Original article

Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes

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A B S T R A C T

The relationship between food web dynamics and hydrological connectivity in rivers should be strongly influenced by annual flood pulses that affect primary production dynamics and movement of organic matter and consumer taxa. We sampled basal production sources and fishes from connected lagoons and the main channel of a low-gradient, floodplain river within the Orinoco River Basin in Venezuela. Stable isotope analysis was used to model the contribution of four basal production sources to fishes, and to examine patterns of mean trophic position during the falling-water period of the annual flood cycle. IsoSource, a multi-source mixing model, indicated that proportional contributions from production sources to fish assemblages were similar in lagoons and the main channel. Although distributions differed, the means for trophic positions of fish assemblages as well as individual species were similar between the two habitats. These findings contradict recent food web studies conducted in temperate floodplain rivers that described significant differences in trophic positions of fishes from slackwater and floodplain versus main channel habitats. Low between-habitat trophic variation in this tropical river probably results from an extended annual flood pulse (ca. 5 mo.) that allows mixing of sestonic and allochthonous basal production sources and extensive lateral movements of fishes throughout the riverscape.

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1. Introduction

Studies using stable isotope analysis increasingly have stressed the importance of algal carbon in supporting river food webs (Hamilton et al., 1992; Forsberg et al., 1993; Thorp and Delong, 1994, 2002; Douglas et al., 2005; Winemiller, 2005), but recent research indicates that sources of organic matter supporting consumers vary spatially and temporally (e.g., Herwig et al., 2004; Zeug and Winemiller, 2008). In some temperate floodplain rivers, environmental conditions related to seasonal changes in hydrological connectivity affect the availability of alternative basal production sources for secondary consumers (Fisher and Willis, 2000; Fisher et al., 2001; Herwig et al., 2004). Such seasonal and temporal changes in hydrological connectivity can contribute to significant variation in the trophic position of secondary consumers (Zeug and Winemiller, 2008; Zeug et al., in press).

The relationship between food web dynamics and hydrological connectivity is influenced both by the passive movement of basal production sources and active movement of consumer taxa (Pringle, 2003; Winemiller, 2005), which in turn are affected by components of the flow regime. Tropical floodplain rivers experience predictable annual flood pulses that have been hypothesized to mix production sources (e.g., Junk et al., 1989); however, a synthesis of research conducted on the Orinoco River floodplain in South America concluded that export of organic carbon sources to the main channel is low due to restricted net lateral movement of water (Lewis et al., 2000). Annual flood pulses also restructure local assemblages of fishes and other aquatic organisms across heterogeneous riverscapes, which may result in significant lateral and longitudinal transport of organic matter (Lowe-McConnell, 1964; Lagler et al., 1971; Welcomme, 1985; Fernandez, 1997; Winemiller and Jepsen, 1998).

In the present study, we used stable isotope analysis (δ^{13}C and δ^{15}N) to examine food web patterns during the descending phase of the annual hydrological cycle in connected lagoons and the main channel of the Cinaruco River. The Cinaruco River is a meandering lowland river in the llanos (savanna) region of southwestern

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Venezuela with strongly seasonal hydrology and an annual flood pulse of approximately 5 months duration (a detailed description appears in Montoya et al., 2006). Here, we modeled differences in the relative importance of the four most important basal production sources supporting fish biomass in floodplain lagoons and the river channel (i.e., benthic algae, seston, terrestrial C_3 plants, and terrestrial C_4 plants), and examined how trophic positions of fishes varied between these habitats.

2. Methods

2.1. Study site

The Cinaruco River is a tributary of the Orinoco River located in the Venezuelan llanos (6°32′N, 67°24′W) and forms the southern boundary of Santos Luzardo National Park (Fig. 1). This black-water floodplain river has oligotrophic and acidic waters, low conductivity, low concentrations of suspended sediments, high amounts of humic acid, and sandy substrates (Montoya et al., 2006). Hydrological regime is strongly seasonal, and the drainage basin is ca. 10,000 km^2. In our study region, aquatic habitats of the Cinaruco River consist of the main channel and numerous floodplain lagoons. Hydrological connectivity of lagoons varies with the hydrological regime, geomorphology, and distance from the main channel, but most lagoons are connected by floodwaters from May to December. In July and August, floodwaters extend into the gallery forest and across hundreds of square kilometers of the llanos. During the period of water recession, from January to April, the aquatic habitat is greatly reduced. More than 280 fish species have been documented in the river, and this assemblage encompasses a great diversity of ecological niches (e.g., Jepsen and Winemiller, 2002). A previous analysis of stable isotope ratios in fish tissues in the Cinaruco River concluded that fishes are mostly dependent upon autochthonous primary production from benthic algae and phytoplankton, and that little carbon is assimilated from C_3 macrophytes and C_4 grasses (Jepsen and Winemiller, 2007).

2.2. Sample collections

Samples of fishes and basal sources for organic matter were collected from lagoons and the main channel during the falling-water period of the dry season (November–April) from 1999 to 2005. Most lagoon samples were from Laguna Larga, a large floodplain lake that is connected to the main channel throughout the annual hydrological cycle. Ecological dynamics are strongly influenced by the highly predictable annual flow regime of the Cinaruco

River, and this interannual consistency justifies pooling seasonal samples across years (Layman et al., 2005b; Arrington and Winemiller, 2006; Cotner et al., 2006; Montoya et al., 2006; Winemiller et al., 2006). Additionally, among-year variation in stable isotope signatures was low for the majority of species (Table 1).

The Cinaruco River supports little aquatic macrophyte growth, especially during the low-water period (Cotner et al., 2006). Thus, we assume this production source is relatively unimportant in supporting consumer biomass, a conclusion supported by Jepsen and Winemiller's (2007) analysis. Elimination of this source pool greatly increased resolution for the other four principal production sources in the IsoSource modeling. Replicate samples of fresh leaves from abundant terrestrial C_3 plants were collected from the riparian zone of lagoons and the main channel ($n = 44$). Twenty-seven of these samples were from the dominant riparian trees *Campsiandra angustifolia* and *Bactris* sp. A single sample of C_4 grass (*Trachypogon plumosus*) was collected from the savanna near the shoreline of a lagoon. The $\delta^{13}C$ value of our C_4 grass sample (-11.8) was very similar to the $\delta^{13}C$ value of C_4 grass from a previous study in the Cinaruco River (-11.5; Jepsen and Winemiller, 2007) and is also within the range of C_4 plants sampled extensively along the Amazon River (-11.6 to -13.6; Martinelli et al., 1991). Samples of filamentous algae ($n = 16$) were removed from substrates (rocks, woody debris) in the lagoons and the river channel and filtered onto pre-combusted (450° for 24 h) Whatman GF/F filters following Zeug and Winemiller (2008). This collection technique was unlikely to produce pure samples, therefore this basal production source, composed of attached filamentous algae and probably other materials (e.g., fine particulate organic matter [FPOM], diatoms, and other microorganisms) is referred to as "benthic algae." Phytoplankton samples ($n = 4$) were collected by filtering water from the lagoon and the main channel onto pre-combusted GF/F filters following Zeug and Winemiller (2008). Samples probably contained both phytoplankton and suspended organic matter; hereafter this source is referred to as "seston." Basal production source samples were frozen and then transported on ice until processing in the laboratory.

Fishes were collected with seines, cast nets, experimental gill nets, and hook and line. Following euthanasia via emersion in a 1% solution of tricaine methanesulfonate, a sample of muscle tissue from each individual was removed from the dorso-lateral region using a scalpel, and then rinsed and preserved in salt. This preservation technique causes minimal isotopic shifts in tissue samples (Arrington and Winemiller, 2002). In order to account for ontogenetic shifts in diet, only tissues from adult consumers were sampled. All samples were transported to the laboratory at Texas
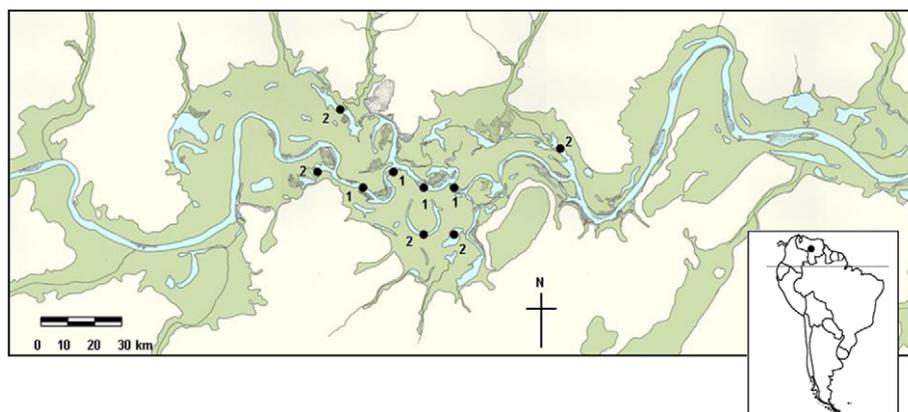

Fig. 1. Map of the Cinaruco River in the llanos savanna region of southwestern Venezuela. The main channel (1), floodplain lagoons (2), and the forested littoral zone are visible (in green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mean and among-year standard deviation of stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) for fish species that were collected over the widest range of years.

Species	Years collected	Mean $\delta^{13}C$	St dev $\delta^{13}C$	Mean $\delta^{15}N$	St dev $\delta^{15}N$
Boulengerella lucius	2002–2005	−28.9	1.0	9.1	0.5
Cichla temensis	2002–2005	−28.9	0.6	8.8	0.6
Metynnis hypsauchen	2001–2005	−23.9	2.2	6.0	0.7
Myleus rubripinnis	1999–2002	−25.2	0.8	5.8	0.7
Piaractus brachypomus	1999–2002	−25.2	1.6	5.2	0.8

A&M University, where tissues were prepared for stable isotope analysis following the methods of Jepsen and Winemiller (2002). Because C/N ratios of samples were relatively low (typically below 3.5), no lipid corrections were necessary (Post et al., 2007). A total of 70 samples of basal production sources and 446 fish samples comprising 91 species and 66 genera were analyzed for stable isotope analysis. We collected 78 fish species from lagoons, 23 species from the main channel, and an additional nine species were collected from both habitats. All of these species have been previously documented to occur in both channel and lagoon habitats (Arrington and Winemiller, 2006; Winemiller, unpublished data). Voucher specimens were deposited at the Venezuelan Museo de Ciencias Naturales de Guanare.

2.3. Stable isotope analysis

IsoSource calculations were performed for the four basal production sources following Phillips and Greg (2003). Because differences in $\delta^{13}C$ between lagoons and the main channel were not significant for riparian C_3 terrestrial plants (Student's *t*-test, $t = 1.23$, $df = 41$, $P = 0.23$), we used the mean of all values as a single input for the IsoSource model. Between-habitat variation of $\delta^{13}C$ was small for our few samples of seston (lagoon mean = −32.0, lagoon st dev = 1.9, main channel mean = −29.8, main channel st dev = 0.1) and benthic algae (lagoon mean = −34.9, main channel value = −31.7), thus these also were averaged to yield a single input value for each source. IsoSource calculations were performed separately for fishes from lagoon and main channel habitats. Trophic fractionation of C isotopes is typically relatively small, therefore $\delta^{13}C$ values of fishes were not corrected for trophic fractionation (McCutchan et al., 2003). Nitrogen values were corrected for trophic fractionation using the mean value of 2.54‰ derived from a meta-analysis (Vanderklift and Ponsard, 2003). The IsoSource tolerance level used to define an acceptable mass balance was 0.1, and source contributions were examined in 1% increments. Minimum and maximum feasible percent contributions for each basal production source supporting fishes in both habitats were reported as ranges for each species and as frequency histograms for the habitat assemblages.

The trophic position (TP) of each fish species was determined using two methods. The first method used a baseline signal that was the mean of the two primary producers estimated to be most important to fish species and their relative mean proportions according to IsoSource. The second used a baseline that was the mean of two common primary consumers in the system (Post, 2002). Trophic position estimates were calculated based on a standard two-source mixing model (Post, 2002) using the equation TP $= \lambda + (\delta^{15}N_{sc} - [\delta^{15}N_{base1} \times \alpha + \delta^{15}N_{base2} \times (1 - \alpha)])/2.54$, where λ was the trophic level of the food base (1 for primary producers, 2 for primary consumers), α was the proportion of nitrogen derived from the base of the first food web pathway, $1 - \alpha$ was the proportion of nitrogen derived from the base of the second

food web pathway, and 2.54‰ was the mean trophic fractionation value. Trophic position calculations with baselines that were primary consumers used two fish species: *Metynnis hypsauchen* (Characiformes: Characidae) which integrates allochthonous C_3 plants, and *Semaprochilodus kneri* (Characiformes: Prochilodontidae) which integrates autochthonous algae and detritus (Layman et al., 2005a,b). The mean trophic position of *M. hypsauchen* calculated using basal production sources was not significantly different between the two habitats (Student's *t*-test, $t = 1.09$, $df = 51$, $P = 0.28$, Fig. 5), therefore $\delta^{15}N_{base1}$ was the mean value averaged between both habitats. All of our *S. kneri* samples ($n = 12$) were collected from lagoons.

3. Results

The IsoSource mixing model indicated that seston had consistently high contribution to fishes in both habitats, as 1st-percentile values were greater than 0 for all species except *Creagrutus phasma* in the main channel (Tables 1 and 2). Benthic algae had 1st-percentile values > 0 for 30 species in lagoons and 5 species in the main channel, and 99th-percentile values ranged from 46 to 57% in the lagoon (Table 1) to 36–56% in the main channel (Table 2), indicating its importance as a contributor to the biomass of certain species. Carbon isotopes did not provide good discrimination for the assimilated fraction from terrestrial C_3 plants in some species. All fishes had 1st-percentile values equal to 0 in both habitats, and many had high 99th-percentile values (Appendices 1 and 2). Terrestrial C_4 grass likely was the least important basal production source supporting fish biomass in both habitats (Fig. 2). Terrestrial C_4 grass apparently contributed little to 35 of 87 species captured from lagoons (Appendix 1) and 6 of 32 from the main channel (Appendix 2), with 1st-percentile values = 0 and 99th-percentile values ≤ 15% in both habitats. However, terrestrial C_4 grass had 1st-percentile values > 0 for 47 species from lagoons and 18 species from the main channel, suggesting minor contributions. *Geophagus abalios* in lagoons and *M. hypsauchen* in the main channel seemed to assimilate larger fractions of carbon from C_4 grass. Overall, fishes collected from the two habitats had similar estimated contributions from basal production sources (Fig. 3). Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) also were similar for the fish species that were sampled from both habitats (Fig. 4; Table 2).

Trophic position estimates using basal sources that were primary producers versus secondary consumers were essentially the same, thus we only present trophic positions based on basal production sources. Because $\delta^{13}C$ and $\delta^{15}N$ for basal production sources were so similar between lagoons and the main channel, trophic positions of fishes were directly comparable between habitats. Mean trophic positions for fishes ranged from 2.0 (*Myleus schomburgki*) to 4.6 (*Catoprion mento*) in lagoons, and from 1.9 (*M. schomburgki*) to 4.3 (*Plagioscion squamosissimus*) in the main channel. Mean trophic positions of conspecifics captured from the two habitats were not significantly different (Student's *t*-test, $t = 0.11$, $df = 16$, $P = 0.92$, Figs. 3 and 5). Although assemblage-wide habitat means were essentially the same (lagoon mean = 3.35, channel mean = 3.26), trophic position distribution seemed to be left-skewed for the species assemblage in the main channel compared to lagoons, implying that piscivores had higher relative abundance in the main channel or they were better sampled than other feeding guilds (Fig. 6).

4. Discussion

The IsoSource mixing model indicated that a mixture of basal production sources was assimilated by fish assemblages in both lagoons and the main channel. Nonetheless, the 1st-percentile
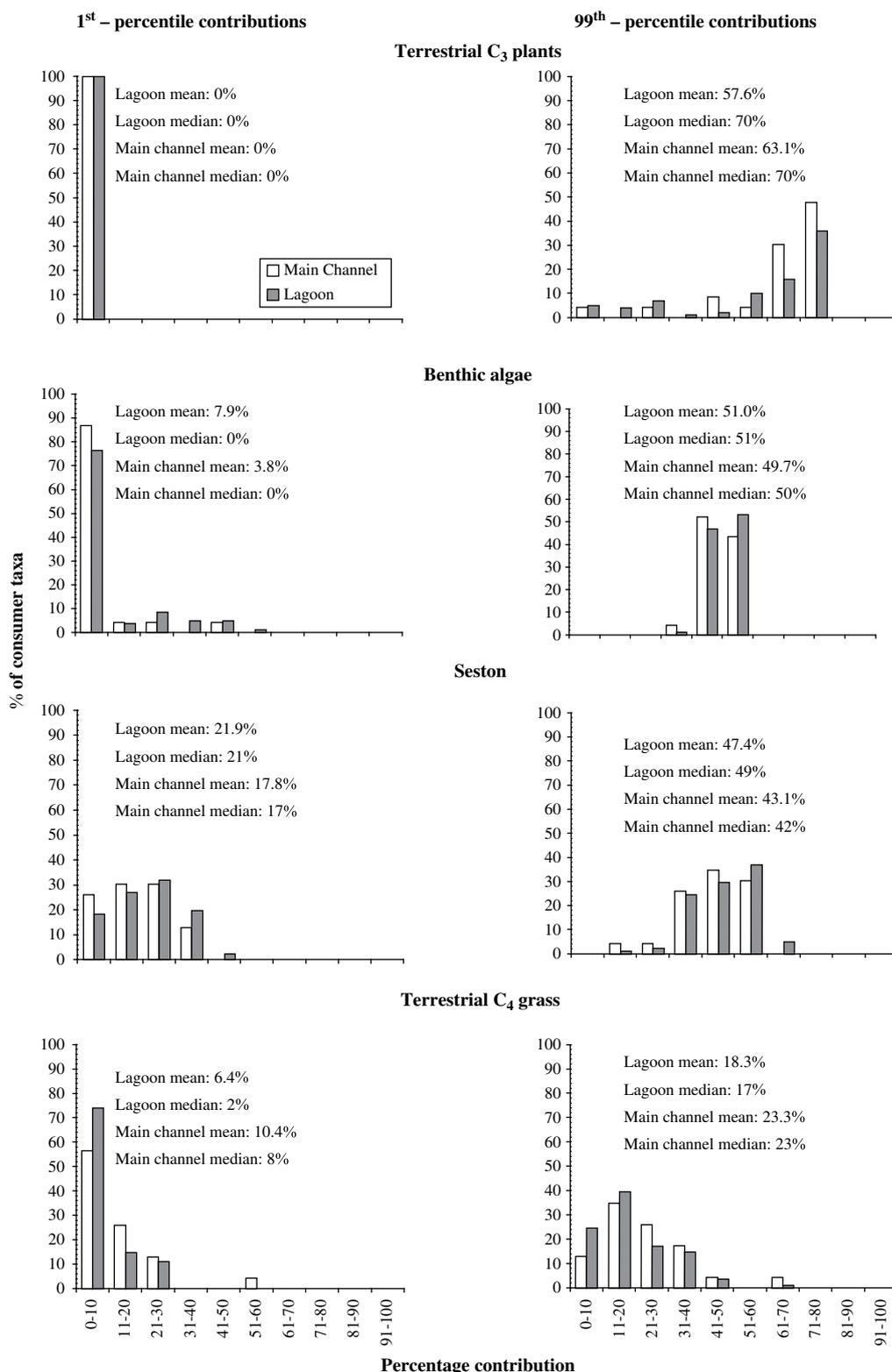
Fig. 2. Frequency histograms of 1st and 99th-percentile estimated contributions of basal production sources to fish biomass for the lagoon and main channel species assemblages.

contributions were highest for seston in both habitats indicating consistently high probability of assimilation of this source. Terrestrial C_4 grass, the dominant vegetation of the region, seems to be the least important production source supporting fishes in both lagoons and the main channel. Other isotopic studies in the Orinoco

River Basin have concluded that phytoplankton and benthic algae are the primary energy sources supporting consumer biomass (Lewis, 1988; Lewis et al., 1990, 2001; Hamilton et al., 1992; Forsberg et al., 1993). In the Cinaruco River, a study measuring net ecosystem production (NEP) within the water column and benthic

Table 2
Student's t-test for stable isotope signatures (δ^{13}C and δ^{15}N) of fish species that were collected in both lagoons and the main channel.

Species	Student's t-test for δ^{13}C			Student's t-test for δ^{15}N		
	t	df	P	t	df	P
Hydrolycus armatus	2.17	12	0.06	2.07	12	0.06
Metynnis hypsauchen	0.18	51	0.13	1.11	51	0.34
Myleus rubripinnis	0.77	22	0.13	0.24	22	0.52
Myleus sp.	1.46	30	0.90	1.60	30	0.89
Mylossoma aureus	1.93	14	0.31	2.94	14	0.98
Piaractus brachypomus	0.19	24	0.27	0.01	24	0.87

habitats in both lagoons and the river channel determined that NEP was always positive, further supporting the conclusion that autochthonous carbon is the principal resource for secondary production (Cotner et al., 2006). Furthermore, NEP was higher in the water column and peaked during the dry season in both habitats, thus organic sources consumed from substrates and assimilated by benthivorous primary consumers may contain a large seston component (Cotner et al., 2006). Additionally, isotopic
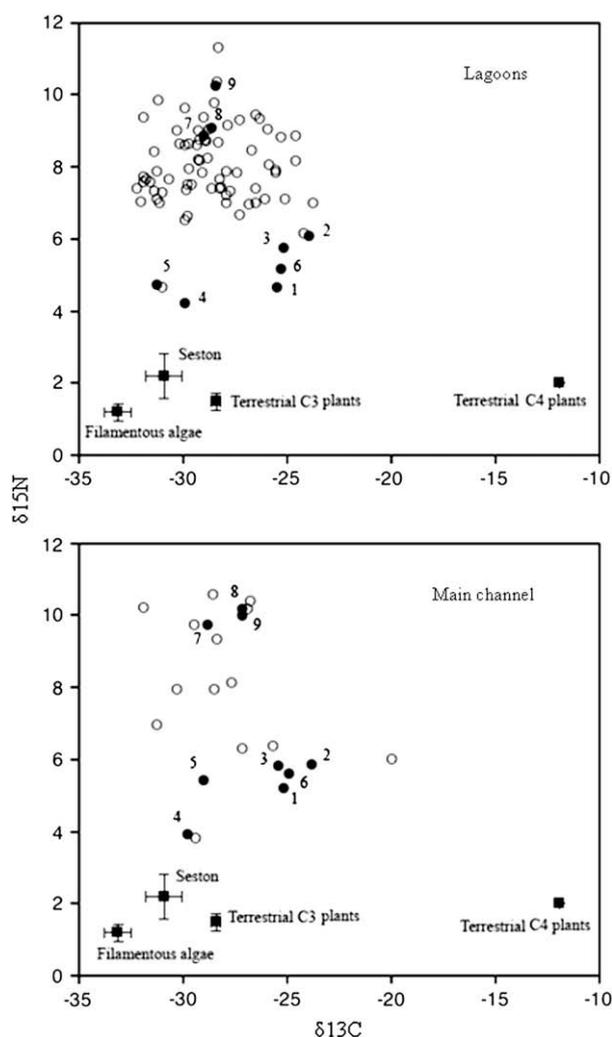
Fig. 3. Carbon and nitrogen isotope ratio biplots of the mean values of four basal production sources, fishes specific to each habitat (unnumbered), and some common fishes taken from lagoons and the main channel (numbered). 1 = *Piaractus brachypomus*, 2 = *Metynnis hypsauchen*, 3 = *Myleus rubripinnis*, 4 = *Myleus schomburgki*, 5 = *Myleus* sp., 6 = *Mylossoma aureus*, 7 = *Boulengerella lucius*, 8 = *Hydrolycus armatus*, 9 = *Serrasalmus manueli*. Error bars indicate 1 standard error.
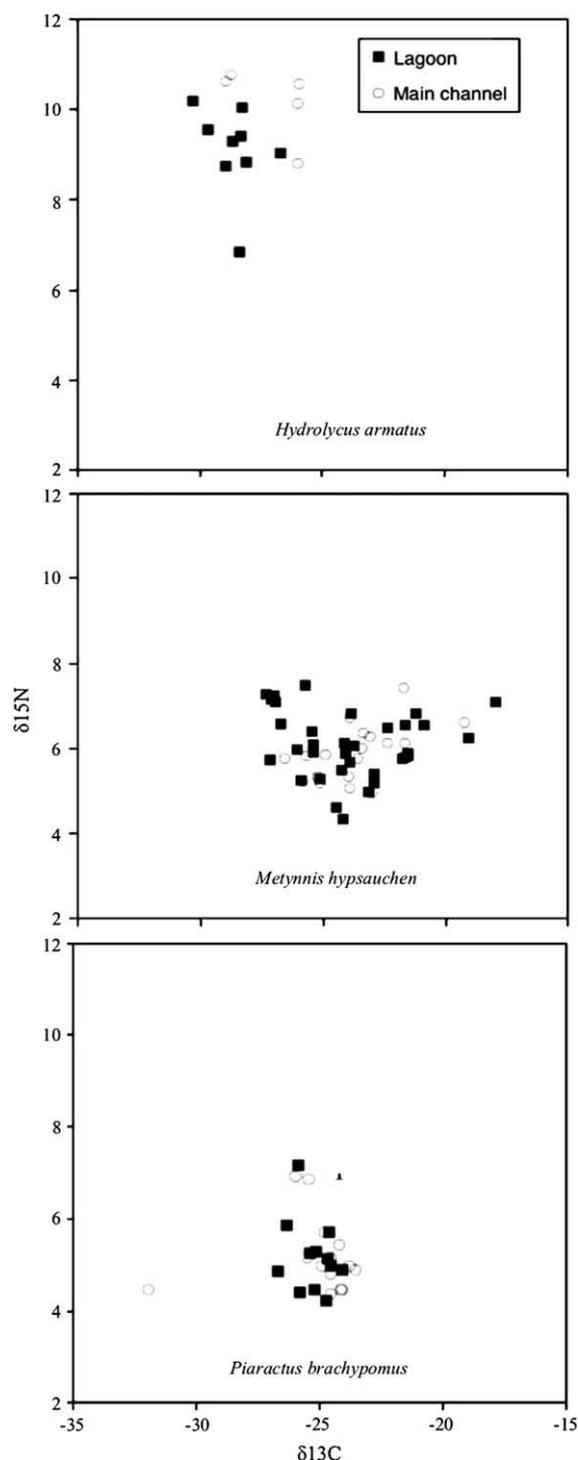
Fig. 4. Carbon and nitrogen isotope ratio biplots of all individuals captured in both lagoons and the main channel for *Hydrolycus armatus*, *Metynnis hypsauchen*, and *Piaractus brachypomus*.

evidence from other Neotropical rivers has estimated that little carbon from macrophytes, particularly C_4 grasses, is assimilated by secondary consumers (Hamilton et al., 1992; Lewis et al., 2001), and a previous isotope study in the Cinaruco River estimated that C_4 grass was a minor contributor to fishes (Jepsen and Winemiller, 2007).

Stable isotopes also have been used to model the flow of organic carbon between habitats in several temperate rivers. For example, variation in stable isotope signatures of secondary consumers has
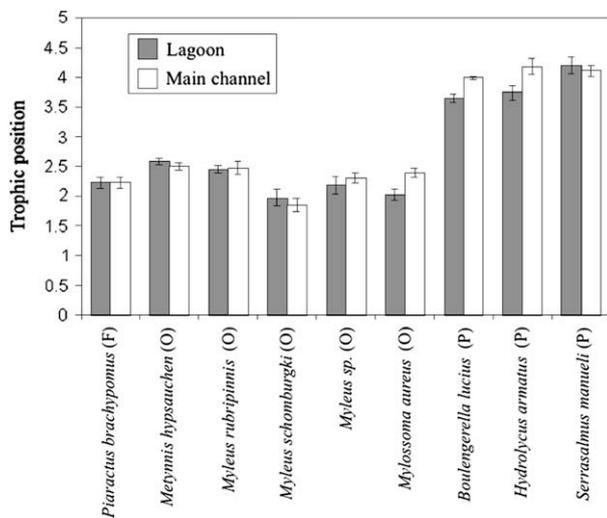
Fig. 5. Mean trophic position of fish species in both lagoons and main channel calculated using basal production sources. F = frugivore, O = omnivore, P = piscivores. Error bars indicate 1 standard error.
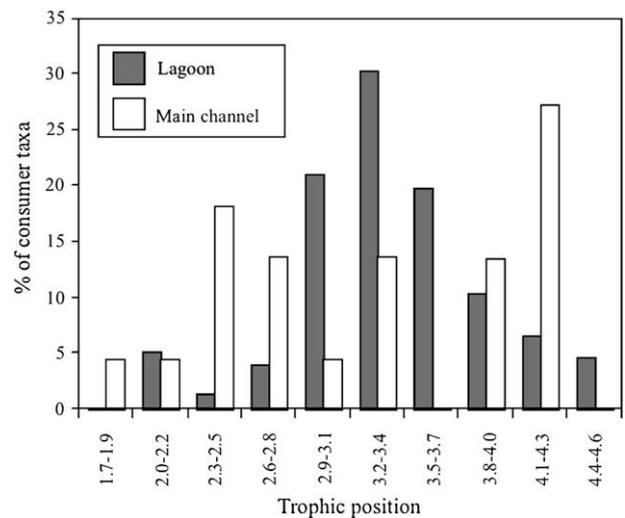

Fig. 6. Frequency histograms of trophic position calculated using basal production sources for species assemblages in lagoons and the main channel.

been found at the reach scale (Finlay et al., 1999, 2002; Walters et al., 2007), the segment scale (Zeug and Winemiller, 2008; Roach et al., 2009), and the drainage network scale (Fry, 2002; Hoeing-haus et al., 2007), suggesting that exchange of production sources and movements of consumer taxa between these habitats are relatively low. In Neotropical floodplain rivers, a few studies have suggested a significant net transfer of organic carbon from flood-plains to the river channel (Junk et al., 1989), whereas others have indicated little lateral exchange of organic materials during the flood pulse (Lewis et al., 2000). The latter study did not examine the role of fishes in the exchange of organic carbon between habitats, and movements by fishes in tropical lotic systems in response to seasonal hydrologic variation are well documented (Winemiller and Jepsen, 1998).

Our findings indicate that proportional contributions from production sources to fishes are generally similar in lagoons and the main channel of the Cinaruco River. Moreover, isotopic varia-tion of fish species sampled from both habitats was low. Mean trophic positions of fish assemblages and conspecifics also were not different between the habitats. This apparent lack of variation in assimilated matter from production sources, stable isotope signa-tures, and trophic positions of fishes between lagoons and the main channel in the Cinaruco River could result from a combination of factors, including lack of spatial variation in stable isotope ratios of basal production sources, transport and lateral mixing of produc-tion sources during the flood pulse, and lateral migrations of fishes.

In floodplain rivers of South America, seasonal changes in water levels are associated with shifts in algal biomass and assemblage structure (Hamilton and Lewis, 1987; Forsberg et al., 1988; Montoya et al., 2006). Low-water conditions in floodplain lagoons result in higher densities of phytoplankton (Rai and Hill, 1984; Putz and Junk, 1997) and benthic algae (Montoya et al., 2006). Differences in species composition and isotopic fractionation related to carbon fixation can cause habitat-associated shifts in $\delta^{13}C$ of basal production sources. For example, in algae, fractionation is associ-ated with uptake of dissolved inorganic carbon, affected by both local availability and boundary layer thickness (Post, 2002). Based on our limited number of samples, we found low spatial variation in stable isotope ratios of seston and terrestrial C_3 plants between lagoons and the main channel. C_4 grass $\delta^{13}C$ also should be similar between habitats; the dominant grass, *T. plumosus*, is found in

a virtual monoculture on the floodplain savanna. We did not collect a sufficient number of benthic algae samples to analyze differences between the habitats; however, other studies show that as flow velocity decreases, ^{13}C content of algae may increase because of decreased boundary layer thickness (Finlay et al., 1999).

The longitudinal and lateral movement of water during the annual flood pulse could transport particulate organic matter (POM) floating on the surface or suspended in the water column (e.g., phytoplankton, autochthonous FPOM, and allochthonous POM). However, benthic algae are less likely than phytoplankton to be transported by water currents. Furthermore, because of limited lateral movements of water during the descending phase of the annual hydrologic cycle, export of basal production sources to the main channel may be low (Lewis et al., 2000). Fish movements thus may be the largest contributor to the lack of spatial variation found in fishes of some Neotropical floodplain rivers with seasonal flood pulses. Extensive movements may allow fishes to assimilate basal production sources from various habitats, resulting in little spatial variability in stable isotope signatures of consumers even when there is spatial variability in production sources. For example, in the low-water period of the Paraná River, one study found significant variability in the stable isotope signatures of phytoplankton and particulate organic carbon between main channel and reservoir habitats, yet *Leporinus friderici* had similar signatures in both of these habitats (Pereira et al., 2007).

Many fishes in the Cinaruco River undertake extensive move-ments that are associated with seasonal changes in hydrology and resource availability. For example, during the falling-water period, some piscivorous species (e.g., *Cichla temensis*) migrate from lagoons to the main channel to exploit large schools of detritivorous fishes (*S. kneri*) that enter the Cinaruco from the Orinoco River and disperse upstream (Winemiller and Jepsen, 2004). During the low-water period, some fish species enter lagoons to spawn (Hoeing-haus et al., 2003). However, because of the relatively long turnover times of tissues from secondary consumers, (i.e., weeks to months; McIntyre and Flecker, 2006), stable isotope signatures during the falling-water period may largely reflect a spatial reshuffling of local fish assemblages that occurs during the preceding flood pulse. Movements of consumers may be sufficient to reduce any locally acquired isotopic differences. Thus, we infer that the lack of spatial variation in stable isotope signatures in fishes of the Cinaruco River is mainly a function of the extended annual flood pulse that allows mixing of sestonic and allochthonous production sources and

extensive lateral movements of fishes. We speculate that movements of newly produced fish biomass from floodplains to the main channel may represent a significant net transfer of organic carbon.

Acknowledgments

Appendix 1

Means and 1–99th percentile ranges (in parentheses) of estimated contributions of basal production sources to fish biomass in lagoons from IsoSource models. Sample sizes for consumers are in parentheses next to species names. Numbers in bold indicate assimilation of that source (1st-percentile values greater than 0). Species in bold were captured in both habitats.

Taxa	Benthic algae	Seston	Terrestrial C_3	Terrestrial C_4
Characiformes				
Anostomidae				
Laemolyta taeniatus (2)	**0.50 (0.41–0.56)**	**0.47 (0.40–0.58)**	0.03 (0.00–0.08)	<0.01 (0.00–0.01)
Leporinus sp. (2)	0.21 (0.00–0.48)	**0.20 (0.06–0.33)**	0.31 (0.00–0.69)	**0.29 (0.22–0.36)**
Characidae				
Acestrorhynchus microlepis (4)	0.22 (0.00–0.51)	**0.34 (0.20–0.48)**	0.33 (0.00–0.74)	**0.11 (0.03–0.18)**
Agoniates anchovia (2)	**0.41 (0.28–0.55)**	**0.47 (0.36–0.60)**	0.10 (0.00–0.24)	0.02 (0.00–0.05)
Argonectes longiceps (2)	0.21 (0.00–0.48)	**0.24 (0.10–0.38)**	0.31 (0.00–0.71)	**0.24 (0.16–0.31)**
Brycon falcatus (9)	0.21 (0.00–0.47)	**0.18 (0.04–0.31)**	0.30 (0.00–0.69)	**0.32 (0.24–0.38)**
Brycon pesu (2)	0.22 (0.00–0.49)	**0.25 (0.12–0.39)**	0.32 (0.00–0.71)	**0.22 (0.14–0.29)**
Myleus rubripinnis (15)	0.21 (0.00–0.48)	**0.20 (0.06–0.34)**	0.31 (0.00–0.69)	**0.29 (0.21–0.36)**
Myleus schomburgki (5)	**0.28 (0.06–0.52)**	**0.41 (0.28–0.54)**	0.26 (0.00–0.55)	0.05 (0.00–0.11)
Myleus sp. (7)	**0.41 (0.29–0.55)**	**0.48 (0.37–0.60)**	0.10 (0.00–0.23)	0.02 (0.00–0.04)
Mylossoma aureus (6)	0.21 (0.00–0.48)	**0.21 (0.08–0.35)**	0.31 (0.00–0.70)	**0.27 (0.19–0.34)**
Piaractus brachypomus (12)	0.21 (0.00–0.48)	**0.21 (0.07–0.34)**	0.31 (0.00–0.69)	**0.28 (0.21–0.35)**
Poptella sp. (1)	0.21 (0.00–0.49)	**0.25 (0.11–0.39)**	0.31 (0.00–0.71)	**0.23 (0.15–0.30)**
Pristobrycon striolatus (2)	0.22 (0.00–0.49)	**0.29 (0.15–0.43)**	0.32 (0.00–0.72)	**0.17 (0.10–0.24)**
Serrasalmus manueli (2)	0.23 (0.00–0.51)	**0.34 (0.20–0.47)**	0.33 (0.00–0.73)	**0.11 (0.04–0.19)**
Tetragonopterus chalceus (2)	**0.28 (0.06–0.52)**	**0.41 (0.28–0.54)**	0.26 (0.00–0.55)	0.05 (0.00–0.11)
Triportheus albus (2)	0.21 (0.00–0.48)	**0.20 (0.07–0.34)**	0.31 (0.00–0.70)	**0.28 (0.21–0.35)**
Chilodontidae				
Caenotropis labrynthicus (1)	**0.28 (0.06–0.52)**	**0.41 (0.28–0.54)**	0.26 (0.00–0.54)	0.05 (0.00–0.11)
Crenuchidae				
Bryconops caudomaculatus (7)	0.23 (0.00–0.51)	**0.36 (0.22–0.50)**	0.33 (0.00–0.74)	**0.08 (0.01–0.16)**
Catoprion mento (2)	0.22 (0.00–0.50)	**0.33 (0.20–0.47)**	0.33 (0.00–0.73)	**0.12 (0.04–0.19)**
Chalceus macrolepidotus (5)	0.21 (0.00–0.48)	**0.21 (0.08–0.35)**	0.31 (0.00–0.70)	**0.27 (0.19–0.34)**
Characidium sp. (2)	**0.36 (0.19–0.54)**	**0.45 (0.33–0.58)**	0.17 (0.00–0.36)	0.03 (0.00–0.07)
Hemigrammus analis (2)	0.22 (0.00–0.49)	**0.33 (0.20–0.47)**	0.33 (0.00–0.73)	**0.12 (0.04–0.19)**
Hemigrammus vorderwinkleri (2)	**0.56 (0.55–0.57)**	**0.43 (0.42–0.45)**	<0.01 (0.00–0.1)	<0.01 (0.00–0.01)
Metynnis argenteus (4)	0.20 (0.00–0.47)	**0.16 (0.03–0.30)**	0.30 (0.00–0.68)	**0.34 (0.27–0.41)**
Metynnis hypsauchen (34)	0.20 (0.00–0.46)	**0.15 (0.01–0.29)**	0.30 (0.00–0.68)	**0.35 (0.28–0.42)**
Moenkhausia browni (2)	0.21 (0.00–0.47)	**0.17 (0.04–0.31)**	0.30 (0.00–0.68)	**0.32 (0.25–0.39)**
Moenkhausia copei (5)	0.23 (0.00–0.51)	**0.37 (0.24–0.51)**	0.33 (0.00–0.71)	0.07 (0.00–0.15)
Moenkhausia lepidura (6)	0.21 (0.00–0.48)	**0.23 (0.09–0.37)**	0.31 (0.00–0.70)	**0.25 (0.17–0.32)**
Moenkhausia sp. 1 (1)	**0.26 (0.03–0.52)**	**0.40 (0.27–0.53)**	0.28 (0.00–0.59)	0.06 (0.00–0.12)
Moenkhausia sp. 2 (3)	0.22 (0.00–0.50)	**0.31 (0.18–0.45)**	0.32 (0.00–0.73)	**0.14 (0.06–0.21)**
Curimatidae				
Cyphocharax oenas (2)	**0.47 (0.37–0.56)**	**0.49 (0.40–0.62)**	0.04 (0.00–0.11)	0.01 (0.00–0.02)
Cyphocharax spilurus (3)	**0.41 (0.29–0.55)**	**0.48 (0.37–0.60)**	0.10 (0.00–0.22)	0.02 (0.00–0.04)
Cynodontidae				
Hydrolycus armatus (9)	0.22 (0.00–0.50)	**0.34 (0.21–0.48)**	0.33 (0.00–0.73)	**0.10 (0.03–0.18)**
Crythrinidae				
Boulengerella lucius (7)	0.23 (0.00–0.51)	**0.36 (0.22–0.50)**	0.33 (0.00–0.74)	**0.08 (0.01–0.16)**
Hoplias malabaricus (1)	0.23 (0.00–0.51)	**0.36 (0.22–0.60)**	0.33 (0.00–0.74)	**0.09 (0.01–0.16)**
Hemiodontidae				
Bivibranchia fowleri (2)	0.22 (0.00–0.50)	**0.33 (0.19–0.47)**	0.33 (0.00–0.73)	**0.13 (0.05–0.20)**
Hemiodus gracilis (2)	0.23 (0.00–0.51)	**0.37 (0.23–0.51)**	0.33 (0.00–0.72)	0.08 (0.00–0.15)
Hemiodus immaculatus (3)	**0.43 (0.31–0.55)**	**0.48 (0.37–0.61)**	0.08 (0.00–0.19)	0.01 (0.00–0.04)
Hemiodus semitaeniatus (1)	**0.40 (0.26–0.55)**	**0.47 (0.36–0.60)**	0.11 (0.00–0.26)	0.02 (0.00–0.05)
Hemiodus unimaculatus (8)	**0.27 (0.04–0.52)**	**0.41 (0.28–0.53)**	0.27 (0.00–0.57)	0.05 (0.00–0.12)

Appendix 1 (*continued*)

Taxa	Benthic algae	Seston	Terrestrial C$_3$	Terrestrial C$_4$
Prochilodontidae				
Semaprochilodus kneri (12)	**0.53 (0.48–0.57)**	**0.45 (0.41–0.52)**	0.02 (0.00–0.05)	<0.01 (0.00–0.01)
Semaprochilodus laticeps (2)	**0.41 (0.28–0.55)**	**0.47 (0.36–0.60)**	0.10 (0.00–0.24)	0.02 (0.00–0.05)
Clupeiformes				
Clupeidae				
Amazonsprattus scintilla (3)	0.23 (0.00–0.51)	**0.37 (0.24–0.51)**	0.32 (0.00–0.70)	0.07 (0.00–0.14)
Engraulidae				
Anchoviella sp. (2)	**0.28 (0.06–0.52)**	**0.41 (0.28–0.54)**	0.26 (0.00–0.55)	0.05 (0.00–0.11)
Myliobatiformes				
Potamotrygonidae				
Potamotrygon sp. (1)	0.22 (0.00–0.50)	**0.33 (0.20–0.47)**	0.33 (0.00–0.73)	**0.12 (0.04–0.19)**
Perciformes				
Cichlidae				
Apistogramma sp. (3)	**0.31 (0.11–0.53)**	**0.43 (0.30–0.55)**	0.23 (0.00–0.48)	0.04 (0.00–0.10)
Biotodoma wavrini (3)	**0.27 (0.04–0.52)**	**0.40 (0.27–0.53)**	0.27 (0.00–0.53)	0.05 (0.00–0.12)
Biotoecus dicentrarchus (2)	0.22 (0.00–0.49)	**0.29 (0.16–0.43)**	0.32 (0.00–0.72)	**0.17 (0.09–0.24)**
Cichla orinocensis (4)	**0.26 (0.03–0.52)**	**0.40 (0.27–0.53)**	0.28 (0.00–0.59)	0.06 (0.00–0.12)
Cichla temensis (16)	0.23 (0.00–0.51)	**0.36 (0.22–0.50)**	0.33 (0.00–0.74)	**0.09 (0.01–0.16)**
Geophagus abalios (2)	0.20 (0.00–0.46)	**0.14 (0.01–0.28)**	0.30 (0.00–0.67)	**0.36 (0.29–0.43)**
Geophagus dicrozoster (2)	0.22 (0.00–0.49)	**0.29 (0.15–0.43)**	0.32 (0.00–0.72)	**0.18 (0.10–0.25)**
Heros sp. (2)	0.22 (0.00–0.50)	**0.34 (0.21–0.48)**	0.33 (0.00–0.73)	**0.10 (0.03–0.18)**
Hoplarchus psittacus (3)	0.21(0.00–0.48)	**0.22 (0.08–0.35)**	0.31 (0.00–0.70)	**0.27 (0.19–0.34)**
Mesonauta insignis (1)	**0.38 (0.24–0.54)**	**0.46 (0.35–0.59)**	0.13 (0.00–0.29)	0.02 (0.00–0.06)
Satanoperca sp. (3)	0.22 (0.00–0.48)	**0.25 (0.12–0.39)**	0.32 (0.00–0.71)	**0.22 (0.14–0.29)**
Satanoperca daemon (5)	0.22 (0.00–0.50)	**0.31 (0.18–0.45)**	0.32 (0.00–0.73)	**0.14 (0.06–0.21)**
Siluriformes				
Auchenipteridae				
Trachycorystes trachycorystes (2)	0.22 (0.00–0.50)	**0.31 (0.17–0.34)**	0.32 (0.00–0.73)	**0.15 (0.07–0.22)**
Cetopsidae				
Scorpiodoras sp. (1)	**0.32 (0.13–0.53)**	**0.43 (0.31–0.56)**	0.21 (0.00–0.45)	0.04 (0.00–0.09)
Doradidae				
Acanthodoras sp. (1)	0.22 (0.00–0.49)	**0.27 (0.13–0.41)**	0.32 (0.00–0.71)	**0.20 (0.12–0.27)**
Orinocodoras eigenmanni (1)	0.22 (0.00–0.49)	**0.26 (0.13–0.40)**	0.32 (0.00–0.71)	**0.21 (0.13–0.28)**
Oxydoras niger (3)	0.23 (0.00–0.51)	**0.36 (0.23–0.50)**	0.33 (0.00–0.73)	0.08 (0.00–0.15)
Platydoras costatus (3)	0.22 (0.00–0.50)	**0.35 (0.21–0.49)**	0.33 (0.00–0.74)	**0.10 (0.02–0.17)**
Loricariidae				
Dekeseria scaphyrhyncha (3)	**0.28 (0.06–0.52)**	**0.41 (0.28–0.54)**	0.26 (0.00–0.54)	0.05 (0.00–0.11)
Glyptoperichthys gibbiceps (2)	**0.45 (0.34–0.55)**	**0.49 (0.38–0.62)**	0.06 (0.00–0.15)	0.01 (0.00–0.03)
Hypostomus sp. (1)	0.23 (0.00–0.51)	**0.35 (0.22–0.49)**	0.33 (0.00–0.74)	**0.09 (0.02–0.17)**
Peckoltia sp. (1)	0.22 (0.00–0.50)	**0.32 (0.18–0.35)**	0.32 (0.00–0.73)	**0.14 (0.06–0.21)**
Rineloricaria sp. (2)	0.22 (0.00–0.50)	**0.33 (0.19–0.47)**	0.33 (0.00–0.73)	**0.12 (0.04–0.20)**
Pimelodidae				
Microglanis poecilus (3)	**0.25 (0.01–0.52)**	**0.39 (0.26–0.53)**	0.30 (0.00–0.62)	0.06 (0.00–0.13)
Pimelodus blochii (2)	0.21 (0.00–0.48)	**0.23 (0.10–0.37)**	0.31 (0.00–0.70)	**0.25 (0.17–0.32)**
Pseudoplatystoma fasciatum (4)	0.22 (0.00–0.50)	**0.31 (0.18–0.35)**	0.32 (0.00–0.73)	**0.14 (0.07–0.22)**
Pseudopimelodidae				
Cephalosilurus apurensis (1)	0.23 (0.00–0.51)	**0.37 (0.23–0.51)**	0.33 (0.00–0.72)	0.08 (0.00–0.15)
Trichomycteridae				
Ochmacanthus alternus (3)	**0.50 (0.41–0.56)**	**0.47 (0.40–0.58)**	0.03 (0.00–0.08)	<0.01 (0.00–0.01)
Symbranchiformes				
Symbranchidae				
Synbranchus marmoratus (2)	0.23 (0.00–0.51)	**0.35 (0.21–0.49)**	0.33 (0.00–0.74)	0.10 (0.02–0.17)

Appendix 2

Means and 1–99th percentile ranges (in parentheses) of estimated contributions of basal production sources to fish biomass in the main channel from IsoSource models. Sample sizes for consumers are in parentheses next to species names. Numbers in bold indicate assimilation of that source (1st-percentile values greater than 0). Species in bold were captured in both habitats.

Taxa	Benthic algae	Seston	Terrestrial C$_3$	Terrestrial C$_4$
Characiformes				
Characidae				
Myleus rubripinnis (9)	0.21(0.00–0.48)	**0.21 (0.07–0.35)**	0.31 (0.00–0.70)	**0.27 (0.20–0.34)**
Myleus schomburgki (2)	**0.26 (0.03–0.52)**	**0.40 (0.27–0.53)**	0.28 (0.00–0.58)	0.06 (0.00–0.12)
Myleus torquatus (3)	0.21 (0.00–0.48)	**0.22 (0.09–0.36)**	0.31 (0.00–0.70)	**0.26 (0.18–0.33)**

Appendix 2 (*continued*)

Taxa	Benthic algae	Seston	Terrestrial C₃	Terrestrial C₄
Myleus sp. (25)	0.23 (0.00–0.51)	**0.36** (**0.22–0.50**)	0.33 (0.00–0.74)	**0.08** (**0.01–0.16**)
Mylossoma aureus (10)	0.21 (0.00–0.47)	**0.19** (**0.06–0.33**)	0.30 (0.00–0.69)	**0.30** (**0.23–0.37**)
Piaractus brachypomus (14)	0.21 (0.00–0.48)	**0.20** (**0.07–0.34**)	0.31(0.00–0.69)	**0.29** (**0.21–0.35**)
Serrasalmus manueli (4)	0.22 (0.00–0.49)	**0.28** (**0.15–0.42**)	0.32 (0.00–0.72)	**0.18** (**0.10–0.25**)
Serrasalmus rhombeus (6)	0.22 (0.00–0.49)	**0.27** (**0.13–0.40**)	0.32 (0.00–0.71)	**0.20** (**0.13–0.27**)
Crenuchidae				
Creagrutus phasma (2)	0.17 (0.00–0.36)	0.05 (0.00–0.12)	0.21 (0.00–0.46)	**0.57** (**0.52–0.62**)
Melanocharacidium dispilomma (2)	**0.32** (**0.13–0.53**)	**0.43** (**0.31–0.56**)	0.21 (0.00–0.45)	0.04 (0.00–0.09)
Metynnis hypsauchen (19)	0.20 (0.00–0.47)	**0.14** (**0.01–0.28**)	0.30 (0.00–0.67)	**0.36** (**0.29–0.42**)
Ctenoluciidae				
Boulengerella cuvieri (2)	**0.24** (**0.01–0.52**)	**0.38** (**0.25–0.52**)	0.31 (0.00–0.65)	0.06(0.00–0.13)
Boulengerella lucius (2)	0.23 (0.00–0.51)	**0.35** (**0.22–0.39**)	0.33 (0.00–0.74)	**0.09** (**0.01–0.17**)
Cynodontidae				
Hydrolycus armatus (5)	0.22 (0.00–0.49)	**0.28** (**0.15–0.42**)	0.32 (0.00–0.71)	**0.18** (**0.11–0.25**)
Raphiodon vulpinus (10)	0.22 (0.00–0.49)	**0.27** (**0.14–0.41**)	0.32 (0.00–0.71)	**0.20** (**0.12–0.27**)
Osteichthyes				
Clupeidae				
Pellona castelnaeana (1)	**0.50** (**0.41–0.56**)	**0.47** (**0.40–0.58**)	0.03 (0.00–0.08)	<0.01 (0.00–0.01)
Perciformes				
Sciaenidae				
Plagioscion squamosissimus (10)	0.23 (0.00–0.51)	**0.34** (**0.21–0.48**)	0.33 (0.00–0.73)	**0.11** (**0.03–0.18**)
Siluriformes				
Auchenipteridae				
Ageneiosus brevifilis (17)	0.22 (0.00–0.51)	**0.33** (**0.20–0.47**)	0.33 (0.00–0.73)	**0.12** (**0.04–0.19**)
Loricariidae				
Hypostomus sp. (1)	0.22 (0.00–0.49)	**0.28** (**0.15–0.42**)	0.32 (0.00–0.72)	**0.18** (**0.11–0.25**)
Peckoltia sp. (1)	0.24 (0.00–0.51)	**0.38** (**0.25–0.52**)	0.32 (0.00–0.67)	0.06(0.00–0.14)
Rineloricaria sp. (1)	**0.41** (**0.29–0.55**)	**0.48** (**0.37–0.60**)	0.10 (0.00–0.22)	0.02 (0.00–0.04)
Pimelodidae				
Pimelodella sp. 1 (2)	0.22 (0.00–0.50)	**0.34** (**0.20–0.48**)	0.33 (0.00–0.73)	**0.11** (**0.03–0.18**)
Pimelodella sp. 2 (2)	0.22 (0.00–0.50)	**0.30** (**0.17–0.44**)	0.32 (0.00–0.72)	**0.15** (**0.08–0.23**)

References

Arrington, D.A., Winemiller, K.O., 2002. Use of preserved biological specimens for stable isotope analysis. Transactions of the American Fisheries Society 131, 337–342.

Arrington, D.A., Winemiller, K.O., 2006. Cyclical flood pulses, littoral habitats and species associations in a Neotropical floodplain river. Journal of the North American Benthological Society 25, 126–141.

Cotner, J.B., Montoya, J.V., Roelke, D.L., Winemiller, K.O., 2006. Seasonally variable riverine production in the Venezuelan llanos. Journal of the North American Benthological Society 25, 171–184.

Douglas, M.M., Bunn, S.E., Davies, P.M., 2005. River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. Marine and Freshwater Research 56, 329–342.

Fernandez, C.C., 1997. Lateral migration of fishes in Amazon floodplains. Ecology of Freshwater Fish 6, 36–44.

Finlay, J.C., Khandwala, S., Power, M.E., 2002. Spatial scales of carbon flow in a river food web. Ecology 83, 1845–1859.

Finlay, J.C., Power, M.E., Cabana, G., 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnology and Oceanography 44, 1198–1203.

Fisher, S.J., Brown, M.L., Willis, D.W., 2001. Temporal food web variability in an upper Missouri River backwater: energy origination points and transfer mechanisms. Ecology of Freshwater Fish 10, 154–167.

Fisher, S.J., Willis, D.W., 2000. Seasonal dynamics of aquatic fauna and habitat parameters in a perched upper Missouri River wetland. Wetlands 20, 470–478.

Forsberg, B.R., Araujo-Lima, C.A.R.M., Martinelli, L.A., Victoria, R.L., Bonossi, J.A., 1993. Autotrophic carbon sources for fish of the central Amazon. Ecology 74, 643–652.

Forsberg, B.R., Devol, A.H., Richey, J.E., Martinelli, L.A., 1988. Factors controlling nutrient concentrations in Amazon floodplain lakes. Limnology and Oceanography 33, 41–56.

Fry, B., 2002. Stable isotopic indicators of habitat use by Mississippi River fish. Journal of the North American Benthological Society 21, 676–685.

Hamilton, S.K., Lewis Jr., W.M., 1987. Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. Limnology and Oceanography 32, 1277–1290.

Hamilton, S.K., Lewis Jr., W.M., Sippel, S.J., 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia 89, 324–330.

Herwig, B.R., Soluk, D.A., Dettmers, J.M., Wahl, D.H., 2004. Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Science 61, 12–22.

Hoeinghaus, D.J., Layman, C.A., Arrington, D.A., Winemiller, K.O., 2003. Movement of *Cichla* species (Cichlidae) in a Venezuelan floodplain river. Neotropical Ichthyology 1, 121–126.

Hoeinghaus, D.J., Winemiller, K.O., Agostinho, A.A., 2007. Landscape-scale hydrologic features differentiate patterns of carbon flow in large-river food webs. Ecosystems 10, 1019–1033.

Jepsen, D.B., Winemiller, K.O., 2002. Structure of tropical river food webs revealed by stable isotope ratios. Oikos 96, 46–55.

Jepsen, D.B., Winemiller, K.O., 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four Neotropical rivers. Ecology of Freshwater Fish 16, 267–281.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodpain systems. In: Dodge, D.P. (Ed.), Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences, vol. 106, pp. 110–127.

Lagler, K.F., Kapetsky, J.M., Stewart, D.J., 1971. The Fisheries of the Kafue River Flats, Zambia, in Relation to the Kafue Gorge Dam. FAO Technical Report SF/Zam 11-1, pp. 1–161.

Layman, C.A., Winemiller, K.O., Arrington, D.A., 2005a. Describing the structure and function of a Neotropical river food web using stable isotope ratios, stomach contents, and functional experiments. In: Moore, J.C., De Ruiter, P., Wolters, V. (Eds.), Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Elsevier/Academic Press, Burlington, Massachusetts, USA, pp. 395–406.

Layman, C.A., Winemiller, K.O., Arrington, D.A., Jepsen, D.B., 2005b. Body size and trophic position in a diverse tropical food web. Ecology 86, 2530–2535.

Lewis Jr., W.M., 1988. Primary production in the Orinoco River. Ecology 69, 679–692.

Lewis Jr., W.M., Hamilton, S.K., Lasi, M.A., Rodriguez, M., Saunders III, J.F., 2000. Ecological determinism on the Orinoco floodplain. Bioscience 50, 681–691.

Lewis Jr., W.M., Hamilton, S.K., Rodriguez, M.A., Saunders III, J.F., Lasi, M.A., 2001. Foodweb analysis of the Orinoco floodplain based on production estimates and stable isotope analysis. Journal of the North American Benthological Society 20, 241–254.

Lewis Jr., W.M., Weibezahn, F.H., Saunders III, J.F., Hamilton, S.K., 1990. The Orinoco River as an ecological system. Interciencia 15, 346–357.

Lowe-McConnell, R.H., 1964. The fishes of the Rupununi savanna district of British Guiana, Pt. 1. Groupings of fish species and effects of the seasonal cycles on the fish. Zoological Journal of the Linnean Society 45, 103–144.

Martinelli, L.A., Devol, A.H., Victoria, R.L., Richey, J.E., 1991. Stable carbon isotope variation in C_3 and C_4 plants along the Amazon River. Nature 353, 57–59.

McCutchan Jr., J.H., Lewis Jr., W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378–390.

McIntyre, P.B., Flecker, A.S., 2006. Rapid turnover of tissue nitrogen of primary consumers in tropical freshwaters. Oecologia 148, 12–21.

Montoya, J.V., Roelke, D.L., Winemiller, K.O., Cotner, J.B., Snider, J.A., 2006. Hydrological seasonality and benthic algal biomass in a Neotropical floodplain river. Journal of the North American Benthological Society 25, 157–170.

Pereira, A.L., Benedito-Cecilio, E., Sakuragui, C.M., 2007. Spatial variation in the stable isotopes of ^{13}C and ^{15}N and trophic position of *Leporinus friderici* (Characiformes, Anostomidae) in Corumbá Reservoir, Brazil. Anais da Academia Brasileira de Ciências 79, 41–49.

Phillips, D.L., Greg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136, 261–269.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Montaña, C.G., Quattrochi, J., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important? Hydrological Processes 17, 2685–2689.

Putz, R., Junk, W., 1997. Phytoplankton and primary production. In: The Central Amazon Floodplain. Springer-Verlag, Heidelberg, pp. 207–222.

Rai, H., Hill, G., 1984. Primary production in the Amazonian aquatic ecosystem. In: Sioli, H. (Ed.), The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin. Dr. W. Junk Publishers, Dordrecht, pp. 311–335.

Roach, K.A., Thorp, J.H., Delong, M.D., 2009. Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the Upper Mississippi River. Freshwater Biology 54, 607–620.

Thorp, J.H., Delong, M.D., 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70, 305–308.

Thorp, J.H., Delong, M.D., 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96, 543–550.

Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. Oecologia 136, 169–182.

Walters, D.M., Fritz, K.M., Phillips, D.L., 2007. Reach-scale geomorphology affects organic matter and consumer δ^{13}C in a forested Piedmont stream. Freshwater Biology 52, 1105–1119.

Welcomme, R.L., 1985. River fisheries. FAO Fisheries Technical Paper (Rome) 262, 1–330.

Winemiller, K.O., 2005. Floodplain river food webs: generalizations and implications for fisheries management. In: Welcomme, R.L., Petr, T. (Eds.), Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, vol. 2. Mekong River Commission, Phnom Penh, Cambodia, pp. 285–312.

Winemiller, K.O., Jepsen, D.B., 1998. Effects of seasonality and fish movement on tropical river food webs. Journal of Fish Biology 53, 267–296.

Winemiller, K.O., Jepsen, D.B., 2004. Migratory Neotropical fish subsidize food webs of oligotrophic blackwater rivers. In: Polis, G.A., Power, M.E., Huxel, G.R. (Eds.), Food Webs at the Landscape Level. University of Chicago Press, Chicago, pp. 115–132.

Winemiller, K.O., Montoya, J.V., Layman, C.A., Roelke, D.L., Cotner, J.B., 2006. Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. Journal of the North American Benthological Society 25, 250–262.

Zeug, S.C., Peretti, D., Winemiller, K.O. Movement into floodplain habitats by gizzard shad (*Dorosoma cepedianum*) revealed by dietary and stable isotope analyses. Environmental Biology of Fishes, in press.

Zeug, S.C., Winemiller, K.O., 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89, 1733–1743.