratory *Prochilodus lineatus* (Valenciennes, 1836), commonly known as curimba, is a fish of commercial interest and consumes inorganic sediment, organic detritus, microinvertebrates, and algae (Fugi *et al.*, 1996), and occurs in all environments of the floodplain of the Upper Paraná River in Brazil (Lowe-McConnell, 1999).

Using $\delta^{13}C$ stable-carbon isotope ratios, this study investigates the contribution of autochthonous resources, including as the main sources: phytoplankton, periphyton and microbial biomass of organic matter in the sediment. Furthermore, the microbial biomass of terrestrial soil organic matter was considered as an allochthonous source of nutrition. This work was conducted under the hypothesis that the carbon source used by detritivorous fish, *P. lineatus*, comes from autochthonous resources.

Material and Methods

Study area. The floodplain of the Upper Paraná River is located in South of Brazil, on the border of the states, Paraná and Mato Grosso do Sul (22º45'S, 53º30'W) (Fig. 1). This study was conducted in the Paraná, Baía, and Ivinheima Rivers form this floodplain area. The Paraná River varies widely in depth, with an average of 4 m but can exceed 15 m during the wet period; the vegetation consists of sparse trees and grasses. The average depth of the Baía River is 3.2 ± 4.26 m, with riparian vegetation and fields affected by human activities (agriculture and cattle-raising activities), as well as fields of floodplains, aquatic macrophytes, and grasses. The Ivinheima River has an average depth of 3.9 m and variation of 2.94 m, with quite diverse vegetation, including herbaceous, grass, wetland and riparian species at different stages of regeneration. This environment presents significant, differentiated and complex characteristics. The hydrological regime is bimodal, with floods from December to March and August to September that reach a depth of up to 4.0 m (Souza-Filho *et al.*, 2004).

Sampling design. The sampling was conducted in July 2010 (dry season) in the floodplain of the Upper Paraná River in three environments: Paraná, Baía, and Ivinheima (Fig. 2). In this period, the connectivity between environments from floodplain is lower than in other periods. In Paraná and Baía rivers, two sites were sampled each, whereas three sites were sampled n Ivinheima River. Unfortunately, the next period of wet has an elevated hydrometric level (Fig. 2), and the points in the majority of environments were submerged and could not be sampled.

The primary sources of energy considered were: phytoplankton and periphyton. The phytoplankton samples were obtained with plankton nets of 15 µm (without zooplankton) and the periphyton by scraping stems of aquatic plants, being composed of five samples of phytoplankton and five samples of periphyton in each environment studied. Samples were retained on glass fiber filters (previously undergone combustion at 550°C for 4 h).

The abiotic data, soil samples (allochthonous), and sediment samples (autochthonous) were taken at three points in each transect in every environment. For the soil samples, a core sampler (5-cm diameter and 0-10 cm depth) was used. For the sediment, samples were collected at 0-5 cm in depth, with the aid of a simplified collector type core sampler for sediment (Boyd, 1995) to avoid the influence of the water column. The sampling of soil and sediment was carried out in a transect composed of four soil samples and three sediment samples. The transects were conducted from the right margin until the left margin, and the samples had 2 m of distance between them. In larger lagoons (Ivinheima River), five sediment samples were collected. The soil samples were collected close to the banks of the lagoons, with a distance of approximately 2 m between the points. In the case of the sediment transect, the samples were taken near the edges and

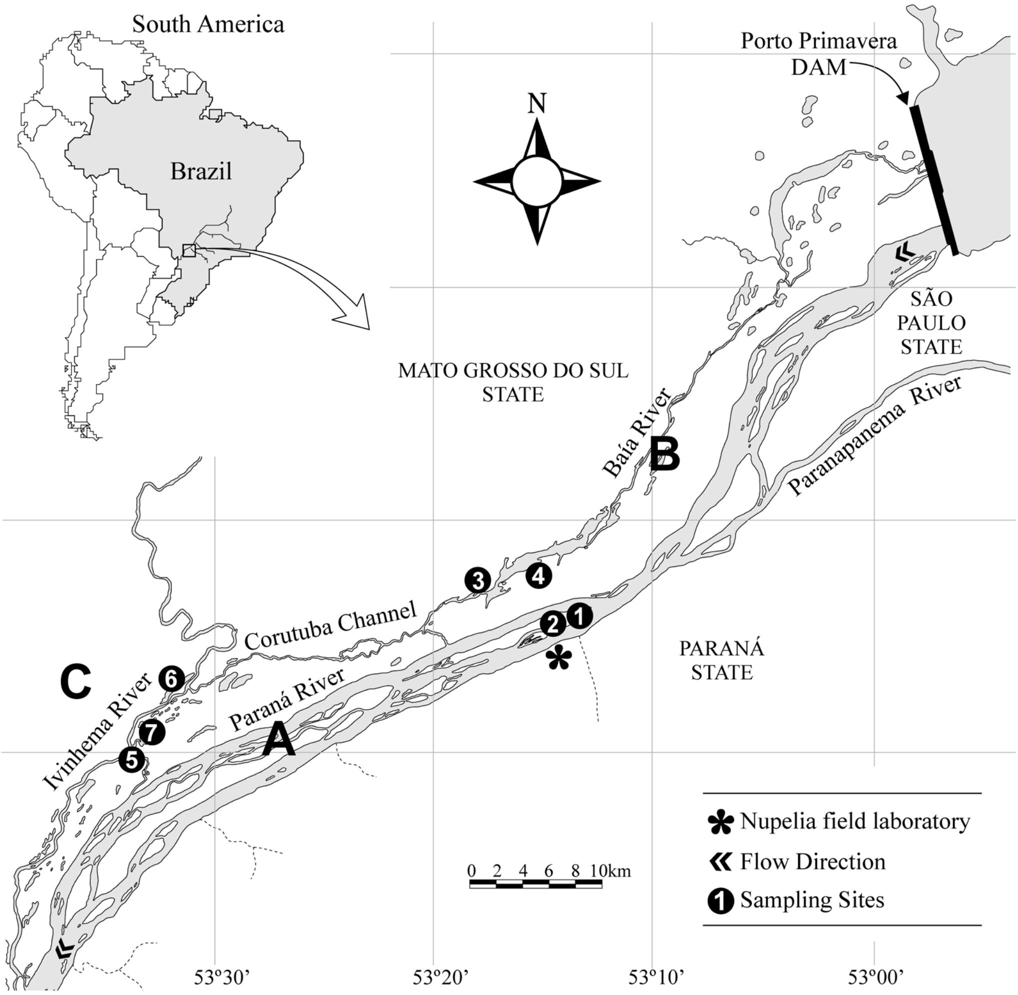

Fig. 1. Map of the floodplain of the Upper Paraná River, highlighting the areas sampled in this study. The subsystems sampled were A = Paraná River, B = Baía River and C = Ivinheima River. The numbers indicate sampled sites in each subsystem.

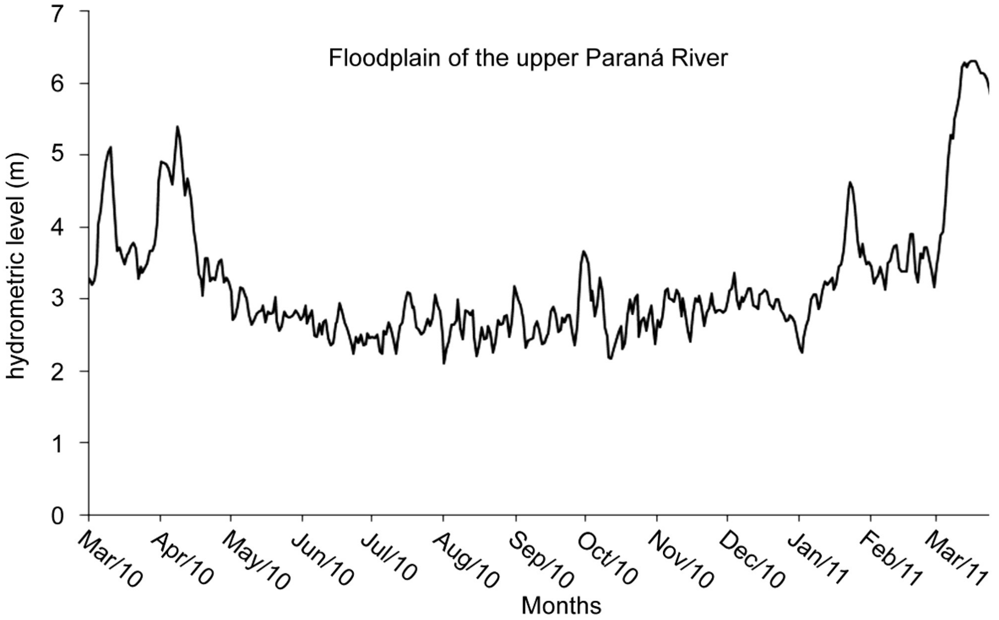

Fig. 2. Hydrometric level from dry and wet periods in the floodplain of the Upper Paraná River.

center of the lagoons. For the larger lagoons, one sample of each sediment was collected close to either margin and three samples additional samples were collected along the transect in the lagoon at approximately similar distances.

The specimens of *P. lineatus* were sampled using gill nets; five fish were collected in each environment studied (Paraná, Baía and Ivinheima rivers). *Prochilodus lineatus* is a migratory fish, and the environments are relatively close. However, the detritivorous feed continuously due to low nutritive values of the diet (Yossa, Araujo-Lima, 1998) and for this reason the isotopic values are significantly different among environments from the floodplain of the Upper Paraná River (Lopes *et al.*, 2007). Some of the collected specimens of *P. lineatus* were deposited in the Ichthyology Collection of NUPELIA (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, Paraná State) (NUP 11092 – http://peixe.nupelia.uem.br/). All adult specimens had a similar standard length (Ls, cm) and total weight (Wt, g), which were determined before a small portion of muscle (located at the base of the dorsal fin) was removed. The muscle samples were dried at 60°C for 36 to 48 h, and ground until obtaining a fine and homogeneous powder, of which approximately 0.001g was weighed into tin capsules for mass spectrometry.

In the Energy Ecology Laboratory at the State University of Maringá, the samples were submitted to a fumigation-extraction method with chloroform according to Vance *et al.*, (1987). The extracts were frozen until sent for analysis of total organic carbon concentration (in Analytical Model 1030 TOC Analyzer, Sercon Ltd., Cheshire, UK) and $\delta^{13}C$ in (PDZ Europa ANCA-GSL Mass Spectrometer, Sercon Ltd., Cheshire, UK).

Data Analysis. The values of the isotope ratios were expressed in delta notation (δ) and in parts per thousand (‰) (Bond, Hobson, 2012) relative to the international standard Viena Pee Dee Belemnite (VPDB). All biological material prepared was sent to the UC Davis Stable Isotope Facility, USA, for analysis of $\delta^{13}C$ (‰) in the isotope ratio mass spectrometer (PDZ Europa ANCA-GSL, Sercon Ltd., Cheshire, UK), according to the expression:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 10^{3}$$

where: R = carbon isotope ratios = $^{13}C/^{12}C$

For the microbial biomass carbon (C) an extraction coefficient (K_{EC}) of 0.45 was used (Wu *et al.*, 1990). To determine the microbial biomass $\delta^{13}C$ ($\delta^{13}C_{MB}$), a mass balance was calculated according to the equation (Werth, Kuzyakov, 2008):

$$\delta^{13}C_{MB} = (\delta^{13}C_{fum} \times C_{fum} - \delta^{13}C_{nfum} \times C_{nfum})/C_{fum} - C_{nfum}$$

where, $\delta^{13}C_{fum}$ and C_{fum} are measured in chloroform-fumigated samples, and $\delta^{13}C_{nfum}$ and C_{nfum} are obtained from samples that were not treated with chloroform (Murage, Voroney, 2007) and the correction factor was 2,22 the total carbon in ppm.

For graphical and statistical analysis, parametric and non-parametric tests were performed with the Statistica program (version 7.0 – StatSoft). One-way ANOVA with the Tukey HSD *post hoc* test was used to compare the differences of means among the isotopic sources of carbon and environments studied. In cases where the assumptions of normality and homoscedasticity were not fulfilled, the Kruskal-Wallis test was used. A 5% level of significance was considered for both tests.

The contribution of energy sources for *P. lineatus* was calculated by the IsoSource program (Phillips, Gregg, 2003). Only $\delta^{13}C$ values were available. Isosource model is helpful at inferring possible diet compositions when a unique solution cannot be calculated (Hopkins, Ferguson, 2012) once uses rules of mass balance to examine all possible source combinations that could result in observed isotope value, and provides range of possible proportional contributions (Layman *et al*., 2012). Although IsoSource does not include sampling and measurement sources of uncertainty in a straightforward way (Phillips *et al*., 2014). For the calculations of carbon sources contributions an isotopic discrimination of 1 ‰ was considered, the tolerance values used were 0.1 for the Paraná and Baía rivers and 0.05 for Ivinheima, and the increment used was 1% in all cases. Tolerance values can range from 0.05 to 0.2 (Phillips, Greg, 2003). Stable isotope missing model presented feasible solutions when performed with small tolerances, in which the frequency and reach of the potential contributions of the source could be determined.

Results

Isotopic values. Isotope ratios for $\delta^{13}C$ from consumers and resources were higher in the Paraná (between -28 ‰ and -19 ‰) and lower for Baía and Ivinheima rivers (between -32 ‰ and -26 ‰) than other floodplain environments the Upper Paraná River (Fig. 3). The $\delta^{13}C$ values of detritivorous *P. lineatus* differed significantly among the rivers (p = 0.01) (Tab. 1).

Tab. 1. Mean values and standard deviations of abiotic parameters from the Paraná, Baía and Ivinheima subsystems in dry season.

Abiotic data	Subsystems		
	Paraná	Baía	Ivinheima
Oxygen (mg l^{-1})	8.2±1.03	8.7±0.53	8.9±1.04
Water temperature (°C)	20.3±0.33	22.8±0.74	17.9±0.25
pH	7.4±0.20	6.8±0.17	7.7±0.80
Conductivity(µS cm^{-1})	65.0±0.54	29.5±0.87	43.3±3.07

Contribution of carbon sources. We found that *P. lineatus* consumed different sources in each environment studied. In the Baía environment, the fish principally used periphyton (77%), followed by phytoplankton (11%). In the Paraná environment, the fish principally assimilated phytoplankton (75%), followed by periphyton (18%), whereas in

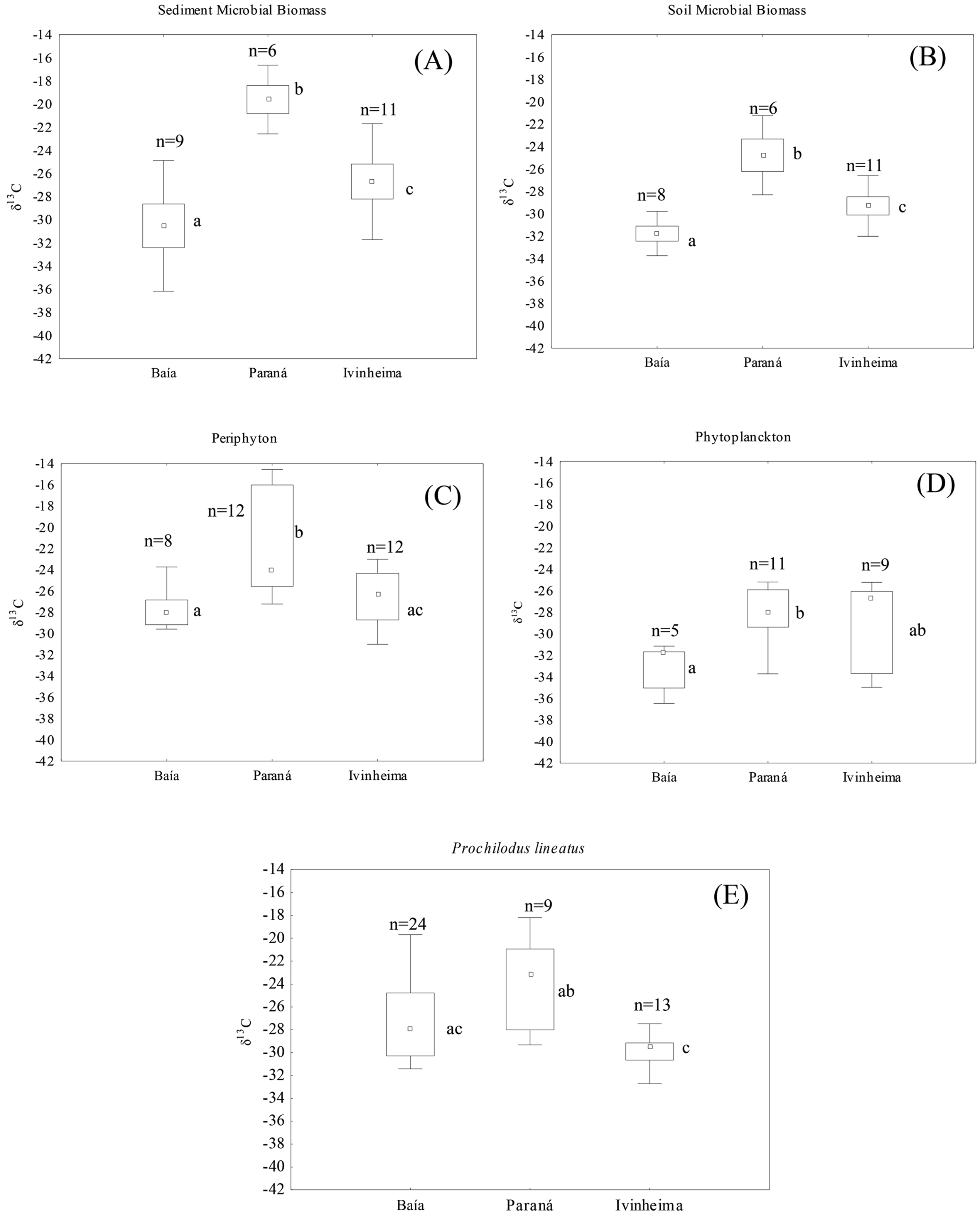

Fig. 3. δ13C values of food sources (A to D) and of *P. lineatus* (E). The box-whisker-plots show the lower and upper quartile (25% - 75%), median (□), minimum and maximum (vertical bars). The small letters represent significant differences between the components studied in Paraná, Baía and Ivinheima subsystems of the floodplain of the Upper Paraná River (n = number of samples).

Ivinheima the species principally assimilated MB sediment (51%) and MB soil (25%) (Tabs. 2-3 and Fig. 4). The algae presented an average contribution higher than 88% in the environments of Paraná and Baía River, and in contrast, it was lower than 21% in Ivinheima.

Tab. 2. The values of results of ANOVA and Kruskal-Wallis tests from carbon sources for *P. lineatus* in the area studied (MB: Microbial Biomass).

	ANOVA		Kruskall-Wallis		
	F	p		H	p
MB sediment	8.99	0.0010	Periphyton	10.25	0.005
MB soil	12.15	0.0002	Phytoplankton	4.90	0.080
			P. lineatus	9.12	0.01

Tab. 3. Contributions of carbon sources to nutrition of *P. lineatus*. Variations in the contribution of the resources are presented in 1-99 (50) percentile and standard deviation (SD) for the consumer in each subsystem studied in the floodplain of the Upper Paraná River. The values in parentheses indicate the median (MB = Microbial Biomass).

Subsystem	Sources (%)			
	MB sediment	MB soil	Periphyton	Phytoplankton
Baía	0-20 (6)	0-14 (4)	63-86 (77)	0-35 (11)
Paraná	0-9 (3)	0-8 (3)	1-34 (18)	62-88 (75)
Ivinheima	1-72 (51)	0-64 (25)	0-1 (1)	0-94 (20)

Discussion

Floodplains are environments with heterogeneous landscapes associated with mosaics of food webs (Bellmore *et al.*, 2013), reinforcing the paradigm that these areas are biophysically complex "hotspots" (Junk *et al.*, 1989; Stanford *et al.*, 2005). Thus, they may also be considered "hotspots" with complex feeding interactions (Bellmore *et al.*, 2013).

In this study, we identified considerable variability in isotopic signatures from carbon sources in different environments, but also in contributing to the energy sources of detritivorous *P. lineatus*. Studies in flooded areas have emphasized the relationship between the structure of fish assemblages and the pathways of organic matter. The flood pulses redistribute organic material, providing interaction between the aquatic and terrestrial environment (Junk *et al.*, 1989; Stanford *et al.*, 2005). This fact may have influenced the isotopic variability observed for the carbon sources and the consumer both in different environments.

In relation to microbial sources, derived from the autochthonous and allochthonous organic matter, isotopic variation can be related to the carbon assimilated by microorganisms in various environments (Pelz *et al.*, 1998), taking into account the basic principle of studies with stable isotopes that the organisms isotopically represent their source of energy (DeNiro, Epstein, 1978).

The floodplain of the Upper Paraná River has high plant diversity associated with forest and shrubby formations (Romagnolo, Souza, 2000), which shows the predominance of species with the C_3 photosynthetic pathway. These plants exhibit **δ**^{13}C values between -32.0‰ and -22.0‰ (Boutton *et al.*, 1998). These characteristics may justify the isotopic value of the allochthonous microbial biomass, which is quite similar to the isotopic signature of vegetation, a result also evidenced by Lopes *et al.* (2007). These authors analyzed other available resources for *P. lineatus*, including phytoplankton and periphyton, which showed similar isotopic values. Thus, although the nutritional variation for detritivorous fish in Neotropical floodplains may be diversified, several studies about food sources have reported the importance of phytoplankton, especially in the dry season (Araujo-Lima *et al.*, 1986; Lopes *et al.*, 2007).

The source of greatest contribution to *P. lineatus* originated from the autochthonous material. Large contributions of phytoplankton were found in Paraná River, periphyton in Baía and the microbial biomass in the Ivinheima River. The higher contribution from autochthonus sources may be a reflex of the dry season and this result may not be repeated during the flood pulses. On the other hand, the origin of allochthonous resources is essential since many consumers use terrestrial organic carbon as a food resource. Outstanding among these consumers are microorganisms (Berggren *et al.*, 2010), zooplankton (Cole *et al.*, 2011), benthic invertebrates (Solomon *et al.*, 2008), and fish (Medeiros, Arthington, 2011; Solomon *et al.*, 2011). However, in contrast, other studies have suggested that the terrestrial organic matter contributes little to the nutrition of aquatic consumers (Brett *et al.*, 2009).

In this context, former studies on stable carbon isotopes in the fish species *Dorosoma cepedianum* (Lesueur, 1818) have to be considered, because like *P. lineatus*, this species also has morphological adaptations to consume detritus from sediment and phytoplankton (Pilati, 2007; Zeug, Winemiller, 2008; Smoot, Findlay 2010a, 2010b). In these studies, *D. cepedianum* assimilated carbon from both allochthonous and autochthonous origin in floodplains. This result was related to hydrology, since according to Wetzel (1990) the proportion of terrestrial inputs is higher on wetlands than rivers, whereas autochthonous production is higher in rivers than wetlands. Another study investigating the isotopic ratios for the same fish species indicated that, although they are dependent on carbon sources from both origins, autochthonous items prevailed, with phytoplankton contributing more than 50% to the production of fish biomass throughout the environments studied (Babler *et al.*, 2011).

Other authors have aimed to explain these results and reported that the consumer prefers items with high carbon and nutrient contents (Higgins *et al.*, 2006). Thus, detritivores have high selectivity, ingesting sediment particles enriched in organic matter, which include detritus of terrestrial plants, algae, and microorganisms (Smott, Findlay, 2010a). Smott, Findlay (2010a, 2010b) also mention that allochthonous organic carbon may contribute indirectly to the detritus biomass, by the fact that autochthonous microorganisms utilized terrestrial detritus as a resource.

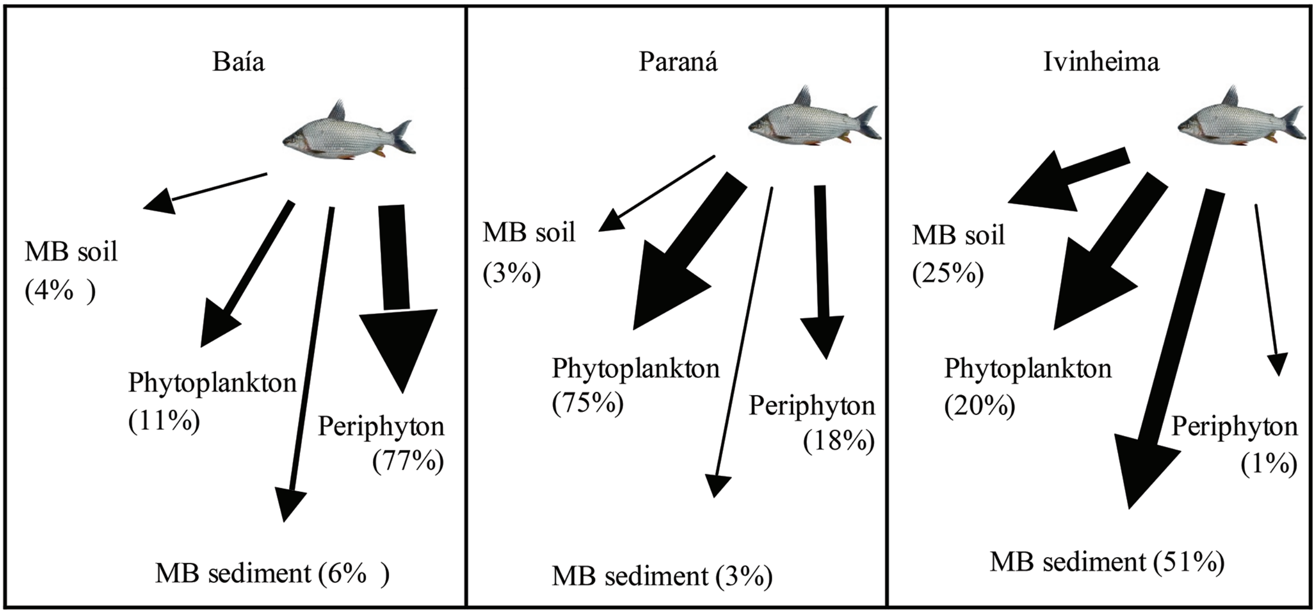

Fig. 4. The average percentage contribution of each carbon source in different subsystems. The width of arrows represents the strength of resource utilization in each environment studied (MB = microbial biomass).

In an experiment in mesocosms, Pilati (2007) added carbon derived from *Zea mays* L. (maize) to the sediment and found (by this natural ^{13}C labeling approach), that the terrestrial carbon was assimilated. It was unclear if the carbon was incorporated directly, or by a pathway of microorganisms that also utilized the detritus coming from maize. This trend was also registered in this study, primarily in the Ivinheima River, where the use of microbial biomass by *P. lineatus* was predominant. Hence, it is possible that the species had assimilated carbon derived from terrestrial sources via the microorganisms pathway. The nutrients and other terrestrial materials originating from agricultural areas may increase phytoplankton production, consequently providing a high amount of phytodetritus for detritivorous fish, explaining the use of autochthonous sources in several studies (Bremigan *et al.*, 2008). It is worth mentioning that the environments of the floodplain of the Upper Paraná River suffer from negative agricultural effects (Agostinho *et al.*, 2004), which might have caused the greater assimilation of autochthonous carbon by *P. lineatus*.

The studies mentioned above show the importance of allochthonous and autochthonous resources for bottom foraging fish species. The phytoplankton was the main resource used by the species. Isotopic studies have shown the significant contribution of phytoplankton algae to aquatic organisms, including detritivorous fish (Araujo-Lima *et al.*, 1986; Benedito-Cecilio *et al.*, 2000; Benedito-Cecilio *et al.*, 2004; Lopes *et al.*, 2015) and zooplankton (Santana *et al.*, 2009; 2011). Among these are studies on the Orinoco River (Venezuela and Colombia), which showed that phytoplankton was among the main carbon sources for fish and invertebrates (Lewis *et al.*, 2001). Similarly, Araujo-Lima *et al.* (1986) found that detritivorous fish from the floodplain of the Amazon River used detritus derived from phytoplankton production. In the floodplain of the Upper Paraná River, the isotopic analysis of muscles of *P. lineatus*, revealed that phytoplankton algae are among the main sources of carbon used by species of fish in the studies developed by Lopes *et al.* (2007). This trend can also be justified by the fact that, in the period from 2000 to 2007, the phytoplankton biomass was considerably higher in the floodplain, while the highest value was registered for the Paraná River, followed by Baía and Ivinheima Rivers (Rodrigues *et al.*, 2009). In Ivinheima the contribution from MB soil was the highest, once that this environment has the greatest ecological integrity, since its banks are more preserved (Agostinho, Zalewski, 1996).

There are many considerations about the resources used by detritivorous fish, and there are many uncertainties (Moore *et al.*, 2004). Detritivores consume a mixture of material composed of terrestrial detritus and microorganisms (Smoot, Findlay, 2010a, 2010b). Besides the importance of phytoplankton for detritivores (Araujo-Lima *et al.*, 1986; Benedito-Cecilio *et al.*, 2000; Benedito-Cecilio *et al.*, 2004; Angelini *et al.*, 2013) other sources (riparian vegetation, particulate organic matter, periphyton, and macrophytes) are also relevant (Manetta *et al.*, 2003; Lopes *et al.*, 2007). Given this contrast, it is important to emphasize that both energy sources are important. However, the major challenge is to determine the factors that regulate the use of these resources by fish species. These factors may be related to the size and characteristics of the aquatic ecosystem. For example, in situations where the allochthonous production decreases with surface area, autochthonous production increases (Pace *et al.*, 2007). Another situation occurs when large aquatic areas receive both terrestrial organic carbon and inorganic nutrients (Wetzel, 1990), often originating from agriculture.

Such nutrients increase phytoplankton production (Vanni *et al.*, 2011).

Considering the above, it appears that the detritivorous fish species *P. lineatus* used autochthonous resources as carbon sources. However, the importance of the wetlands was highlighted, because they have a large input of organic material (due to their inherent characteristic of seasonal floods) (Agostinho, Zalewski, 1996). The authors have reported that these environments are dynamic and with high species diversity. However, the authors highlight that the Upper Paraná River is a region that has considerable anthropogenic influence, which is reflected in the biotic community. This basin has the greatest demographic density in the country and, thus, has of large water demand. Agostinho, Zalewski (1996) point out that the water for irrigation in the intense agriculture, the livestock activities, the inadequate soil management, the pesticides used, and the degradation of riparian vegetation have harmed the quality of water for human use and aquatic life. For these authors, the largest anthropogenic impact is the dams because they have significantly modified the physiographic characteristics of this basin, affecting all principal affluents and the hydrological regime of the Paraná floodplain.

This study showed the importance of phytoplankton and periphyton as an energy source for *P. lineatus*. However, the finding that this fish species consumed these sources differently in each environment provide evidence of the importance of environmental factors for food selectivity. Therefore, studies should employ an eco-hydrological approach that quantifies the magnitude of energy subsidies, as well as assesses routes to aquatic consumers. It is also important to clarify under what conditions the input of organic matter is dependent on allochthonous or autochthonous sources, and why and how the consumers select energy resources to be assimilated. For this, it is essential to gain knowledge about the selectivity of the species, the size of the watershed, the extent of allochthonous resources, phytoplankton productivity, and different land uses. Such studies are important to trace the influence of these pathways in the carbon cycle of aquatic food chains, but also to protect and conserve aquatic species.

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