Carbon sources of Amazonian fisheries

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Abstract

Variation in the seasonal and spatial isotopic composition of plant C4 (aquatic macrophytes) and C3 (forest, C3 aquatic macrophytes and algae), and that of fish [Prochilodus nigricans Agassiz, Mylossoma duriventre (Cuvier), Colossoma macropomum (Cuvier), Semaprochilodus insignis (Schomburgk) and S. taeniurus Steindachner] in the Amazon floodplain were analysed to test whether the fisheries deliver plant carbon to the population of Manaus in the same proportion as it is available in the floodplain. The contribution of C4 plants was significantly lower in δ13C during the season of high water levels and increased toward the west of the basin. Mylossoma duriventre and C. macropomum changed δ13C levels, while the δ13Co of P. nigricans and C. macropomum shifted spatially. The contribution of C4 to the fisheries yield was small. C3 plants (excluding phytoplankton) also contributed less than expected. This was explained by the importance of detritivores to the yield of the fisheries and the dependence of these species on algal carbon.

KEYWORDS: Amazon, carbon, δ13C, fisheries, floodplain, stable isotopes.

Introduction

Fisheries play an important role in the economy of the Amazon. Fish provide the main protein source and a substantial commercial income for the people in most of the basin (Bayley 1989). An understanding of the factors responsible for fisheries production is of crucial importance for effective management of the resources of the Amazon fisheries. Fish production can be viewed as the final step in the series of carbon (or energy) transformations beginning with carbon dioxide fixation by plants (Forsberg, Araujo-Lima, Martinelli, Victoria & Bonassi 1993). Aquatic macrophytes, including aquatic grasses, flooded forest, phytoplankton and periphytic algae are the main primary producers in the region, and as such, form the energy base supporting fisheries production. These plants can be classified into two groups with different photosynthetic pathways, i.e. C3 and C4 plants. C4 plants, which are mostly represented by
aquatic grasses in the Amazon, are the most productive plant group in the region, accounting for approximately 52% of total plant production (Junk 1985; Bayley 1989). The rest (48%) of total plant production is provided by C₃ plants. The most important C₃ producers are the trees of the flooded forest and C₃ macrophytes, and less importantly, planktonic and benthic algae.

Carbon isotopes provide an excellent means of tracing the carbon from these two sources through the aquatic food web. Because of higher selectivity for the lighter isotope during carbon fixation, C₃ plants are significantly enriched in ¹²C (Forsberg et al. 1993). Therefore, as opposed to the expected result, analysis of the stable isotope in plants and fish indicates that phytoplankton is the main energy source for many species of detritivores, and that C₃ plant production supports most of the fish fauna of the Amazon floodplain (Araujo-Lima, Forsberg, Victoria & Martinelli 1986; Forsberg et al. 1993). The above authors suggested that the energy base of fish production on the floodplain is concentrated in only half of the total primary production. However, they evaluated the contribution of plants to the production of the entire fish community, rather than the commercial species in particular. Fisheries exploit the fish community selectively, and results from experimental fishing and analyses of fish diversity are not necessarily applicable to their harvest.

Araujo-Lima et al. (1986) and Forsberg et al. (1993) considered the average values of δ¹³C in calculating the contribution of plants as carbon sources for fish of the central Amazon. The above authors did not take into account spatial and seasonal variation in the isotopic composition of plants and fish. There can be 2–3‰ spatial and seasonal variation in the δ¹³C values of plants, which may lead to errors in the estimation of energy sources for consumers (Martinelli, Devol, Victoria & Richey 1991; Victoria, Martinelli, Trivelin, Matsui, Forsberg, Richey & Devol 1992; Boon & Bunn 1994; France 1996).

In the present paper, the contribution of autotrophic carbon sources to the commercial fisheries which support the people of Manaus, the largest city in the central Amazon, is recalculated. In contrast to previous studies, the seasonal and spatial variation in δ¹³C values of plant and fish were included in calculating the relative contribution of plants to fish in a section of the Amazon River and the participation of C₄ plants as a carbon source for the fisheries. The hypothesis tested was that fisheries production delivers plant carbon to people in the same proportion as its availability in the floodplain ecosystem.

**Materials and methods**

The spatial and seasonal variations in 495 samples of plants and five fish species were sampled along a 1800 km west-to-east (i.e. upstream–downstream) transect of the Amazon River between 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. The sampling sites were classified in relation to the linear distance of these areas from Manaus (Fig. 1). Plant samples included tree parts (i.e. leaves, fruits and seeds), C₃ and C₄ aquatic macrophytes, and periphytic algae. Determining the δ¹³C of phytoplankton is problematic because of contamination with carbon from vascular plants. The δ¹³C of zooplankton was strongly negative and comparable only to the δ¹³C of phytoplankton (Forsberg et al. 1993; del Giorgio & France 1996). Therefore, the δ¹³C of zooplankton was determined, and from this value, the present authors calculated the
value for phytoplankton, considering the fractioning of the $\delta^{13}C$ in $\%$ for each trophic level. The fish species examined were: tambaqui, *Colossoma macropomum* (Cuvier); curimatã, *Prochilodus nigricans* Agassiz; pacu, *Mylossoma duriventre* (Cuvier); and jarajuis, *Semaprochilodus insignis* (Schomburgk) and *S. taeniurus* (Steindachner). These contributed 50–70% of the yield recorded between 1976 and 1986 (de Merona & Bittencourt 1988), and in 1996 (IBAMA 1997). Fisheries data were not available at the same spatial scale as isotope data, but were grouped in six river stretches (Fig. 1) which overlapped the area where plant and fish were sampled for isotope analyses: (SOL3) upper region of the Solimões River; (SOL2) middle region of the de Solimões River; (SOL1) section of the de Solimões River near Manaus city; (NEGRO) Negro river; (AMA1) section of the Amazon River from Manaus to the Madeira River; and (AMA2) downstream region of the Amazon River. Martinelli *et al.* (1991) provided additional information about isotopic composition of Amazon plants. Details of sample preparation and isotope analysis are described elsewhere (Araujo-Lima *et al.* 1986; Forsberg *et al.* 1993).

The seasonal changes in $\delta^{13}C$ of plants were tested using paired $t$-tests of the means of sample sites. The relationship between the $\delta^{13}C$ values of plants and the sampling sites was analysed using linear regression. Seasonal and spatial changes in the $\delta^{13}C$ of fish were analysed with an analysis of covariance (ancova). Whenever more than one statistical test was performed in testing a hypothesis, a Bonferroni correction was applied.

The maximum and minimum plant contributions to fish were estimated from a mass balance equation using the mean $\delta^{13}C$ values of plants according to published information on fish diet. For the three detritivore species (*P. nigricans*, *S. taeniurus* and *S. insignis*) which eat particulate organic carbon (POC), three potential sources of plant carbon were considered: C$_4$ macrophytes, C$_3$ plant leaves and algae (periphyton and phytoplankton). Since these fish are detritus feeders, they consume the sediment phytoplankton and do not filter the water. Stomach content analyses of detritivorous fish revealed occasional fragments of leaves in the diet, but never wood or seeds (Yossa & Araujo-Lima 1998). The maximum and minimum contributions of each plant group were estimated by considering the contribution of the component of the end member as 0. Calculating the mass balance equation involved determination of the contribution of C$_3$ plants to the fish. However, the equation was solved normally by considering the

participation of phytoplankton. Therefore, when fish δ\(^{13}\)C was lower than the phytoplankton for a given site, the only possibility was that phytoplankton comprised 100% of the plant contribution. When fish δ\(^{13}\)C was lower than C\(_3\) leaves for a site, this indicated that phytoplankton, the most negative end member, must have been in the diet.

The diet of *C. macropomum* consisted mostly of zooplankton and C\(_3\) seeds, but on a few occasions, young individuals (> 30 and < 60 cm) were found eating C\(_4\) grasses and roots of C\(_3\) macrophytes (Araujo-Lima & Goulding 1997). When adult, *M. duriventre* is an omnivore eating mostly tree fruits, macrophyte seeds and roots, but also zooplankton, algae and occasionally insects (Paixão 1980). The δ\(^{13}\)C values of seeds, C\(_3\) macrophytes and periphytic algae are not significantly different (Forsberg *et al.* 1993). The maximum and minimum contributions of C\(_4\) plants and phytoplankton were estimated based on the contribution of C\(_3\) plants. The contribution of C\(_3\) plants to fish was estimated using the amount of C\(_3\) plant material in the diet and the digestibility rate of fruits (Moreira da Silva, Pereira-Filho & Oliveira-Pereira 1999). The leaves and roots of C\(_3\) plants have a lower digestibility rate than seeds, while periphytic algae have the highest digestibility rate. Periphytic algae occurred in the diet in very low volumes. Therefore, despite the counterbalancing effects of the digestibility rates, it is possible that the contribution of C\(_3\) plants group was slightly overestimated. Fractionation from producer to consumer was considered +1‰ per trophic level (DeNiro & Epstein 1978; Fry & Sherr 1984).

To estimate the contribution of plants to fisheries per fish species and river stretch, the δ\(^{13}\)C values for the middle stretches were used. The fisheries yield was calculated using the catch of the Manaus fishing fleet in stretches of the Solimões/Amazon River and its floodplain during 1986. This represented approximately 50% of the total catch for that year. These values have not changed much since that time (IBAMA 1997). Additional information about the fisheries was presented by de Merona & Bittencourt (1988).

Results

Variation in δ\(^{13}\)C in plants and zooplankton

The δ\(^{13}\)C values of plant groups showed different seasonal trends (Fig. 2). The C\(_3\) plants did not change with hydrological season, but C\(_4\) plants were significantly depleted during high water (*P* < 0.05), in contrast to POC, which was \(^{13}\)C-enriched during high water (*P* < 0.01). The δ\(^{13}\)C of zooplankton was not significantly different between seasons and did not change along the river. The average was –36.2‰ as the best estimator, leading to a mean of δ\(^{13}\)C for phytoplankton of –37.2‰, a value similar to that in Venezuelan floodplain lakes (Hamilton & Lewis 1992).

Spatial variation in δ\(^{13}\)C only occurred in C\(_4\) plants, which increased significantly from east to west (*r* = 0.68; *P* < 0.01), as previously reported by Martinelli *et al.* (1991) (Fig. 2). Periphytic algae and C\(_3\) forest leaves showed no spatial trend. The average δ\(^{13}\)C values for periphytic algae, C\(_3\) macrophyte leaves, and forest seeds and leaves were –28.3‰ and –30.0‰, respectively, which are the best estimates throughout the basin.

Seasonal variation in δ\(^{13}\)C of fish occurred only in *M. duriventre* (ANOVA; *n* = 14; *F* = 4.6; *P* < 0.05) and *C. macropomum* (ANOVA; *n* = 21; *F* = 5.6; *P* < 0.05), two fish species which
feed heavily on seeds from the flooded forest (Fig. 2). Spatial variation in $\delta^{13}C$ was significant in *P. nigricans* (ancova; $n = 30$; $F = 34.8$; $P < 0.01$) and *C. macropomum* (ancova; $n = 21$; $F = 11.6$; $P < 0.01$), the latter only during low water. In both cases, fish muscle was more depleted in $^{13}C$ in the western than the eastern part of the basin (Fig. 3).

**Source carbon for fish**

The maximum and minimum contributions of C4 plants, C3 plants and phytoplankton to fish species were calculated by integrating the seasonal and spatial variation of plants and fish (*P. nigricans*) per stretch of river. The strongly negative $\delta ^{13}C$ values suggest that *S. insignis*, *S. taeniurus* and *P. nigricans* received up to 15% of their carbon from C4 plants in stretches of the

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**Figure 2.** Spatial variation in the mean $\delta^{13}C$ of (a) C4 plants ($r = 0.68$; $P < 0.01$), (b) forest leaves, (c) particulate organic carbon, (d) periphyton and (e) zooplankton in the Solimões/Amazon River: (E) east; and (W) west.
western part of the Amazon River. The contribution of C₄ plants to the latter species reached 32% in the eastern stretches of the river. Algal carbon (phytoplankton) contributed at least 54% of carbon to the detritivores in sections SOL2 and SOL3 of the river, corresponding the most important energy source. Detritus from C₃ plants other than phytoplankton could contribute 46% of *S. taeniurus* and *S. insignis* carbon production, and up to 56% of *P. nigricans* carbon production upriver from SOL1 (Table 1).

The maximum carbon contribution of aquatic C₄ grasses was higher in *C. macropomum* and *M. duriventre*, but always less than 38%. Most of the stomach contents (≈ 86%) of adult *C.*

**Figure 3.** Spatial and seasonal variation in the δ¹³C of *Mylossoma duriventre*, *Colossoma macropomum* (*r* = 0.79; *P* = 0.01), *Semaprochilodus insignis*, *S. taeniurus* and *Prochilodus nigricans* (*r* = 0.72; *P* < 0.01) in the Solimões/Amazon River: (●) high water; (○) low water; (E) east of Manaus; and (W) west of Manaus.
Table 1  Percentage seasonal contributions of C₄ plants (C₄), C₃ plants (C₃) and phytoplankton (algae) to fisheries by fish species and river stretches based on mass balance (the range represents the minimum and maximum contribution of primary producers)

<table>
<thead>
<tr>
<th>Section</th>
<th>Semaprochilodus taeiniurus</th>
<th>Semaprochilodus insignis</th>
<th>Prochilodus nigricans</th>
<th>Mylossoma duriventre</th>
<th>Colossoma macropomum</th>
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macropomum during the high water season consisted of C₃ seeds, which have a 44% digestibility rate (Araujo-Lima & Goulding 1997; Moreira da Silva et al. 1999). If it is accepted that 38% of the energy of C. macropomum comes from C₃ seeds, then the fish must assimilate 10% of C₄ carbon and 52% of phytoplankton carbon (through zooplankton) to attain the average δ¹³C-value of −30‰. Fish eat much less fruit and seeds during low water, when the floodplain is dry. Seeds averaged only 8% of the stomach contents (Araujo-Lima & Goulding 1997), resulting in C₃ contributing only 4% of all carbon assimilated by the fish. Fish δ¹³C also changed spatially from −34 to −24‰ from west to east. To reach these values, the fish would have to have received 58–87% of algal carbon and 38–9% C₄ carbon, respectively. Likewise, M. duriventre assimilated 46% of the C₃ plants which it eats during high water and 22% during low water. To have δ¹³C of −27.3 and −28.7‰ during low and high water, respectively, this species would have had to receive 51–52% phytoplankton carbon and 26–27% grass carbon during low water, and 41–42% phytoplankton carbon and 12–13% grass carbon during high water.

Fisheries

The fishing fleet at Manaus landed ≈ 20 000 t of the five fish species in 1986. The minimum and maximum mean contributions of C₄ plant carbon to this yield were 10% and 15%, respectively. Therefore, C₃ plants, including phytoplankton, contribute more than 85% to fish yield. Phytoplankton carbon may account for as much as 56–57% of fish yield and other C₃ plants contribute 8–40%.

Discussion

The carbon isotope composition of an animal depends on the δ^{13}C of the assimilated food. Intraspecific variations are related to habitat, seasonality, sex and age (Hughes & Sherr 1983; France & Steedman 1996). Because of the water level fluctuations of the Amazon floodplain, it can be assumed that there will be a seasonal variation in δ^{13}C of the plants, which would be reflected in the consumers (Hamilton & Lewis 1992). Only the δ^{3}C of C_{4} plants was more negative during high water. The POC was more depleted in δ^{13}C during low water.

Atmospheric CO_{2} is the main carbon source for primary production. During the high water season, decomposition of floodplain vegetation is accelerated, generating biogenic light carbon through respiration, which can lead to the more negative values found in C_{4} plants during this period (Martinelli et al. 1991). Phytoplankton carbon is normally lighter than vascular plant carbon (Hamiton & Lewis 1992; Victoria et al. 1992). The higher values found for the δ^{13}C of POC during the high water season may result from the incorporation of heavier carbon from vascular plants of the floodplain and/or river sediments into the seston. During the dry season, lake water has a low sediment load and the input of allochthonous carbon is greatly reduced, leading to a POC pool enriched in light phytoplankton carbon.

The δ^{13}C values of dissolved inorganic carbon change spatially, probably because of changes in primary production, respiration and the solubility of carbonates (Angradi 1994). Gradients of stable isotopes of carbon may exist in an ecosystem and influence the isotopic composition of the plants. Upstream waters are 1.5–2 times more saturated and have lower δ^{13}C than downstream waters because of respiration (Quay, Wilbur, Richey, Hedges, Devol. & Victoria 1992; Lajtha & Marshall 1994). Consequently, the CO_{2} flux from river to atmosphere increases downriver, and since this CO_{2} is relatively depleted in ^{13}C, the plants which use this carbon source also may become more negative. This effect could explain variation in δ^{13}C of C_{4} plants along the river. However, a similar effect should also occur in the periphytic algae, trees of flooded forest or C_{3} macrophytes, and should influence the δ^{13}C of POC. Since this did not happen suggests that other unexplained factors also influence δ^{13}C.

Two fish species, *M. duriventre* and *C. macropomum*, changed their δ^{13}C between the seasons of high and low water. *Prochilodus nigricans* and *C. macropomum* were the only species whose δ^{13}C changed spatially. These changes were most likely linked to a shift in the diet rather than to changes in the isotopic composition of the plants.

Detritivores consume POC, which has an isotopic signature which changes seasonally, but these fish are highly selective during the assimilation of this food. Yossa & Araujo-Lima (1998) demonstrated that *P. nigricans* used only a very small fraction of the detritus (2–3%). The δ^{13}C of this fraction is not known, and it is possible that it has a unique isotope signature, and therefore, does not reflect seasonal change.

The value of the assimilation rate of tree seeds is needed to estimate the contribution of the other plant groups. The values used (50% in *M. duriventre* and 44% in *C. macropomum*) were determined experimentally by Moreira da Silva et al. (1999) using three different tracers. These rates were only slightly lower than the average values reported for herbivorous fish (50–60%) by Brett & Groves (1979). If such higher rates were used, then these would increase the
contribution of C3 plants to 52–54% and reduce phytoplankton contribution by approximately 10%. The average contribution of C4 plants to both species was very small, but consistent, because few individuals of these species had relatively high $\delta^{13}C$. This result can only be explained by assuming that the fish assimilate heavy grass carbon. However, this contribution is seasonal, and in the case of *C. macropomum*, clustered in the eastern part of the basin. It is reasonable to infer that consumption of C4 grasses is higher during low water, when C3 fruits are less available. However, it is not clear why the contribution of C4 grasses is higher and phytoplankton is lower in *C. macropomum* in the eastern part of the basin because floodplain lakes in the lower Amazon are larger, favouring plankton production. The amount of C4 grasses does not seem to change spatially and the data were previously corrected for spatial variation in the $\delta^{13}C$ value of C4 plants.

The mean contribution of C4 plants to the fisheries yield was 10–15%, which is much less than the contribution of this plant group to total primary production in the Amazon floodplain. This estimate of the C4 contribution is lower than that previously reported by Forsberg et al. (1993). The contribution of C3 plants other than phytoplankton algae was also relatively low compared to their availability in the ecosystem. In part, this can be explained by the greater importance of detritivores to the total yield and their dependence on algal carbon (Araujo-Lima et al. 1986). This dependence on algae can be explained by the low digestibility of C4 grasses, selective grazing and the higher protein content of zooplankton (Forsberg et al. 1993).

In conclusion, there is no correlation between carbon availability in the ecosystem and its delivery to Manaus via fisheries. Fisheries production is equally dependent on phytoplankton and vascular plant production. However, this result is applicable only to those five commercially important fish species and vascular plants are seldom important to the more than 200 other species which live in the Amazon floodplain. It is possible that the present fisheries scenario (1986–1996) reflects the destruction of the flooded forest habitat. Seed eaters such as *C. macropomum* were the most important species for Amazon fisheries in 1978 (Bayley & Petrere 1989) and now rank in fourth position.

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