BIOTA AMAZÔNIA
OPEN JOURNAL SYSTEM
ARTICLE
DOI: http://dx.doi.org/10.18561/2179-5746/biotaamazonia.v9n4p8-12

Contribution of C_3 and C_4 autotrophic sources for juvenile Characiformes in the aquatic herbaceous plants in the Solimões River, Central Amazon, Brazil

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ABSTRACT

Understanding the factors that control production of commercially important fishes in the Amazon are necessary to effectively manage fisheries resources in the region. The first step of this understanding demands the identification of plants that contribute to the energy flow in fish's food web. The objective of this study was to investigate which group of plants supports the production of Characiformes during their juvenile life phase, in which these fish inhabit an environment formed by C_3 and C_4 plants. A carbon isotope analysis was conducted for juvenile Characiformes collected from herbaceous aquatic stands of the Solimões River floodplain. The diet of these fishes was also analyzed to identify possible trophic links. The results indicate that although C_3 plants are the main energy sources of juveniles, the juvenile stage is that the sampled species have higher contribution from group of C_4 plants. A diet analysis revealed that juveniles of *Brycon amazonicus*, *Mylossoma duriventre* and *Triportheus angulatus* consume energy sources through invertebrate herbivores, while *Semaprochilodus insignis* fed the sources directly on detritus. The dependence of juvenile fish diets on both C_3 and C_4 plants suggests that the maintenance of herbaceous aquatic environment is extremely important for fish communities in Amazonian floodplains.

Keywords: Fish; stable isotopes; food web; floodplain; diet.

Contribuição de fontes autotróficas C_3 e C_4 para Characiformes juvenis em plantas herbáceas aquáticas no rio Solimões, Amazônia Central, Brasil

RESUMO

A compreensão dos fatores que controlam a produção de peixes comercialmente importantes na Amazônia é necessária para gerenciar efetivamente os recursos pesqueiros da região. O primeiro passo deste entendimento exige a identificação de plantas que contribuem para o fluxo de energia nas redes alimentares dos peixes. O objetivo deste estudo foi investigar qual grupo de plantas suporta a produção de Characiformes durante a fase juvenil, estágio em que estes peixes habitam um ambiente formado por plantas C_3 e C_4. Uma análise isotópica de carbono foi conduzida para Characiformes juvenis coletados em plantas herbáceas aquáticas na planície de inundação do rio Solimões. A dieta desses peixes também foi analisada para identificar possíveis elos tróficos. Os resultados indicam que embora as plantas C_3 sejam as principais fontes de energia dos juvenis, o estágio juvenil é a fase que as espécies amostradas têm maior contribuição do grupo de plantas C_4. A análise da dieta revelou que juvenis de *Brycon amazonicus*, *Mylossoma duriventre* e *Triportheus angulatus* consomem fontes de energia através de invertebrados herbívoros, enquanto *Semaprochilodus insignis* alimenta-se diretamente através de detritos. A dependência das dietas dos peixes juvenis das plantas C_3 e C_4 sugere que a manutenção do ambiente das herbáceas aquáticas é extremamente importante para as comunidades de peixes nas várzeas da Amazônia.

Palavras-chave: peixe, isótopos estáveis, teia alimentar, várzea, dieta.

Introduction

In floodplains of the Solimões River herbaceous aquatic plants are considered the main producers due to contribute with 65% of the total biomass being followed by the trees of the flooded forest (28%), periphyton (5%) and phytoplankton (2%) (COSTA et al., 2017). In general herbaceous aquatic stands in Central Amazon are composed of a mixture of C_4 (Hatch-Slack photosynthetic path) and C_3 (Calvin cycle photosynthetic path) plants, the C_4 vegetation dominate both in abundance and biomass (SOARES et al., 2014), however, previous studies has indicated that C_3 plants are the principal autotrophic energy source for Characiformes fish species in the floodplain, for both larval and adult life stages (LEITE et al., 2002; MORTILLARO et al., 2016).

In order to effectively manage fisheries resources in the Solimões River, an understanding of the factors that control production of fisheries biomass is required (SANTOS et al., 2017). One of the first steps involves identifying the autotrophic carbon sources that sustain fish food webs at all stages of development of these animals (CARVALHO et al., 2017; KAYMAK et al., 2018).

The use of carbon stable isotopes has been an important tool in studies of fish trophic ecology over the past 25-30 years (JENNINGS; COGAN, 2015; DENG et al., 2018). Carbon stable isotopes ($\delta^{13}C$) are normally used as biological delineators of energy flux (CARABALLO et al., 2016; ZULUAGA-GÓMES et al., 2016; SOUSA et al., 2016). The information obtained by traditional methods such as stomach content analysis is only able to indicate what the fish ingested in a specific moment, rather than identifying the energy sources that were assimilated into the fish tissues (MORTILLARO et al., 2016). As juvenile Characiformes exclusively inhabit the dense stands of herbaceous aquatic in the floodplain during this developmental stage (MOUNIC-SILVA; LEITE, 2013), one would expect that the principal autotrophic energy sources of these fish to be derived from within the plant community, as opposed to externally derived sources. Juvenile fish, depending on their feeding strategies, could ingest C_4 plants directly, including bits of leaves, seeds, roots or detritus (MOTTA; UIEDA, 2005), or utilize the energy derived from these plants indirectly via consumption of aquatic and terrestrial invertebrates found within herbaceous stands (DIAS et al., 2017; KAYMAK et al., 2018).

In this context, to improve the understanding of the factors that sustain the production of fish populations in floodplains of the Amazon drainage basin the objective of this study was to evaluate the dynamics of energy in the food chain of juveniles of *Brycon amazonicus*, *Mylossoma duriventre*, *Semaprochilodus insignis* and *Triportheus angulatus* collecteds in herbaceous stands along a stretch of the Solimões River, combining the analysis of carbon isotopic composition with the analysis of the feeding of these species.

Material and Methods

Study area

Fish samples were collected in herbaceous aquatics stands, at a total of forty sites located in two areas of the Solimões River: ten sites upstream (■) and ten sites downstream (●) of the confluence of Solimões River with the Lake Coari (3º54'42,9"S, 63º17'29,6"W - 3º59'073"S, 62°52'23,8"W, respectively); and ten sites upstream (□) and ten sites of the downstream (▲) of the confluence of the Solimões River with the Negro River (3°16'72,7"S, 60º03'43,3"W - 3°02'68,1"S, 59º46'88,9"W) (Figure 1), the distance between each site was one kilometer. The objective of this sampling methodology was to examine the spatial variation in carbon stable isotope ratios of the species sampled (Figure 1).

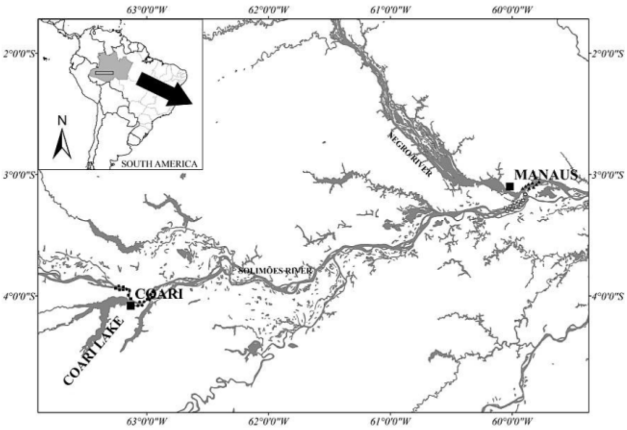

Figure 1. Geographic locations of the fish collection areas in floodplain habitats along the Solimões River, Central Amazon, Brazil.

Sampling was conducted monthly between December 2007 and April 2008 during the rising water period, which coincides with the spawning period of the migratory fishes' species (BAYLEY; PETRERE, 1989). The initial development of these species occurs in the main river channel where they feed off their yolk reserves, but after the total absorption of these reserves, Characiforme larvae colonize places where they find food and protection against predators (GOULDING, 1980; BAYLEY; PETRERE, 1989). The selection of species was based on their commercial importance (BARTHEM; GOULDING, 2007). *B. amazonicus*, *M. duriventre*, *S. insignis* e *T. angulatus* were frequent in the group Characiforme which represents more than 50% of the total juveniles captured in the herbaceous aquatics stands of the Solimões River.

Sampling methodology

Fishes were collected using dip-nets (1.1 x 0.8 m diameter and 5 mm mesh size) and seine nets (10 x 3 m diameter and 5 mm mesh size). Upon capture, specimens were placed on ice before being preserved in 10% formalin and transported to ichthyoplankton laboratory of the National Institute of Amazonian Research (INPA) in Manaus, AM, Brazil.

In the laboratory, fishes were identified to the level of species based on ontogenetic sequence and counting of vertebrae and patterns of pigmentation (ARAÚJO-LIMA et al., 1993; ARAÚJO-LIMA; DONALD, 1988; ARAÚJO-LIMA; HARDY, 1987). Juveniles were also identified with the help of experts and compared with specimens previously identified in the Ichthyoplankton Laboratory. Later, with the objective of verifying the progressive ontogenetic variation in feeding due to the increase in size during the juvenile development, the specimens were divided into two classes of development according to their standard length (SL) constituting class I (juveniles between 15 to 30 mm) and class II (juveniles between 31 and 60 mm).

Stomach content analysis

Stomach content analysis was performed for each species and analyzed in relation to size class and collection area. Diet composition was determined according to the following recognized categories: fish (including fins, scales and muscle tissue); zooplankton (including cladocerans, copepods, ostracods and rotifers); detritus (particulate organic matter); insects (adults, larvae, pupae and dismembered pieces); spiders; and vegetable matter (including pieces of leaves, fruits, roots and plant stock). The importance of each food item was calculated according to the feeding index proposed by Kawakami and Vazzoler (1980).

Stable isotope analysis of carbon ($\delta^{13}C$)

Individuals from each species and size class were sampled for stable isotope analysis of carbon. A small sample of muscle tissue was removed from the dorsal area, rinsed with distilled water and oven dried at 60ºC for 48 hours. After drying, the samples were ground into a fine powder using a mortar and pestle, placed in tin capsules and shipped to the Environmental Stable Isotope Center in the Bioscience Institute at the State University of São Paulo, Botucatu Campus, SP, Brazil for analysis of carbon isotope ratios using an elemental analyzer (EA 1108 CHN) coupled with a isotope ratio mass spectrometer (DELTA-S Finningan MAT). The carbon ($\delta^{13}C$) isotope ratios was expressed by the following formula:

$$Sample(\%) = \frac{R_{sample} - R_{standard}}{R_{standard}} x1000$$

Later, the carbon isotope values were corrected because the samples were preserved in formalin solution and this substance caused a 1.65‰ reduction in carbon isotopic signatures (SARAKINOS et al., 2002). To determine the relative contribution of C_4 plants for each fish species was used the following two end-member mixing model (FORSBERG et al., 1993):

$$\%C_4 = [1 - \delta^{13}C_{fish} - \delta^{13}C_{C4}/\delta^{13}C_{C3} - \delta^{13}C_{C4}]100$$

Where: $\%C_4$ is the percentage of contribution of C_4 plants, $\delta^{13}C_{fish}$ is the mean value of $\delta^{13}C$ for fish, $\delta^{13}Cc_3$ is the mean value of $\delta^{13}C$ for C_3 plants and $\delta^{13}Cc_4$ is the mean value of $\delta^{13}C$ for C_4 plants.

In the present study, was used the carbon isotope data of local autotrophic sources registered at Benedito-Cecílio et al. (2000) because they are representative of the region studied: C_4 = -13.4‰, Periphytic algae = -28.3‰ and Phytoplankton = -37.2‰. These values were obtained from spatial and seasonal variations in 495 samples of plants along an 1800 km west-to-east (i.e. upstream-dowstream) transect of Amazon River between the cities of Vargem Grande (3° 16' S, 67° 55' W) and Óbidos (1° 55' S, 55° 30' W), Brazil during the low and high water seasons between October 1983 and July 1998.

In order to verify if there was a significant influence of juvenile development stage on the isotopic ratios of $\delta^{13}C$ and if there were significant variations among the species, the Student's t-test was used with the Shapiro-Wilk and Levene tests *a priori* and Tukey's test ($p<0.05$) *a posteriori*. The analyzes were conducted with the aid of the Statistical Program *PAleontological STatiscs* - PAST, version 3.15 (HAMMER, 2017).

Results

Average $\delta^{13}C$ values and standard deviation of the juvenile fish ranged from a maximum of -24.6‰ ± 1.0 for class II of *B. amazonicus*, in the confluence of the Solimões River with the Negro River (Manaus) to a minimum of -31.2‰ ± 1.2 for class II of *T. angulatus*, in the confluence of Solimões River (Coari) with the Lake Coari (Table 1).

Table 1. Averages and standard deviations of ^{13}C values and estimates of minimum and maximum contributions of C_4 plants for *Brycon amazonicus, Mylossoma duriventre, Semaprochilodus insignis* and *Triportheus elongatus.* (n) = number of samples; Min. = minimum; Max. = maximum; SD = standard deviation; Size classes: I- 15 to 30; II- 31 to 60 mm SL.

Species	Size classes	COARI					MANAUS				
		^{13}C			C_4 contribution (%)		^{13}C			C_4 contribution (%)	
		n	Avg.	SD	Min.	Max.	n	Avg.	SD	Min.	Máx.
Brycon amazonicus	I	20	-28.6	1.0	2	35	20	-25.8	2.2	20	50
	II	28	-27.6	1.1	10	40	28	-24.6	1.0	20	50
Mylossoma duriventre	I	20	-27.0	9.5	10	40	20	-28.3	1.5	0	40
	II	24	-28.1	1.3	10	40	24	-27.4	1.0	10	40
Semaprochilodus insignis	I	20	-25.9	1.5	20	50	20	-25.5	0.5	20	50
	II	39	-27.5	1.2	10	40	39	-27.6	1.8	10	40
Triportheus angulatus	I	20	-30.3	0.5	10	30	20	-28.2	0.7	10	40
	II	40	-31.2	1.2	20	30	40	-27.4	1.6	10	40
AVG					11.5	38.1				12.5	43.8

The normality assumptions and homocedasticity were met and later it was verified with the t test that there was no significant difference between development classes of each species ($p>0.05= 0.3254$; $t= 0.5966$) therefore, sampling site were pooled across developmental class of the species for both sampling regions: Coari and Manaus.

Only the species *T. angulatus* and *B. amazonicus* significantly differ between the sampling sites because values of $\delta^{13}C$ were lower in Coari and higher in Manaus (Tukey $p<0.05 = 0.0132$). There were also significant differences between development classes of both species (Tukey $p<0.05 = 0.0001$). *T. angulatus* was enriched in $\delta^{13}C$ in Manaus and impoverished in Coari, while *B. amazonicus* enriched in $\delta^{13}C$ in Coari and Manaus with increasing (Figure 2d; 2a). There was no significant difference between the classes of development of *M. duriventre* and *S. insignis* ($p>0.05=0.5853$) (Figure 2b; 2c).

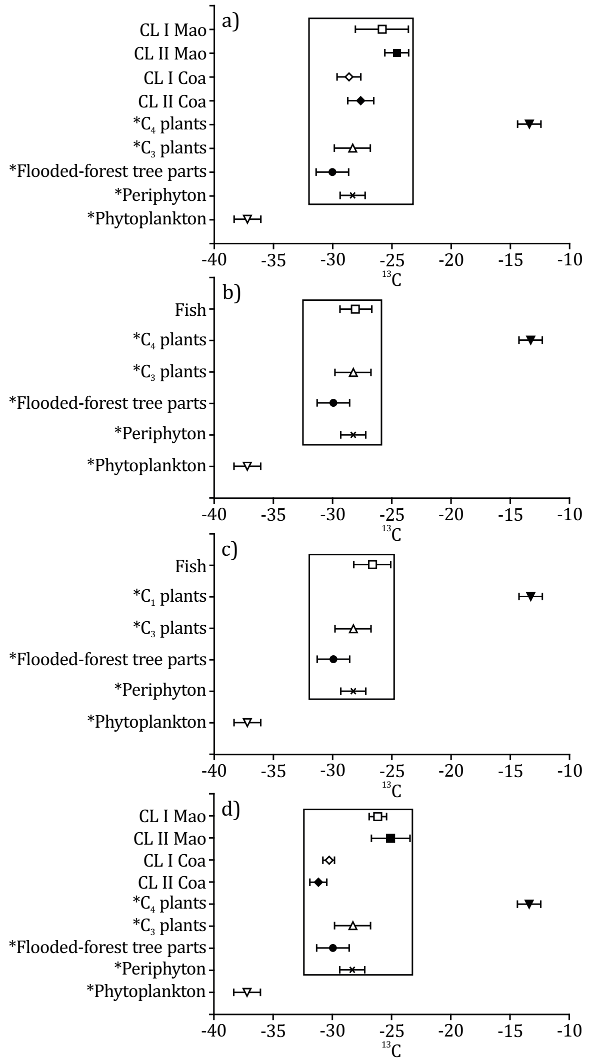

Figure 2. Averages and standard deviations of $\delta^{13}C$ (‰) of a) *Brycon amazonicus,* b) *Mylossoma duriventre,* c) *Semaprochilodus insignis* and d) *Triportheus angulatus* collected in aquatic herbaceous plants. *Mean $\delta^{13}C$ of plants from de Amazon floodplain reported by Benedito-Cecílio et al. (2000) for the same region. For species that there was no significant difference between the classes of development and/or sampling sites (*M. duriventre* and *S. insignis*) is shown only mean $\delta^{13}C$ of species. The rectangle indicates the range of autotrophic sources in which the values of $\delta^{13}C$ juveniles are inserted. COA = Coari; MAO = Manaus; Size classes (mm SL): I - 15 to 30; II - 31 to 60.

The analysis performed with the two end-member mixing model revealed variations in relative contributions of C_4 plants between the two collection sites, because the species *B. amazonicus* and *T. angulatus* in Manaus presented in their two classes of development a contribution of plants C_4 superior greater that in Coari, while the relative contribution of plants C_4 to *M. duriventre* and *S. insignis* did not present changes (Table 1). The estimates of average relative contributions of C_4 grasses to the autotrophic energy sources of the juvenile fish varied from a minimum of 11.5% to a maximum of 38.1% in Coari and a minimum of 12.5% to a maximum of 43.8% in Manaus (Table 1).

For stomach content analyzes were used 1250 stomachs, of which 1181 (94.5%) contained food items. Stomach content analysis did not present significant differences in the diet of the species with respect to the collection areas (Coari and Manaus, downstream and upstream locations) ($p>0.05=0.6318$). Therefore, the analysis was only applied to the development classes of each species, eliminating the need to analysis by geographic location. The diet of juveniles of *B. amazonicus*, *M. duriventre* and *T. angulatus* were high in animal content, principally insects and zooplankton, presenting a higher percentage in class I (88.3%) than class II (57.5%) (Figure 3a; 3b; 3d). For the same species, there were also large differences in plant matter content, which varied from 1.3% in class I to 33.9% in class II. In comparison, *S. insignis* presented a diet low in animal content (21% in class I and 19% in class II), composed only of zooplankton, while 60% constituted a mixture of detritus and algae (Figure 3c).

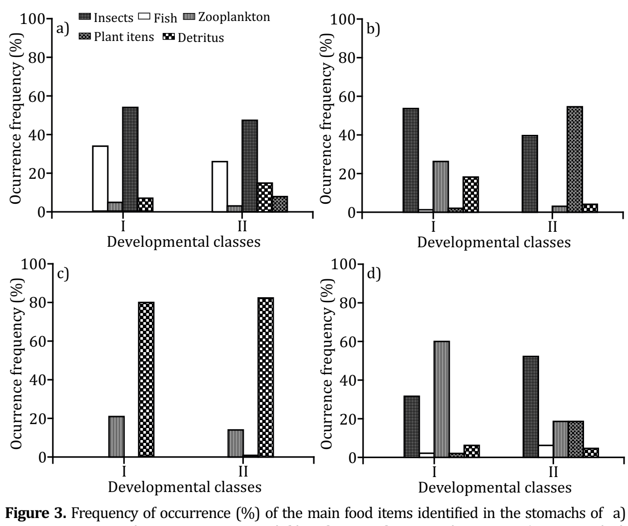

Figure 3. Frequency of occurrence (%) of the main food items identified in the stomachs of a) *Brycon amazonicus* (n= CL I: 124; CL II: 96), b) *Mylossoma duriventre* (n= CL I: 165; CL II: 128), c) *Semaprochilodus insignis* (n= CL I: 122; CL II: 109) and d) *Triportheus angulatus* (n= CL I: 215; CL II: 222) collected in aquatic herbaceous plants.

Discussion

The $\delta^{13}C$ values of *B. amazonicus*, *M. duriventre*, *S. insignis* and *T. angulatus* indicate that although such juveniles inhabit an environment where plants of the group C_4 predominates over the group C_3, it is likely they selectively consume and/or assimilate C_3 plants, following patterns observed in adult fish.

These results reiterate the studies that indicate that the fish present food selectivity being this tendentious to the consumption of plants of the group C_3 (GINDERDEUREN et al., 2014; NANDI; SAIKIA, 2015; DENG et al., 2018).

In this sense, previous studies have shown that herbivorous and detritivorous fish generally avoid C_4 plant foods because these plant sources, because they are rich in fiber, have low levels of nutrients and phenolic compounds that reduce their digestibility and palatability (FORSBERG et al., 1993; MORTILLARO et al., 2015). On the other hand, C_3 plants have nutritional characteristics that attract herbivores and detritivores, since herbaceous C_3 leaves, all algae, seeds and fruits of the trees have the highest average levels of minerals and proteins, are poorer in fiber and are, therefore, a source of energy assimilated more quickly by the body and also more nutritious (MORTILLARO et al., 2016; DENG et al., 2018).

However, the results of this study suggest that the juvenile stage is the only stage of development in which the fish show greater consumption of C_4 plants. This observation derives from the fact that while the maximum contribution of the C_4 plants to juveniles of the analyzed species was 38.1% in Coari and 43.8% in Manaus while the largest contribution of C_4 plants to the larvae of *Brycon cephalus*, who was later identified the *Brycon amazonicus* (LEITE, 2004), *M. duriventre*, *S. insignis* and *T. angulatus*, collected in amazonian floodplain lakes, was only 22% (LEITE et al., 2002). Likewise, for adult specimens of *T. angulatus*, *M. duriventre* and *S. insignis*, the maximum contributions of C_4 plants calculated by Forsberg et al. (1993) were 0%, 20% and 23.4%, respectively. These results probably reflect the large dilution of C_4 plant energy by the assimilation of C_3 plant energy during the adult phase of development, which occurs mainly in the flooded forest where C_3 plant sources dominate. It is likely that movements among habitats during different growth phases explain the varying groups contributions of plant sources, corroborating the studies of Hobson and Clark (1992), who suggested that the isotopic signals encountered in animals' tissues depend on a mixture of diet and habitat displacements.

On the other hand, Oliveira et al. (2010) found that juvenile Characiformes, of the species *Colossoma macropomum*, fed in an artificial environment, synthesized muscle tissue more rapidly with diet of C_3 plants. In addition, the quality of the dietary amino acids C_4 plants is inadequate to promote the development of the species. As this study is based fish captured in the wild, the most plausible explanation for the great contribution from C_4 plants at this stage of development of Characiformes is effect of the higher abundance of C_4 group. Although stands of herbaceous is an association of C_3 and C_4 plants, the C_4 herbaceous are the most abundant plant within the group herbaceous aquatic community in the Solimões river floodplain, resulting in a greater volume of organic matter from that group of plants and available aquatic environment (SOARES et al., 2014).

The analysis of the diet of the species revealed that the juveniles assimilate the energy of the C_3 plants in an indirect way, that is, through trophic links, among which are the herbivorous invertebrates of autochthonous and allochthonous origin that inhabit the herbaceous stands. These results confirm the importance of trophic links in the transfer of autotrophic energy to the sustenance and maintenance of the aquatic food chain (POST, 2002; CAMPOS et al., 2015). In addition, it is also possible that subtle variations in the isotopic composition of species such as *B. amazonicus* and *T. angulatus* are due to the consumption of aquatic invertebrates which is susceptible to variations depending on the fish's food preference and the availability of the resource in the environment (UIEDA; PINTO, 2011; DIAS et al., 2017).

Although it is not possible to state with precision which plant group C_3 was the most important source for *S. insignis*, apparently these juveniles do not use phytoplankton as their main source of autotrophic energy because its isotopic signature remained in the range of sources as periphyton C_3, C_3 herbaceous and flooded parts of the forest, plants that are common on the banks of herbaceous, probably because *S. insignis* forages exclusively on herbaceous bank because Araújo-Lima and Hardy (1987) reported these juveniles sucking submerged stems of herbaceous aquatic structures in which they adhere periphytic algae, detritus and other organic materials. Since for adults of *S. insignis* in the Amazon floodplain, the phytoplankton is indicated as the main source of carbon because this phase of life this specie forage in other environments where the phytoplankton is abundant as per example, in the open waters of the floodplain lakes and the main river (ARAÚJO-LIMA et al., 1986; FORSBERG et al., 1993; BENEDITO-CECÍLIO; ARAÚJO-LIMA, 2002).

Conclusion

In conclusion, the analysis of carbon isotope showed that the contribution of C_4 plants to the development of juveniles is higher than for larvae and adults because the juvenile stage is the only period in which the analyzed species live and forage exclusively in herbaceous banks. In combination with diet analysis, was observed that the consumption of energy sources by autotrophic juvenile of the species *B. amazonicus*, *M. duriventre* and *T. angulatus* occurs by the invertebrate herbivores in these fish's food chains and in *S. insignis* occurs directly through detritus. Although large contribution of C_4 plants to juveniles' diets, C_3 plants are the most important energy source for the four species throughout the juvenile phase. Therefore, the results of this study indicate that C_3 and C_4 plant groups together can ensure future fish stocks, therefore the maintenance of herbaceous aquatic environments is extremely important for the fish communities in the floodplains of the Amazon.

Acknowledgements

This work was part of the master's thesis of the first author, supported by Conselho Nacional de Pesquisa (CNPq) (Proc. 132841/2008-8) and financial support of the project Socio-environmental Intelligence in the Amazon (PIATAM IV-FINEP/PETROBRAS).

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