Research Article

Carbon sources of fish in an Amazonian floodplain lake

A. Cristina B. Oliveira[1]*, M. Gercilia M. Soares[2], L. Antonio Martinelli[3] and M. Zacarias Moreira[3]

[1] Universidade Federal do Amazonas, Departamento Ciências Pesqueiras, 69077-000, Manaus, AM, Brazil
[2] Instituto Nacional de Pesquisas da Amazônia, CP 478, 69011-090, Manaus, AM, Brazil
[3] Universidade de São Paulo, Centro de Energia Nuclear na Agricultura, CP 96, 13470-900, Piracicaba, SP, Brazil

Abstract. In a tropical floodplain lake in central Amazon (L. Camaleão), we investigated seasonal shifts in primary carbon sources for commercially important fish species over an hydrological cycle. Carbon and nitrogen stable isotope and stomach content analyses were conducted to investigate the feeding preferences of six species with different feeding habits: *Cichla monoculus* (piscivorous species), *Schizodon fasciatus* (herbivorous), *Prochilodus nigricans* (detritivorous), and the omnivorous species *Triportheus angulatus*, *Colossoma macropomum* and *Mylossoma duriventre*. Stomach content and isotopic analyses exhibited a high seasonal variation for four out of the six species. The dominant food items were fruits and seeds, plant material, zooplankton and aquatic and terrestrial insects. Over the hydrological cycle, C_3 plants were the major carbon source for all fish species. In addition, seston and aquatic C_4 macrophytes were very important carbon sources for most species. Our findings underpin the complex trophic linkages between floodplain lakes and the aquatic terrestrial transition zone as postulated by the Flood Pulse Concept.

Key words. Carbon; nitrogen; food source; feeding habits; Amazon floodplain.

Introduction

Floodplains along the sediment-laden rivers in the Amazon basin become very fertile upon being flooded, making new environments available to be colonized by a rich and diverse ichthyofauna (Bayley, 1983; Junk et al., 1997; Merona and Bittencourt, 1993; Saint-Paul et al., 2000). These floodplains (locally called várzeas) support commercially valuable fish populations and the resulting fishery-related activities are the main income and food source for riverine communities (Cerdeira et al., 1997; Ruffino and Isaac, 1994).

The fish fauna of the floodplains have life cycles related to river level fluctuations (Junk et al., 1989). At rising and high water stages, the huge aquatic terrestrial transition zone provides shelter, protection and a wide range of food items. At falling and low water, the fish either have to remain in the floodplain lakes or migrate to connecting channels and the main river channel. Under the latter situation, survival conditions become difficult particularly due to the limited food resources (Lowe-McConnel, 1964; Goulding, 1980; Soares et al., 1986; Araújo-Lima and Goulding, 1998; Silva et al., 2000; Yamamoto et al., 2004).

The organic carbon sources for fish production in floodplain lakes originate from four primary producers. Based on the mean rate of aquatic carbon production and the area occupied by plants, Melack et al. (1999) estimated the contribution of herbaceous macrophytes to be 65%; floodplain forests, 28%; periphyton, 5% and phytoplankton, 2%. The distribution and production dynamics of each of these plant groups vary with the temporal variations in lake morphology, geochemistry, and flooding patterns (Melack et al., 1999). Traditional diet analy-

sis by gut content examination does not supply the necessary data for evaluating the relative contributions of the primary carbon sources of fish. These analyses only show what food was ingested by the fish at a specific moment and not what was consumed over a longer period, nor what was assimilated and incorporated into fish tissue. The ratio between the stable isotopes of some elements makes it possible to trace the flow of those elements through the food chain. This method is being used in feeding ecology studies which reconstruct diets and evaluate the relative importance of different components (Pearson et al., 2003).

In the Amazonian region, stable carbon isotopes have been used for determining the autotrophic energy sources of different fishes. In most studies that have investigated the temporal and spatial variations of the carbon sources, phytoplankton has been pointed out to be one of the main sources of energy for fish in the Amazon floodplain (Araújo-Lima et al., 1986; Forsberg et al., 1993; Benedito-Cecilio et al., 2000; Benedito-Cecilio and Araújo-Lima, 2002) and Orinoco River floodplain (Hamilton et al., 1992; Lewis et al., 2001). The conclusion that phytoplankton, which contributes only a small fraction (2%) to the total primary production on the floodplain (Melack et al., 1999), could support entire fisheries still remains unclear. Autotrophic energy source estimates based on isotopic values can vary depending on the method used in calculating these estimates. Within this context, the present study investigates the primary carbon sources of six commercially important fish species from Lake Camaleão, a floodplain lake in the central region of the Amazon River. By combining the use of stable isotope mixing models and stomach content analyses, we determine the primary carbon sources for floodplain fishes and evaluate the seasonality of these autotrophic energy sources.

Materials and methods

Our study was conducted in Lake Camaleão on Marchantaria Island (Brazil, 30° 15′ 12″ S and 59° 57′37″ W) on the Solimões River upstream from the confluence of the Negro River and the Amazon River (Fig. 1). At this location, mean annual water level fluctuation of the Amazon River is about 10 m. The water level starts to rise in November or early December and peaks in late June. Lake Camaleão is an elongated floodplain lake which at low water level is 7 km long and 50 m wide and 2.5 m deep, at high water level it is 8 km long, 300 m wide, and 10 m deep.

Between May 1999 and July 2001, we collected 728 specimens of six commercially important fish species with different feeding habits: the piscivorous species *Cichla monoculus* (locally called tucunaré; N = 53;
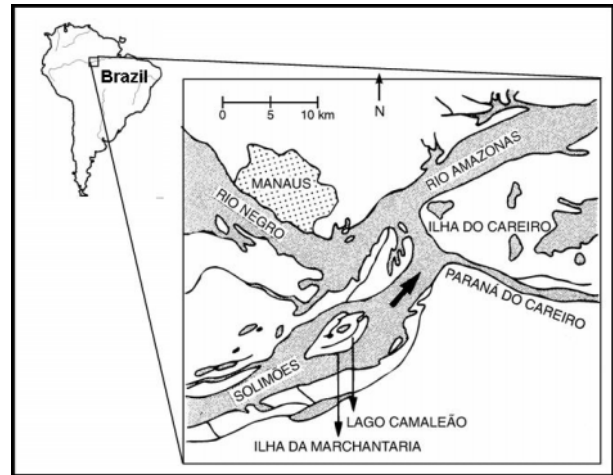

Figure 1. Map showing Marchantaria Island and Lake Camale, Amazon, Brazil, South-America (Modified after Junk et al., 1983).

standard length, Ls = 8.5–28.5 cm), the herbivorous species *Schizodon fasciatus* (aracú; N = 95; Ls = 7–26 cm), the detritivorous species *Prochilodus nigricans* (curimatã; N = 95; Ls = 13–24,5 cm), and the three omnivorous species *Triportheus angulatus* (sardinha, N = 126; Ls = 4.5–17.5 cm), *Colossoma macropomum* (tambaqui, N = 201; Ls = 8–38 cm), and *Mylossoma duriventre* (pacu, N = 158; Ls = 6–19.5 cm). We used 25×2 m gillnets with a bar mesh ranging from 30 to 200 mm that were extended from the shore to the middle of the lake for 24 h. The fish were sampled every 6 h, put on ice and taken to the field laboratory where they were measured (Ls within 0.1-cm precision) and analysed for stomach content. Fish were sampled monthly, however for analyses purposes were grouped according to the water level stage, that is, the rising water period (March to May); high water period (June and July); receding water period (October and November), and dry water period (December to February).

Stomach content analyses were performed on 654 specimens, which is the number that possessed more than a quarter of their stomach filled with food. Distinct food items were grouped into the following categories: Insects - which includes adult insects, larvae, nymphs, and pieces of insects; Crustaceans – shrimps; Fish – whole fish, pieces, fins and scales; Zooplankton – cladocerans, copepods, ostracods and rotifers; Molluscs – whole or fragmented animals; Fruit and seeds – whole fruit and seeds, pieces of fruit; Plant material – fragments of branches, bark, leaves, flowers and roots; Algae – unicellular, filamentous or colonial algae; and POM - amorphous particulate organic matter. The frequency of occurrence (OF) of each ingested item was calculated according to Hyslop (1980).

Stable isotope values of primary carbon energy sources from várzea floodplain lakes have presented little

variation. For example, the C_4 plants were depleted only at high water and C_3 plants did not show any change during the hydrological period (Benedito-Cecílio et al., 2000). In this study, the principal food sources for floodplain fish identified in the specimens' stomachs were collected in the field for isotopic analysis during the hydrological period when they occurred with greater frequency in the stomach content. Therefore, the isotopic values of the food sources correspond to the time when that particular food item was eaten. These are: 16 samples of terrestrial and aquatic C_3 plants (fruit, seeds and leaves), two samples of aquatic C_4 macrophytes – grasses (leaves and root), collected during high water; four samples of zooplankton, during falling and low water; 11 samples of insects associated with aquatic macrophytes and the flooded forest, during falling and low water; 6 samples of molluscs, during low water; four samples of shrimp, during falling water; and five particulate organic material samples (POM) from the bottom of the lake, collected during the low water period. Due to difficulties in acquiring pure samples of phytoplankton, three samples of seston were obtained during the falling and low water periods. These were collected by filtering water through a 53 μm mesh net to eliminate the zooplankton and large particles of detritus, and again through a 25 μm mesh net to retain the fine particulate matter (live phytoplankton, organic detritus and bacteria).

Six hundred and eleven (611) eviscerated fish samples and 51 samples of food items were dried at 60 °C and ground in a grinder until a fine powder was obtained for use in determining the isotopic composition. The isotopic analyses were performed at the Centro de Energia Nuclear na Agricultura – CENA, in the Isotopic Ecology Laboratory at the University of São Paulo. Combustion of the samples was performed under a continuous flow of helium in an elemental analyser (Carlo Erba, CHN – 1110), coupled with the Thermo Finnigan Delta Plus mass spectrometer. CO_2 and N_2 gases, resulting from the combustion of the samples, were analysed in duplicate, with an analytical error of 0.3‰ and 0.5‰, respectively. The isotopic ratios for carbon and nitrogen are expressed as deviations in parts per thousand from the PDB limestone and from atmospheric air nitrogen international standards, respectively, by:

$$\delta X(\text{‰}) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000 \qquad (1)$$

where: R_{sample} and $R_{standard}$ are the ratios $^{13}C : ^{12}C$ or $^{15}N : ^{14}N$ of the sample and the standard, respectively.

The relative contributions of the different primary carbon sources of the fish species studied were estimated by the concentration-weighted linear mixing model proposed by Phillips and Koch (2002). This model assumes that for each element, the contribution of food source to a consumer is proportional to the assimilated biomass times the elemental concentration in that source. Two isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) are used to determine the proportional contributions of three food sources, X, Y and Z (end-members) to a mixture, M (fish). The system can be solved using matrix algebra. A spreadsheet found at http://www.epa.gov/wed/pages/models.htm was used for the calculations.

The three sources to be used in the mixing model were selected among the four existing in the lake (herbaceous macrophytes, C_3 or C_4 plants; floodplain forests, C_3 plants; periphyton, and phytoplankton). The diet composition of the fish in each hydrological period was analyzed to determine this selection. The items with the highest occurrence frequency identified two primary sources: C_3 plants and C_4 aquatic macrophytes. Seston was chosen as the third source because several studies have concluded that phytoplankton is the main primary source for fish (Araújo-Lima et al., 1986; Hamilton et al., 1992; Forsberg et al., 1993; Araújo-Lima et al., 1998; Benedito-Cecílio et al., 2000 and Lewis et al., 2001). Due to a fractional contribution of each food source to the consumer's diet, these end-members were corrected according to fractioning values of 2.5‰ per trophic level for $\delta^{15}N$ and 1‰ for $\delta^{13}C$, as calculated by Oliveira (2003). For each fish species, the trophic level corrections of the energy sources were based on results of stomach content analyses, which indicated either direct ingestion (one trophic level) or indirect ingestion (two trophic levels) of each end-member. In the case of tambaqui, stomach content analyses showed that fruits and seeds, plant material and zooplankton were the food items most frequently encountered. Therefore, the end-members C_3 plants and aquatic C_4 macrophytes, which were ingested directly by the tambaqui, were corrected by only one trophic level. Seston, in contrast, which was ingested indirectly through direct consumption by zooplankton, was corrected by two trophic levels for the $\delta^{15}N$ and $\delta^{13}C$ values.

The data was analyzed using ANOVA and Tukey's multiple range tests for mean comparisons (Zar, 1996).

Results

Diet

Plant material was the dominant food item during the full hydrological cycle; however, fruit and seeds were found only during high and receding water (Fig. 2). Fruit and seeds were also important food items for the omnivorous species, i.e. *C. macropomum*, *T. angulatus*, and *M. duriventre*, especially during the high and receding water periods when fish have access to the flooded forest (Fig. 2). During the rising and low water period, plant material became as important as fruit and seeds for *C. macropomum* and *M. duriventre*. For *T. angulatus*, fruits and seeds

were more important during the receding water period. *C. macropomum*, *T. angulatus*, and *M. duriventre* also add items such as zooplankton and insects to their diet, and the occurrence frequency of these types of prey in-

creases as the water level falls. For the carnivorous *C. monoculus*, the main food item was fish throughout the entire year. For *P. nigricans*, a detritivorous species, POM was present year-round (Fig. 2).
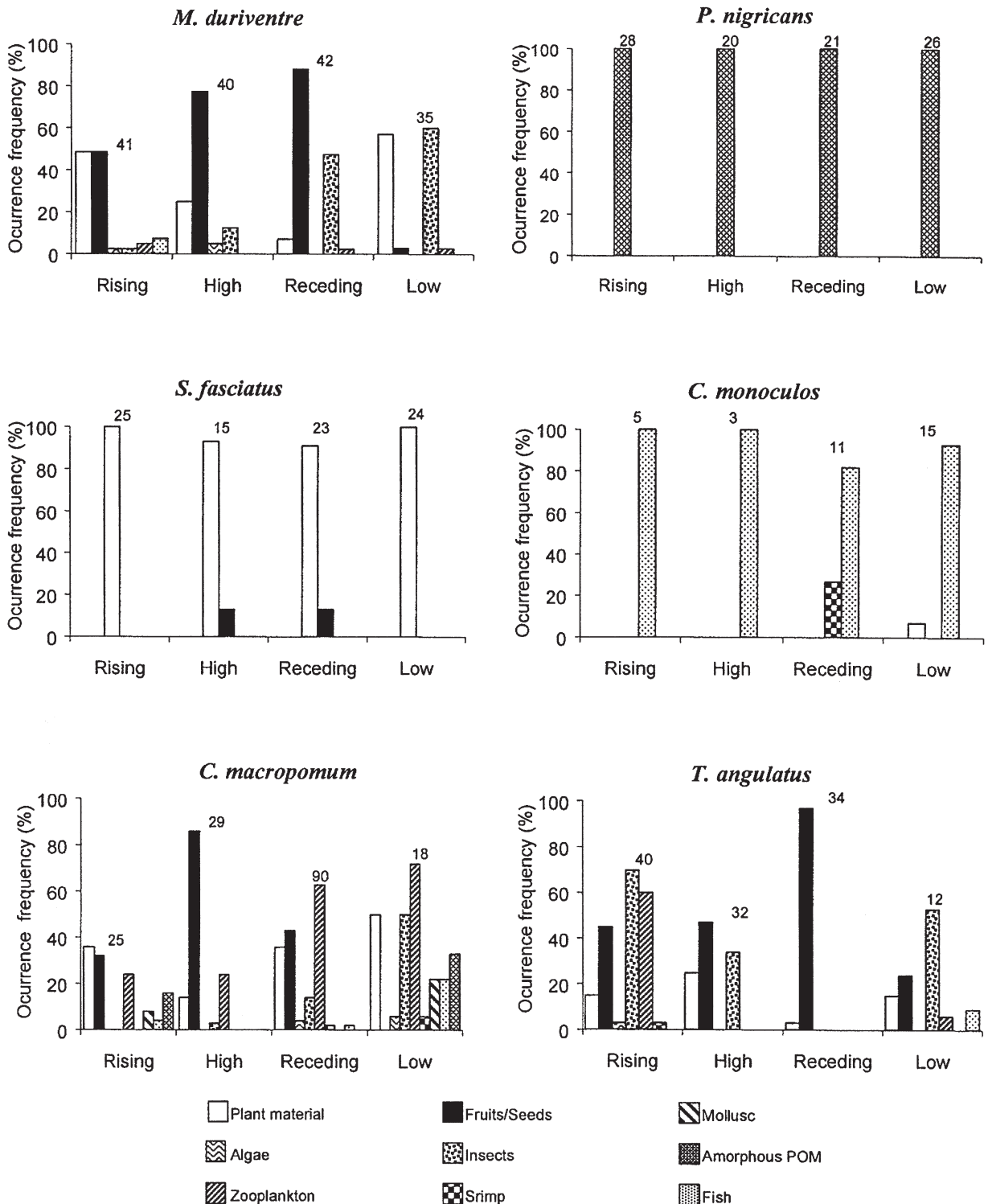

Figure 2. Occurrence frequency (%) of the main food items identified in the stomachs of the fish species. Numbers of analyzed fish are given on top of the set of bar graphs of each season.

$\delta^{13}C$ and $\delta^{15}N$ values of the food sources

The mean $\delta^{13}C$ and $\delta^{15}N$ values of 16 fruits and seeds were –29.3‰ and 4.5‰, respectively, indicating a C_3 plant origin (Fig. 3). Two aquatic C_4 macrophyte species, *Echinochloa polystachya* and *Paspalum repens,* presented mean $\delta^{13}C$ and $\delta^{15}N$ values of –12.9‰ and 6.6‰, respectively, showing more enrichment than that of C_3 plants in ^{13}C and ^{15}N. Seston samples presented mean $\delta^{13}C$ and $\delta^{15}N$ values of –36.1‰ and 6.6‰, respectively, which are similar to results reported by Hamilton et al. (1992) and Benedito-Cecílio et al. (2000). In addition to these primary carbon sources, the isotopic compositions of secondary sources (carbon derived from autotrophic sources) were also determined (Fig. 3). Zooplankton presented $\delta^{13}C$ values which were less enriched in ^{13}C than that of seston, with an average of –37.7‰. In comparison, the mean $\delta^{15}N$ value of zooplankton was 7.3‰, demonstrating more enrichment in ^{15}N than seston. Samples of POM and insects inhabiting C_3 plants presented mean $\delta^{13}C$ values similar to those of fruit and seeds (–29.4‰ and –28.8‰, respectively). However, the mean $\delta^{15}N$ values for both (5.8‰ and 6.0‰, respectively) were more enriched than in fruit and seeds (Fig. 3). Insects inhabiting C_4 plants also presented isotopic signals similar to that of the aquatic C_4 macrophytes with mean $\delta^{13}C$ and $\delta^{15}N$ values of –15.0‰ and 6.0‰, respectively. Both molluscs and shrimps presented mean $\delta^{13}C$ values of approximately –24‰, yet with distinct $\delta^{15}N$ values. The mean $\delta^{15}N$ value for shrimps was nearly 9.5‰, while molluscs presented a mean $\delta^{15}N$ value of 4.5‰ (Fig. 3).

$\delta^{13}C$ and $\delta^{15}N$ values of the fish

$\delta^{13}C$ values of the fish varied seasonally yet were also different depending on the species. *S. fasciatus* (Fig. 4C) was more enriched in ^{13}C during the rising water period

Table 1. Mean values of $\delta^{13}C$ and $\delta^{15}N$ ($\mu \pm$ S.D.) and elemental carbon and nitrogen of the end-members.

	Terrestrial C_3 plants	Aquatic C_4 macrophytes	Seston
$\delta^{13}C$ (‰)	–29.1 ± 1.2	–12.9 ± 0.7	–36.1 ± 0.2
$\delta^{15}N$ (‰)	4.5 ± 2	6.7 ± 0.1	6.6 ± 0.2
C (%)	45.8	32.1	33.4
N (%)	1.7	1.4	6.1

(–18.6 ± 3.4‰) than during the receding water period (–22.5 ± 3.9‰) (P < 0.05). *M .diriventre* (Fig. 4D) was also more ^{13}C-enriched during rising water (–20.5 ± 3.8‰) than during both the high water (–23.7 ± 3.7‰) and receding water (–23.5 ± 4.3‰) periods (P<0.05). *P. nigricans* (Fig. 4E), *T. angulatus* (Fig. 4F), and *C. monoculus* (Fig. 4B) presented similar seasonal variations. They were more ^{13}C-enriched in rising water (–26.1 ± 2.0‰; –26.4 ± 2.9‰ and –23.6 ± 2.5‰, respectively) than in low water (–28.8 ± 2.4‰; –28.5 ± 1.6‰ and –26.4 ± 2.1‰, respectively) (P < 0.05). *C. macropomum* (Fig. 4A) presented more values enriched in ^{13}C (–26.2 ± 2.3‰) (P < 0.05) during the rising water period than during the other periods.

With respect to $\delta^{15}N$ values, only *T. angulatus* and *C. monoculus* didn't present any seasonal variations. Mean values were 9.9‰ (±1.1) and 10.4‰ (±0.8), respectively (Figs. 4F and 4B). *C. macropomum* was more ^{15}N-enriched during low water (10.7 ± 2.2‰), compared to the receding (9.9 ± 1.3‰) and high (8.4 ± 1.3‰) water periods (P < 0.05) (Fig. 4A). *S. fasciatus* presented more ^{15}N-enriched values during rising water (9.9 ± 2.2‰) than during high water (7.8 ± 1.2‰) (P < 0.05) (Fig. 4C). *M. duriventre* also presented the most ^{15}N-enriched values

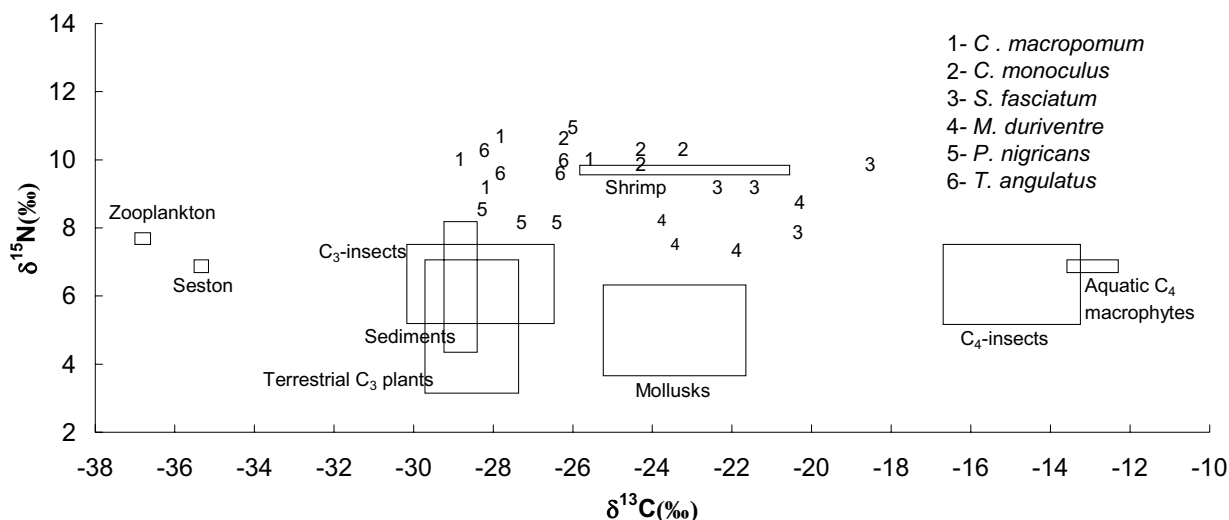**Figure 3.** Relationship between the $\delta^{13}C$ and $\delta^{15}N$ values of fish and carbon sources at Lake Camaleão. Numbers indicate mean values of fish in each period: rising, high, receding and low.

during rising water (8.8 ± 1.2‰), compared to the receding (7.3 ± 0.8‰) and low water periods (7.3 ± 0.7‰) (P < 0.05) (Fig. 4D). *P. nigricans* was also more ¹⁵N-enriched during the rising water period (11.0 ± 2.4‰), and this value differed (P < 0.05) from the other hydrological periods (Fig. 4E).

Primary carbon source of the fish
The results showed that C₃ plants constitute the main carbon source incorporated in the biomass of the fish over the entire hydrological cycle (Fig. 5). The contribution of C₃ plants was greatest during the high water and receding water periods in *C. macropomum* (81 and 63 %); *M. duriventre* (73 and 72 %) and *C. monoculus* (79 and 71 %), respectively. The smallest C₃ plants source contribution, 33 %, occurred during the low water period in *C. macropomum* (Fig. 5). The seston source presented the greatest contribution at low water with maximum values of 47 %, 36 % and 36 %, respectively, in the biomass of *C. macropomum*, *T. angulatus* and *P. nigricans*. The greatest contribution of aquatic C₄ macrophytes occurred in *S. fasciatus* (59 %) and *M. duriventre* (47 %) during the rising water period. C₃ plants and aquatic C₄ macrophytes were the only important carbon sources for these two species during the whole hydrological cycle (Fig. 5).
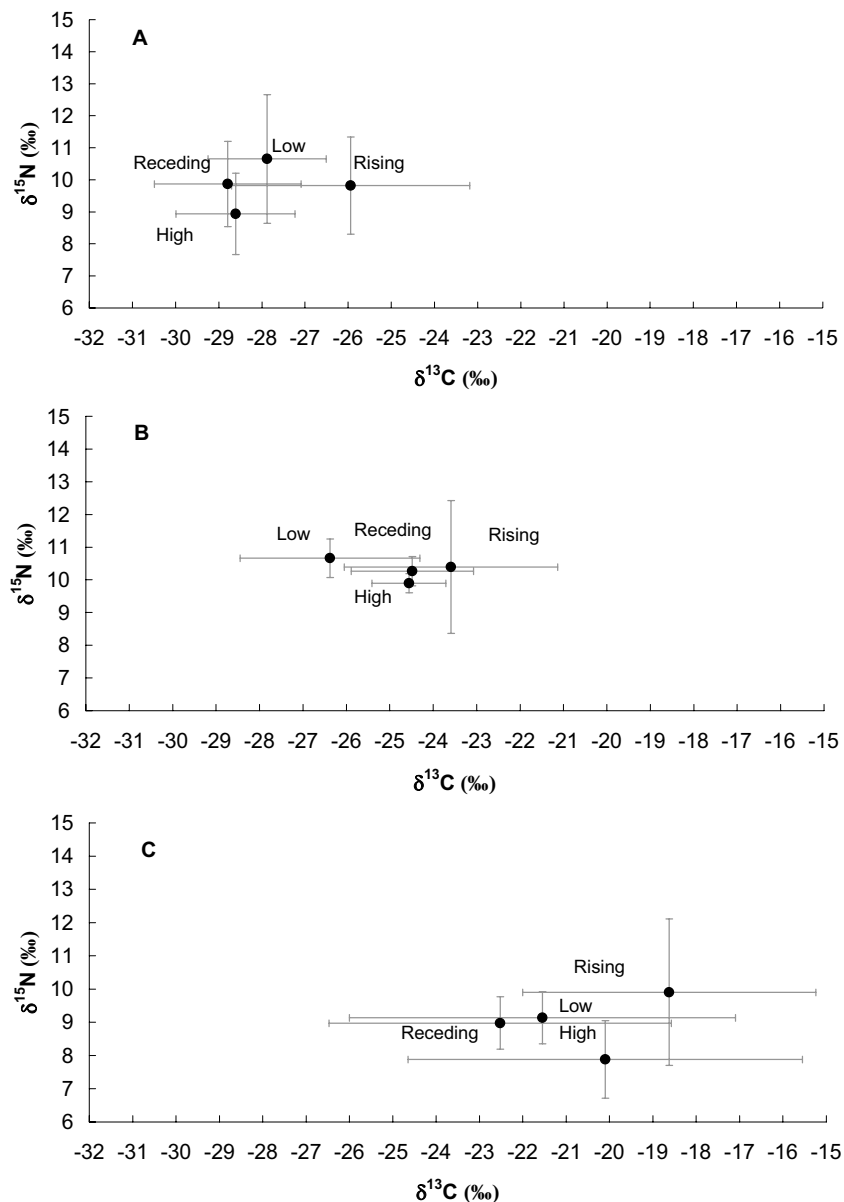

Figure 4. The δ¹³C and δ¹⁵N (μ ± S.D.) values of fish in each period: rising, high, receding and low for A) *C. macropomum,* B) *C. monoculus,* C) *S. fasciatus,* D) *M. duriventre,* E) *P. nigricans* and F) *T. angulatus.*

Discussion

Results from a combination of stomach content and stable isotope analyses demonstrated seasonality in the autotrophic energy sources of fish from Lake Camaleão, which is also related to changes in diet composition. *C. macropomum*, *M. duriventre* and *T. angulatus* are omnivorous fish that principally consume fruit and seeds during the rising water, high water and receding water periods, while during the low water period feed mainly on plant material, insects, and zooplankton. In contrast, the herbivorous *S. fasciatus*, the detritivorous *P. nigri-*

cans and the piscivorous *C. monoculus* did not show any temporal changes in their diet and consumed the same food items throughout the hydrological cycle: plant material, POM, and fish. These findings are similar to those encountered in other floodplain areas (Soares et al., 1986; Wantzen et al., 2002; Yamamoto et al., 2004,) and rivers (Lowe-McConnell, 1964; Goulding, 1980).

Estimates of relative contributions of autotrophic energy sources for the fish species examined in this study, utilizing the concentration-weighted linear mixing model, determines that C_3 plants are the major carbon source for these fish. In *C. macropomum* tissue, C_3 plants con-
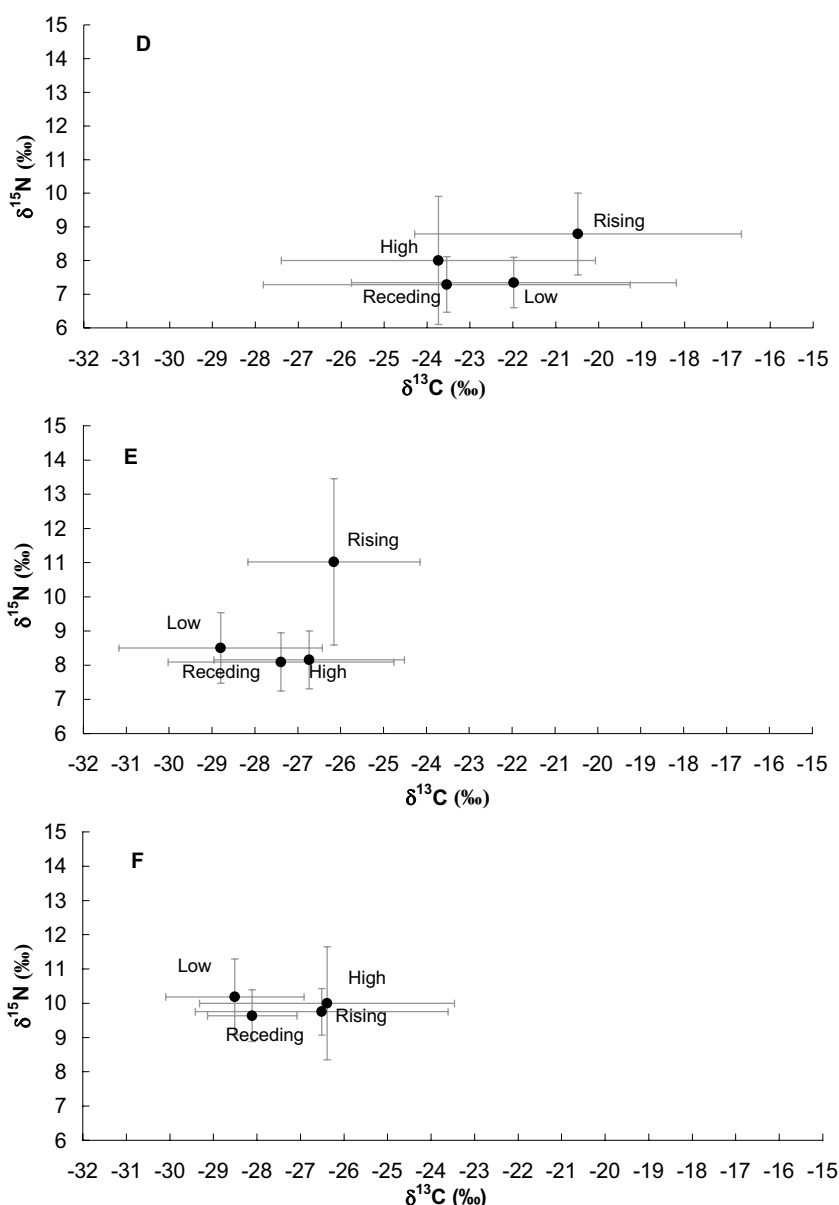

Figure 4. D–F

tributed a minimum of 33 % of the isotopic signal at low water and a maximum of 88 % in *P. nigricans* at high water. The high C_3 plant source contribution to the fish during the full hydrological cycle differs considerably from those estimated by Araújo-Lima et al. (1986), Forsberg et al. (1993), Araújo-Lima et al. (1998), Benedito-

Cecílio et al. (2000) and Lewis et al. (2001). These authors indicate phytoplankton as the most important source of carbon for floodplain fish.

Our results indicate that C_3 plants and other food sources with a similar isotopic composition can be locally more important than phytoplankton for floodplain
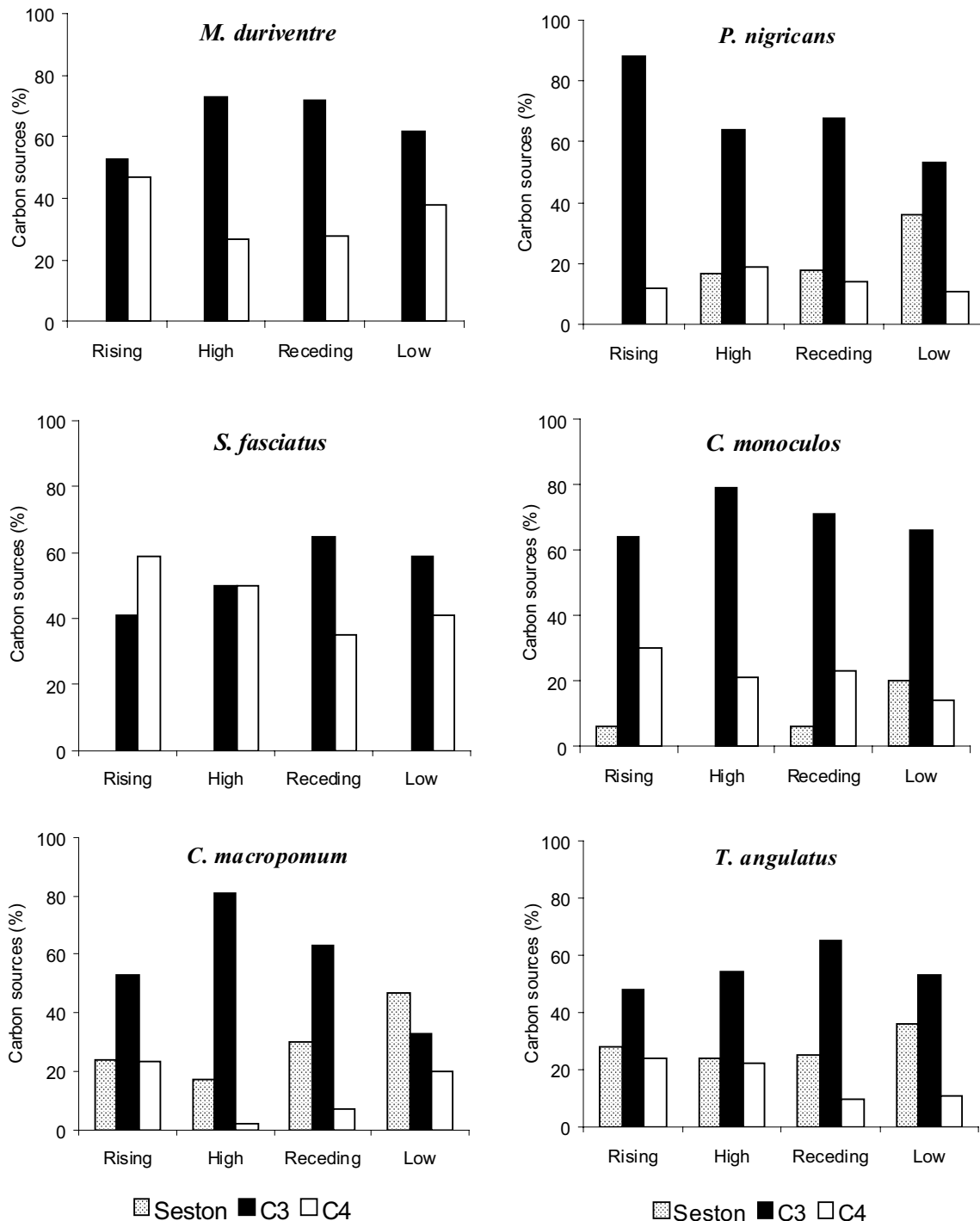

Figure 5. Seasonal estimates of relative contributions of three primary carbon sources for *M. duriventre, S. fasciatus, C. macropomum, P. nigricans, C. monoculus* and *T. angulatus* from Lake Camaleão.

fish species. For example, POM and insects that feed on C_3 plants have a similar isotopic composition and were frequently found in the stomach content. These items may represent important secondary carbon sources, mainly during the low water period. Other terrestrial inputs, such as insects or pollen, were also considered by Post (2002) to be important carbon sources for fish, at least for short periods of time.

Seston which is consumed directly by zooplankton was determined to be the second most important carbon source of *C. macropomum*, *T. angulatus* and *P. nigricans*, mainly during the low water period. In the case of *C. macropomum*, stomach content analyses indicated an occurrence frequency of 72% for zooplankton. Due to this finding, a similar result was expected in terms of the relative contribution of seston to the carbon sources of *C. macropomum*. However, we found that the seston contribution to the isotopic signal of *C. macropomum* tissue was only 47%. This value is much lower than the 74% reported for phytoplankton by Benedito-Cecílio et al. (2000) for *C. macropomum* during the same period.

T. angulatus, as in the case of *C. macropomum*, also consumed zooplankton during the low water period, however the maximum contribution of seston was 36%. The detritivorous *P. nigricans* and the piscivorous *C. monoculus* presented higher seston contributions of 36% and 20%, respectively, during the low water period compared to the other periods. Although seston was the second largest carbon source for *P. nigricans*, it represented a much lower contribution than the 85% of phytoplankton reported for *P. nigricans* in the Solimões River (Benedito-Cecílio et al., 2000). In this study, seston demonstrated the same $\delta^{13}C$ value (–36.1‰) as that reported by Hamilton et al. (1992) and Benedito-Cecílio et al. (2000) for phytoplankton. However, the comparatively small contribution of seston encountered in this research was due to it being a minute component of the POM composition. Furthermore, it can be observed that seston is much less enriched in ^{13}C than that of POM (Fig. 3); clarifying the distinction between these two carbon sources.

Although the aquatic C_4 macrophytes are responsible for over 65% of the primary productivity in floodplain lakes (Melack et al., 1999), their importance as an autotrophic energy source for fish seems to be restricted to only a few species. Among those that consume aquatic C_4 macrophytes directly, such as *S. fasciatus* and *M. duriventre*, maximum contributions of 59% and 47%, respectively, occurred during the rising water period. During this period, the availability of aquatic C_4 macrophytes in the lake is greater than that of C_3 plants. Benedito-Cecilio et al. (2000) estimated a maximum carbon contribution of 27% of aquatic C_4 macrophytes for *M. duriventre*. For *C. macropomum*, the maximum contribution of 23% occurred during the rising water period. This is much higher than the 5% reported by Araújo-Lima et al.

(1998), and is close to the 22% calculated by Benedito-Cecilio et al. (2000). The low proportion of aquatic C_4 macrophytes as a primary carbon source in the fish biomass is probably related to the low nutritional value of the plant roots accessible to the fish (Howard-Williams and Junk, 1977; Forsberg et al., 1993). However, it is important to mention that the isotopic signal of aquatic C_4 macrophytes can be incorporated into the fish not only by direct ingestion, but also indirectly through the ingestion of insects, molluscs and shrimps, which have an isotopic signal or part of it originating from aquatic C_4 macrophytes. The $\delta^{13}C$ values of the insects inhabiting aquatic C_4 macrophytes were much heavier than that of the insects found close to C_3 plants. Similar $\delta^{13}C$ results for insect species were reported by Adis and Victoria (2001). These insects acquired their carbon sources both from C_4 macrophytes and C_3 plants.

Our findings confirm the importance of the flooded forest and aquatic macrophytes for the maintenance of fish stocks in floodplains, regardless of the species' feeding habits. Even *C. monoculus*, a piscivorous fish, obtains a minimum 64% contribution from C_3 plants, which is probably related to its preference for prey that consume C_3 plants.

The differences in the results presented in this research to those of Araújo-Lima et al., (1986), Hamilton et al. (1992), Forsberg et al. (1993), Benedito-Cecilio et al. (2000) and Lewis et al. (2001), which all indicate phytoplankton as the principal carbon source for floodplain fish, can be attributed to a number of different factors. First, in this study there was a much greater number of fish samples collected than in the previous studies. Second, the fish samples were collected in only one várzea lake, as opposed to collecting in different environments on the floodplain over a large geographical area. Third, the model utilized in this research to establish the estimates of relative contributions of carbon sources was a concentration-weighted mixing model and not a mass balance model, allowing for more precision in determining the proportional contributions of three food sources or end-members to the fish. Finally, the stomach content analyses provided complementary in interpreting the stable carbon and nitrogen isotope results, enabling the estimates of the carbon energy sources to be more reliable.

Carbon and nitrogen stable isotope values of *S. fasciatus*, *C. macropomum*, *M. duriventre*, *T. angulatus*, *P. nigricans* and *C. monoculus* reflect the seasonality of their primary carbon sources in Lake Camaleão. The seasonal feeding patterns of the examined species reflects the river's flood pulse. A similar phenomenon was also observed in the Pantanal of Mato Grosso, a large floodplain on the upper Paraguay River (Wantzen et al., 2002). The mixing model underlines the importance of C_3 plants and their contribution as a major carbon source for the

fish species in floodplain lakes, regardless of differences in feeding habits. It also confirms the statement in the Flood Pulse Concept that complex land-water interactions and habitat heterogeneity lead to complex aquatic food webs (Junk and Wantzen, 2004; Junk in press).

Acknowledgments

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