PRIMARY RESEARCH PAPER

Autotrophic energy sources for *Paracheirodon axelrodi* (Osteichthyes, Characidae) in the middle Negro River, Central Amazon, Brazil

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Abstract The cardinal tetra (*Paracheirodon axelrodi*) is the most abundant species of the Brazilian ornamental fish trade, constituting more than 80% of the ornamental fish collected in the middle Negro River basin. Stable isotope analyses were used to identify the autotrophic carbon sources and trophic position for the cardinal in relation to the plant groups at the base of its foodchain. Filamentous algae, tree and plant leaves and cardinals were collected in stream habitats, flooded forest and interfluvial swamps (campos) during peak flood, falling water and low water periods. $\delta^{15}N$ values of the cardinal in relation to the plants at the base of the food chain indicated a trophic position of omnivore. Values of $\delta^{13}C$ for the plants ranged from −43.1 to −26.4‰, with averages of −37.6, −30.4, and −29.4‰ for filamentous algae, flooded forest leaves, and campo leaves, respectively. The $\delta^{13}C$ values for the cardinal ranged from −35.0 to −27.9‰, with an average of −31.4‰. Relative contributions of plants to fish

carbon were estimated in a two end-member mixing model which determined that the leaves (flooded forest and campo leaves combined) and filamentous algae had average relative contributions to cardinal carbon of 71% and 29%, respectively. However, seasonal variation in the relative contributions was encountered throughout the hydrological cycle. The cardinals least enriched in ^{13}C were encountered in November during the falling water period, indicating that they had perhaps recently migrated down from interfluvial campos where filamentous algae production is significant. Considering that algal production has been reported to be less than 1% of total primary production in the Negro River, these results could suggest some evidence of selective herbivory in the cardinal's food chain.

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Introduction

Paracheirodon axelrodi (Weitzman and Fink, 1983) is a brilliant neon fish whose geographic distribution extends through the mid-upper Negro and Orinoco River drainages of South America. The middle Negro, the primary fishing grounds for the ornamental fish industry in the Amazon Basin, produces about 20 million live fish annually, generating over

US$2 million per year for the State of Amazonas in Brazil (Prang, 2004). The ornamental fish industry provides approximately 60% of the total income generated in Barcelos (Prang, 2004), a community of 16,000 located 400 km upriver from Manaus. The municipality of Barcelos, which covers an area of 122,490 km^2 of largely intact forest (and is geographically the largest municipality in the world), has passed bylaws prohibiting both industrial logging and gold mining in order to protect the ornamental fish industry. *Paracheirodon axelrodi* (cardinal tetra) is the most important ornamental fish species, constituting more than 80% of the ornamental fish exported from the middle Negro (Chao et al., 2001). In order to develop effective strategies for the conservation and management of the cardinal, more basic information is needed on its life cycle and ecology. An important first step will be to identify the primary producers which sustain the food chain of the cardinal.

During its annual hydrological cycle the Negro River inundates an extensive lateral floodplain, covered predominantly with seasonally flooded forest (*igapó*). Like many fish species which inhabit this region, the cardinal uses the *igapó* forest for refuge, to reproduce and to feed during seasonal floods (Goulding et al., 1988). When the river begins to rise in late February–March, cardinal tetras move laterally from stream channels into the *igapó* forest and some migrate to interfluvial swamps (Geisler & Annibal, 1986; Prang, 2002; Marshall, 2004). In both *igapó* and interfluvial environments, a variety of food is available to fish including algae, aquatic and terrestrial plants, seeds and fruits, and aquatic and terrestrial invertebrates (Junk et al., 1997). As the water level drops during the falling water period and ensuing dry season, the fish are forced to return to the shallow stream and river beds where a high density of organisms compete for a smaller availability of food resources (Winemiller, 1993; Winemiller, 1998).

Aquatic food chain research conducted in small streams and flooded forests in the acidic waters of the Negro River basin, utilizing phosphorous tracers (^{32}P) and observations of feeding strategies, have identified forest leaves and coarse litter as the principal source of energy for aquatic organisms, including small fish, in these systems (Walker et al., 1991; Walker, 1995). However, there is also evidence that algae are an important energy source for aquatic

food chains in the middle Negro River (Marshall, 2004).

The *igapó* forests of the Negro River offer vast quantities of substrata for the attachment of periphytic algae, which grows on submerged logs and on the roots of aquatic plants (Goulding et al., 1988; Putz & Junk, 1997). However, due to the relatively dense nature of these flooded forests, periphytic algae production tends to be restricted to a narrow zone at the interface with the stream or river canal where light penetration is greatest (Forsberg et al., 2001). In the interfluvial swamps (campos) at the headwaters of many tributaries in the middle Negro, minimal forest cover combined with shallow, transparent waters creates a much more favorable environment for the development of loosely attached filamentous algae, especially during the rising water and peak flood periods (B. Marshall, personal observations). In this environment, filamentous algae grow between clusters of rooted aquatic plants in thick mats close to the water surface (B. Marshall, personal observations). The vegetation of the interfluvial campos is generally characterized by mono-specific stands of palms such as *Mauritia flexuosa*, low-lying shrubbery (e.g. *Platycarpum egleri*, *Macairea scabra*, *Bactris campestris*) and aquatic sedges and grasses (e.g. *Cyperus ligularis*, *Panicum orinocense*); the latter of which provide excellent substratum for filamentous algae production (B. Marshall, personal observations). Filamentous algae, in turn, not only serves as a direct and indirect food source for invertebrates and fish (Putz & Junk, 1997), but also provides shade and protection for small prey species like the cardinal, which find refuge from direct sunlight under the thick mats (B. Marshall, personal observations).

The cardinal, depending on changes in the water level, utilizes different habitats and capitalizes omnivorously on a diverse selection of food resources, including algae (Geisler & Annibal, 1986; Marshall, 2004; Walker, 2004). In a study of stomach contents of cardinals collected in streams and *igapó* forest, Walker (2004) concluded that the cardinal is principally a predator of small invertebrate prey, feeding mainly on microcrustaceans and chironomid larvae. While this information is important to understand short-term feeding patterns, it does not necessarily demonstrate what has been incorporated and assimilated into the tissues of the fish. Also, since Walker's collections were made during a single

period in a limited number of habitats, the results may not reflect the full spatial and temporal variability in the diet. The use of carbon and nitrogen stable isotopes offers an alternative and more efficient means to investigate trophic relationships between plants and animals in aquatic ecosystems, permitting direct identification of the relative contributions of different autotrophic energy sources to heterotroph food chains (Peterson & Fry, 1987). Once carbon is fixed by a plant the ratio of ^{13}C to ^{12}C remains relatively constant as it passes through the food chain (DeNiro & Epstein, 1978; Fry & Sherr, 1984). Furthermore, when different plant groups are isotopically distinct from each other, it is frequently possible to determine the plant carbon source(s) of an animal directly from its carbon isotope ratio (Forsberg et al., 1993).

In this study, the natural variation in stable carbon isotope ratios of plants was used to investigate seasonal changes in the autotrophic energy sources of the cardinal. Nitrogen stable isotope analyses were also used to investigate the trophic position of the cardinal in relation to these autotrophic energy inputs.

Materials and methods

Study area

The main channel of the middle Negro is characterized by high concentrations of dissolved organic matter and low nutrient and electrolyte levels (Stallard and Edmond, 1983). The principal autotrophs in the river system are flooded-forest (*igapó*) trees and algae (filamentous and periphytic algae and phytoplankton). Thomé-Souza (2005) reported that leaves, fruits and seeds that fall from igapó forests are responsible for over 99% of autotrophic production in the middle Negro. However, considering that autotrophic production in interfluvial regions has not been studied, a basin-wide estimate for algal production without information on these habitats could be erroneous.

Fifty-one leaves, fifteen filamentous algae, and fifty-four cardinal samples were collected from stream, flooded forest, and campo habitats in four different areas in the middle Negro River (Fig. 1) during the period of June 2003 to March 2004. Six
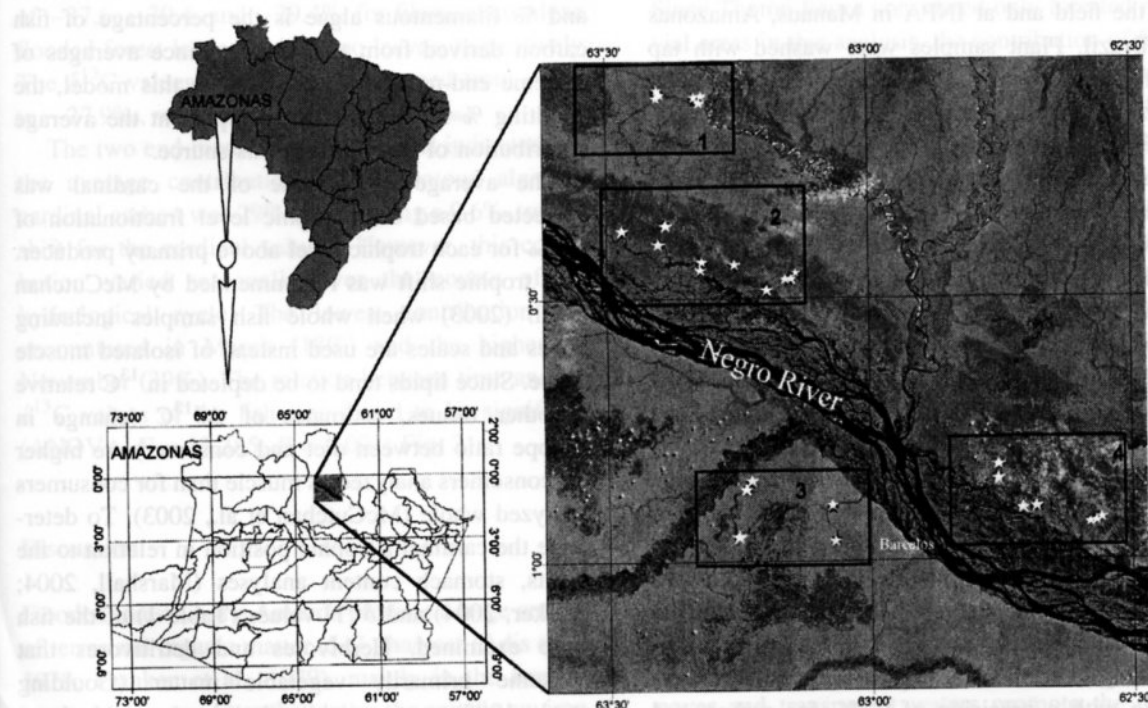
Fig. 1 Map of study area in the middle Negro River basin, Municipality of Barcelos, Amazonas State, Brazil. The map shows the location of the town of Barcelos and the four different sampling areas, with the collection points of cardinal tetras marked in white

samples of phytoplankton were also collected and analyzed, however we suspect that the samples might have been contaminated by terrestrial organic matter due to inconsistencies in the carbon/chlorophyll ratios obtained for this material. Considering these potential problems, the phytoplankton samples were not included in this study.

The leaf samples were collected from the flooded forests and campos mainly during the falling water and dry season when the leaf fall from the trees and shrubs was greatest. The filamentous algae samples were collected from interfluvial campos during the peak of the flood using 800 and 275 μm sieves to remove large detritus particles and macro invertebrates. The cardinals were collected during high, falling and low water periods. The fish were collected from streams using a *rapiché* (a local type of dip net) and from the flooded forest and campos utilizing a *cacurí* (a vertical trap net of regional design). Each cardinal sample was composed of a mixture of 10 or more specimens from each collection point. The fish were frozen in liquid nitrogen upon capture and transported to INPA (Instituto Nacional de Pesquisas da Amazônia) for processing.

Preliminary processing of the samples was carried out in the field and at INPA in Manaus, Amazonas State, Brazil. Plant samples were washed with tap water followed by a 1 M HCL solution, rinsed with deionized water and then dried at 60°C. After drying, samples were ground to a fine powder with mortar and pestle. The heads and stomachs of the fish were removed, then dried and ground as above. Further processing and isotopic analysis were carried out at the Centro de Energia Nuclear na Agricultura (CENA) in Piracicaba, São Paulo, Brazil. About 1 mg of each dry sample was combusted at 1,700°C in continuous flux by CF-IRMS (Continuous Flow Isotopic Ratio Mass Spectrometry) in a Carlo Erba element analyzer (CHN-1110). The CO_2 and N_2 released on combustion was purified by passage through an alcohol-dry ice trap and collected with liquid N in a specially adapted high vacuum line. A secondary standard calibrated to PDB limestone was utilized to calibrate carbon isotope analyses while nitrogen isotope analyses were calibrated with atmospheric N_2. All of the samples were analyzed in triplicate with a precision of 0.3‰ for carbon and 0.5‰ for nitrogen. Carbon and nitrogen isotope ratios were determined in a Finnigan Delta Plus mass spectrometer fitted with double inlet and double collector systems and expressed relative to the PDB and N_2 standards as:

$$\delta X(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1,000 \qquad (1)$$

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.

To determine the relative importance of different autotrophic energy sources (plants) for the cardinal, we applied a linear mass balance mixing model (Forsberg et al., 1993) using two end-members; filamentous algae and leaves:

$$\% \text{ filamentous algae} = 1 - \frac{\delta^{13}C_{cardinal} - \delta^{13}C_{algae}}{\delta^{13}C_{leaf} - \delta^{13}C_{algae}} \times 100 \qquad (2)$$

where $\delta^{13}C_{cardinal}$ is the average $\delta^{13}C$ value of the fish's carbon source (corrected for trophic fractionation), $\delta^{13}C_{algae}$ is the average $\delta^{13}C$ value for filamentous algae (the least enriched end-member), $\delta^{13}C_{leaf}$ is the average $\delta^{13}C$ value for flooded forest and campo leaves (the most enriched end-members), and % filamentous algae is the percentage of fish carbon derived from this source. Since averages of extreme end-members were used in this model, the resulting % filamentous algae represent the average contribution of carbon from this source.

The average $\delta^{13}C$ value of the cardinal was corrected based on a trophic level fractionation of 0.3‰ for each trophic level above primary producer. This trophic shift was recommended by McCutchan et al. (2003) when whole fish samples including bones and scales are used instead of isolated muscle tissue. Since lipids tend to be depleted in ^{13}C relative to other tissues, estimates of $\Delta\delta^{13}C$ (change in isotope ratio between diet and consumer) are higher for consumers analyzed as muscle than for consumers analyzed whole (McCutchan et al., 2003). To determine the cardinal's trophic position in relation to the plants, stomach content analyses (Marshall, 2004; Walker, 2004) and $\delta^{15}N$ values (Table 1) of the fish were examined. Herbivores and detritivores that consume primarily vegetable matter (Goulding et al., 1988) were considered to be 1 trophic level and omnivores 1.5–2 trophic levels above the plants at the base of the food chain (Fisher et al., 2001;

Table 1 δ^{13}C and δ^{15}N values for the fish and plants. None of the values have been corrected for trophic fractionation

Plants	N	δ^{13}Avg.	SD	Min	Max	δ^{15}Avg.	SD	Min	Max
Filamentous algae	15	−37.6	4.1	−43.1	−34.0	4.0	2.0	−1.6	6.7
Flooded forest leaves	35	−30.4	1.7	−33.4	−26.4	2.5	2.1	−1.4	6.0
Campo leaves	16	−29.4	2.4	−32.8	−25.8	4.2	3.3	−2.1	9.9
Cardinal	54	−31.4	1.6	−35.0	−27.9	8.6	0.8	6.9	10.9

Jepsen & Winemiller, 2002). Since the cardinal is predominantly a predator of micro crustaceans and chironomid larva (Marshall, 2004; Walker, 2004), a 2.0 trophic level correction was applied resulting in a trophic shift of 0.6‰ for the fish. A similar correction was obtained using the average difference in δ^{15}N values between plants and fish (4.2‰), assuming a fractionation of 2.1‰ per trophic level for animals analyzed whole (McCutchan et al., 2003).

Results

δ^{13}C and δ^{15}N values obtained for fish and plants are shown in Table 1 and Fig. 2. Values of δ^{13}C for the plants ranged from −43.1 to −26.4‰, with averages of −37.6, −30.4, and −29.4‰ for filamentous algae, flooded forest leaves and campo leaves, respectively. The δ^{13}C values for the cardinal ranged from −35.0 to −27.9‰, with an average of −31.4‰.

The two end-member mixing model indicated that the average contribution of filamentous algae to cardinal carbon was 29% (considering a 0.6‰ trophic shift for the cardinal values). However, this contribution varied seasonally over the course of the hydrological cycle. The lowest contribution was encountered in March (18%) and the highest in November (39%). The relation between time and the δ^{13}C values of the fish was found to be significant (ANOVA, F = 13.385, P = 0.001; Fig. 3).

Discussion

Flooded forests in the Amazon produce a large amount of terrestrial organic matter (5–7 t/ha/year (Adis et al., 1979; Franken et al., 1979), mainly in the form of leaves and coarse litter that enters the aquatic environment and is potentially available to consumer food webs. Considering this large input of allochthonous

carbon in a mainly heterotrophic system, it is not surprising that this plant group is the principal autotrophic energy source of the cardinal. However, the results here indicate that filamentous algae also contributes significantly to the carbon balance of the cardinal and that this contribution varies throughout the year, accounting for a peak of 41% of fish carbon during late falling water period. This sizeable percentage is impressive considering the relatively small levels of filamentous algae production when compared to other plant groups. It has been estimated that periphytic algae accounts for only 5–8% of total aquatic primary production along the central Amazon floodplain (Junk et al., 1985; Melack & Forsberg, 2001). Thomé-Souza (2005) estimated that periphytic algae contributed even less (0.6%) to aquatic production in the middle Negro. Since Thomé-Souza considered only forested interfluvial areas in this analysis, the contribution of filamentous algae may have been underestimated. However, it is unlikely that their input exceeds that encountered in other environments. The disproportionate contribution of filamentous algae to fish carbon is probably due its high nutritional quality (Forsberg et al., 1993; Thorp and Delong, 2002). Forsberg et al. (1993) compared the nutritional characteristics of different plant materials present in the Amazon River system and concluded that algae was the plant group highest in protein and nutrients and lowest in fiber, making it the preferred food of herbivores and detritivores in all aquatic food webs.

Migrations between habitats linked to water level changes could be responsible, in part, for the large seasonal variation observed in the contribution of filamentous algae to fish carbon. During high water periods, flooded environments provide a conduit for fish to migrate between the lower reaches of streams and interfluvial wetlands, where reduced forest cover and transparent waters promote the development of filamentous algae. The cardinals most enriched in ^{13}C were collected in stream beds in

Fig. 2 Avg. $\delta^{13}C$ and $\delta^{15}N$ values with standard deviation bars of the fish and plants. $\delta^{13}C$ values of the fish have been corrected for trophic fractionation
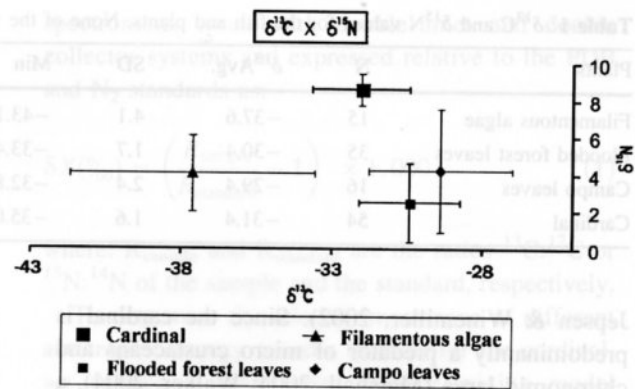
Fig. 3 Relation between time of year and $\delta^{13}C$ values of the cardinal. $\delta^{13}C$ values have been corrected for trophic fractionation
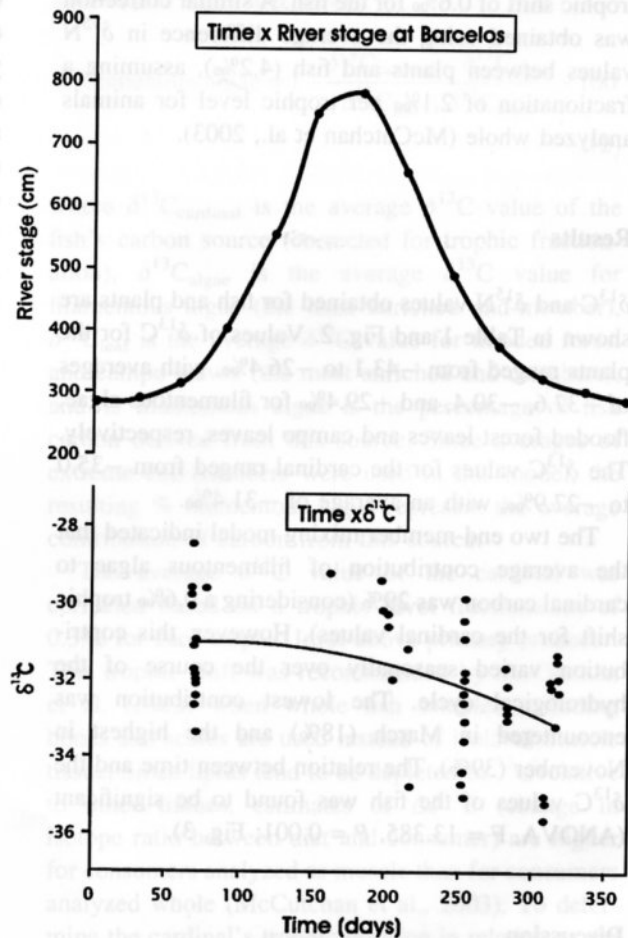
March when the water level was at its lowest. This suggests that the primary carbon source of the cardinal tetras collected in this habitat originated from the flooded forest. The aquatic food web of the flooded forest has been found to involve the breakdown of forest litter by fungi, which, in turn

are eaten by micro crustaceans and chironomid larva (Walker et al., 1991; Walker, 1995), which are then preyed upon by small fish like the cardinal tetra (Marshall, 2004; Walker, 2004).

The isotopically lightest cardinal samples (least enriched in ^{13}C, closest to filamentous algae) were

collected in stream beds in late November during the receding water period, when cardinals were already beginning to migrate out of the interfluvial campos. The lighter isotopic value, in this case, suggests that these fish had derived much of their carbon from a filamentous algae-based food web. As the food chain in this environment may be shorter than that found in flooded forest habitats, the trophic enrichment factor for the cardinal during the falling water period would be less, putting the cardinal at 1.5 levels above the plants instead of the two levels presumed for the flooded forest food web. Unfortunately, information on tissue turnover time which would be beneficial in interpreting the isotope values of cardinals captured in different habitats, is currently not available.

In a stable isotope analysis of lotic foodwebs in streams with basins ≥ 10 km^2, Finlay (2001) observed a transition from terrestrial to algal carbon sources between the headwaters and lower reaches of streams. He concluded that the observed transition to algal carbon sources is related to increasing autochthonous primary production in channels as forest cover declines in larger streams, although decreasing retention or quality of terrestrial carbon may also play a role. The pattern found in the Negro system was quite different due to the large interfluvial wetlands seasonally connected to tributary headwaters. High levels of filamentous algae production in these relatively open environments provide significant amounts of autochthonous energy to the local aquatic food webs while allochthonous forest inputs tend to fuel food chains further downstream, exactly the opposite to the trend described by Finlay (2001).

Algae have often been found to be an important energy source for aquatic consumers in ecosystems dominated by vascular plants. Planktonic and periphytic algae have been shown to be the principal autotrophic carbon sources in tropical riverine food webs (Araújo-Lima et al., 1986; Hamilton et al., 1992; Forsberg et al., 1993; Benedito-Cecílio et al., 2000; Lewis et al., 2001). In all of these systems algae have also been shown to account for only a small part of total aquatic production, although their relative contributions to heterotroph carbon are significant. Hecky & Hesslein (1995), analyzing contributions of benthic algae to lake food webs with stable isotopes, concluded that up to 50% of the carbon assimilated by a broad range of fish species worldwide was originally fixed by periphytic algae.

The consumption of periphytic algae by benthic macro invertebrates has been identified as a major energy pathway in fish food webs (Vadeboncoeur et al., 2002). James et al. (2000), studying the carbon flow of a macrophyte-dominated lotic system in New Zealand, found that periphytic algae were the dominant primary producers in littoral regions and that trichopteran and chironomid larvae mediated the flow of this production to fish.

Thorp and Delong (2002) stated that the relative contributions of different carbon sources to the total organic carbon in transport are not necessarily matched with their relative importance to metazoan biomass production within riverine food webs because of differences in assimilation rates and consumer feeding preferences. In addition, they hypothesized that autochthonous plant carbon supports most metazoan production in large river systems, especially at higher trophic levels where the algal-grazer food web pathway dominates. They also argue that since accurate measurements of algal production in river-floodplain systems are difficult to obtain, the contribution of this group to total aquatic production has been underestimated in many rivers (Bayley, 1989; Murkin, 1989; Hamilton et al., 1992). This problem is especially acute in systems like the Negro where remote interfluvial wetlands have been largely ignored from basin-wide estimates of algal productivity (Melack & Forsberg, 2001).

The average δ^{13}C value for filamentous algae in this study (-37.6‰) was much lower than that reported by Forsberg et al. (1993) for periphytic algae collected in white water environments along the central Amazon floodplain (-26.2‰). This is most likely due to a difference in the δ^{13} of the source CO_2 in these two systems. Dissolved CO_2 concentrations in aquatic environments in the Amazon are generally supersaturated due to the overwhelming influence of microbial metabolism on the inorganic carbon balance (Richey et al., 1988) and the δ^{13}C value of CO_2 is usually similar to that of the dominant aquatic plant group (Waichman, 1996). C4 grasses are the dominant plant group and the principal organic carbon source for planktonic bacteria in white water floodplain environments (Waichman, 1996; Melack & Forsberg, 2001). The δ^{13}C of dissolved CO_2 in this system is thus expected to be similar to that of C4 plants (δ^{13}C $= -12.8$‰, Forsberg et al., 1993). Since the dominant aquatic autotrophs in Negro River

wetlands are all C3 plants, the $\delta^{13}C$ of dissolved CO_2 in this system is expected to be similar to the average plant value ($\delta^{13}C = -29.2‰$; average for flooded forest, campo shrub and campo grass leaves in this study). Using these $\delta^{13}C$-CO_2 values and an average photosynthetic fractionation factor of $-13‰$ for freshwater algae (Bade et al. 2006), the $\delta^{13}C$ of periphytic algae in Amazon white water and Negro River wetlands would be expected to be -25.8 and $-42.2‰$, respectively. The predicted value for periphytic algae in white water environments was almost identical to the average value reported by Forsberg et al. (1993), while the value predicted for filamentous algae from Negro River wetlands was within the observed range of values (Table 1). The similarity between predicted and observed values indicates that the assumptions used in these calculations were reasonable and that the observed difference in $\delta^{13}C$ was due primarily to the isotopic variability of dissolved CO_2 between systems.

Despite the apparent small contribution of filamentous algae to regional primary production, this plant group proved to be an important autotrophic carbon source for the cardinal. The differentially large contribution of filamentous algae to fish carbon is apparently due to its high nutritional value which makes it the preferred food for herbivores and detritivores in the cardinal food web. The relative contribution of filamentous algae to fish carbon varied seasonally as fish migrated between environments with different food webs and plant energy sources. All habitats and food webs used by the cardinal during its brief life cycle will have to be conserved to effectively manage this commercially important population. Better estimates of aquatic production for algae and other aquatic plant communities are needed to evaluate their relative importance to this and other food webs in the Negro basin.

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