

# Landscape-Scale Hydrologic Characteristics Differentiate Patterns of Carbon Flow in Large-River Food Webs

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## ABSTRACT

Efforts to conserve, restore, or otherwise manage large rivers and the services they provide are hindered by limited understanding of the functional dynamics of these systems. This shortcoming is especially evident with regard to trophic structure and energy flow. We used natural abundances of carbon and nitrogen isotopes to examine patterns of material flow in ten large-river food webs characterized by different landscape-scale hydrologic characteristics (low-gradient river, high-gradient river, river stretches downstream of reservoirs, and reservoirs), and tested predictions from three ecosystem concepts commonly applied to large-rivers: The River Continuum Concept, The Flood Pulse Concept and the Riverine Productivity Model. Carbon derived from aquatic C<sub>3</sub> plants and phytoplankton were the dominant energy sources supporting secondary consumers across the ten large-river food webs examined, but relative contributions differed significantly among landscape types. For low-gradient river food webs, aquatic C<sub>3</sub> plants were the principal carbon source, contributing as much as 80% of carbon assimilated by top consumers, with phytoplankton secondarily important. The estimated relative importance of

phytoplankton was greatest for food webs of reservoirs and river stretches downriver from impoundments, although aquatic C<sub>3</sub> plants contributed similar amounts in both landscape types. Highest 99th percentile source contribution estimates for C<sub>4</sub> plants and filamentous algae (both approximately 40%) were observed for high-gradient river food webs. Our results for low-gradient rivers supported predictions of the Flood Pulse Concept, whereas results for the three other landscape types supported the Riverine Productivity Model to varying degrees. Incorporation of landscape-scale hydrologic or geomorphic characteristics, such as river slope or floodplain width, may promote integration of fluvial ecosystem concepts. Expanding these models to include hydrologically impacted landscapes should lead to a more holistic understanding of ecosystem processes in large-river systems.

**Key words:** flood pulse concept; river continuum concept; riverine productivity model; stable isotopes; river impoundment; neotropical rivers; Paraná River.

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## INTRODUCTION

Freshwater ecosystems, especially large rivers, are some of the most threatened on the planet (Allan and Flecker 1993; Jackson and others 2001). Perhaps the greatest impact to the functioning of large river ecosystems is alteration to the global water cycle through water diversion and impoundment (Postel and others 1996; Rosenberg and others 2000; Bunn and Arthington 2002; Foley and others 2005). At the global scale, few large rivers remain in relatively natural states (Gore and Shields 1995; Rosenberg and others 2000; Nilsson and others 2005). The vast majority of temperate-zone rivers are heavily regulated (Dynesius and Nilsson 1994), and construction of large dams for the production of hydroelectric power and flood control is widespread and continuing in tropical latitudes (Dudgeon 2000; Pringle and others 2000).

Efforts to conserve, restore or otherwise manage large rivers are hindered by limited understanding of the functional dynamics of natural and modified systems, especially with regard to energy flow (Johnson and others 1995; Delong and Thorp 2006). Despite the relative paucity of food web studies conducted in large rivers, three general concepts of ecosystem functioning are widely cited, each stressing the importance of a different principal energy source driving large-river food webs: the River Continuum Concept (RCC—Vannote and others 1980), the Flood Pulse Concept (FPC—Junk and others 1989) and the Riverine Productivity Model (RPM—Thorp and Delong 1994, 2002).

The RCC (Vannote and others 1980) called attention to longitudinal connections of natural river systems, which “present a continuous gradient of physical conditions.” Biological communities should be predictably distributed according to functional relationships with “patterns of loading, transport, utilization, and storage of organic matter” that change along the river continuum. Consumers in headwater streams are predicted to rely on carbon derived from riparian inputs, with the addition of attached algae as a carbon source in intermediate reaches. In the RCC, secondary production in large-river food webs is attributed to the assimilation of terrestrially derived organic carbon leaked downstream due to inefficient processing by consumers in headwaters and intermediate reaches.

With a greater focus on downstream low-gradient rivers systems, the FPC (Junk and others 1989) was intended to be complementary to the RCC by accounting for two basic limitations: the RCC had been extrapolated to rivers in general even though

it was developed on small temperate streams, and the RCC was restricted to habitats that were permanent and lotic. Junk and others (1989) argued that with increasing floodplain size and river discharge, flood predictability and duration increase, resulting in “distinct geomorphological and hydrological systems” characterized by a greater proportion of area which is periodically lentic rather than lotic. Adaptations of biota in these river–floodplain ecosystems are distinct from those in either stable lotic or lentic ecosystems. According to the FPC, seasonal floodplain inundation drives ecosystem dynamics, with most secondary production directly or indirectly attributed to aquatic macrophytes and periodically submerged floodplain vegetation.

The RPM (Thorp and Delong 1994) emphasized the refractory nature of transported organic material, and proposed that consumers in large rivers preferentially assimilate labile autochthonous production, and to a lesser degree moderately labile direct inputs from the riparian zone, rather than allochthonous carbon leaked from upstream inefficiencies. In its original form (Thorp and Delong 1994), the RPM was intended to apply to large rivers with naturally constricted channels. The revised RPM (Thorp and Delong 2002) expanded its application and simultaneously increased the predicted relative importance of autochthonous production to consumers, stating that “the primary, annual energy source supporting overall metazoan production and species diversity in mid- to higher-trophic levels of most rivers ( $\geq 4$ th order) is autochthonous primary production entering food webs via algal-grazer and decomposer pathways.”

Whereas each of the above concepts makes predictions about the dominant sources of energy supporting river food webs, studies testing the predictions of these models are rare (Thorp and others 1998) and typically address only a single river or river type. River impoundment has been addressed only to a limited degree (Ward and Stanford 1983, 1995), even though the above concepts have explicit longitudinal and lateral contexts that are disrupted by reservoirs in most of the world’s river systems. Large-scale comparative studies of energy flow in multiple river types, including hydrologically impacted rivers, are needed to reconcile current river ecosystem concepts and provide a more holistic view of energy flow in large river food webs (Johnson and others 1995).

In the present study, we used stable isotopes of carbon and nitrogen to estimate material flow through aquatic food webs of five natural and five hydrologically impacted river stretches (low-gradi-

ent rivers, high-gradient rivers, reservoirs, and rivers just below reservoirs) of a large South American river basin, and estimated the relative importance of different carbon sources supporting dominant metazoan trophic pathways of each species-rich food web. Estimated source contributions for each food web are used to test predictions of the above-mentioned ecosystem models, and to describe potential effects of landscape-scale hydrological characteristics and river impoundment on material flow in large-river food webs.

## METHODS

### Regional Description

The Paraná River is the tenth largest river in the world in annual discharge ( $5.0 \times 10^8 \text{ m}^3 \text{ y}^{-1}$ ) and fourth in drainage area ( $2.8 \times 10^6 \text{ km}^2$ ). The upper third of the Paraná River Basin ( $891,000 \text{ km}^2$ ) is almost completely in Brazilian territory, including the most densely populated region of Brazil (Agostinho and others 1995). The Upper Paraná is one of the most extensively dammed river basins in the world (Figure 1), with over 130 major reservoirs (dam height  $\geq 10 \text{ m}$ ) on the eastern side, among which 20% are larger than 10,000 ha (Agostinho and others 2000; Gomes and Miranda 2001).

The last free-flowing stretch of the Upper Paraná River is approximately 230 km, located between Porto Primavera Reservoir and Itaipu Reservoir. It is accompanied by a wide floodplain ( $\leq 20 \text{ km}$ ) on the west margin and experiences a relatively predictable seasonal flood pulse influenced by several important tributaries that flow into the Paraná in this stretch. Due to impoundments in the upper basin, floodplain inundation is of shorter duration and lower magnitude than historically observed (Agostinho and others 2004). Eastern margin tributaries (for example, Ivaí and Piquiri Rivers) have higher elevational gradients and restricted floodplains. Seasonal rainfall results in inundation of the floodplain and lowland rivers of the western margin (for example, Ivinheima and Iguatemi Rivers) from December through April.

More than 600 fish species have been recorded in the Paraná Basin (Bonetto 1986), with about 170 species known to occur between Itaipu Reservoir and the mouth of the Paranapanema River (Agostinho and others 1997). Large-scale reproductive migrations of several fish species (for example, *Prochilodus lineatus*, *Pseudoplatystoma corruscans*, *Salminus brasiliensis*) coincide with rising water levels and wet season flooding (Agostinho

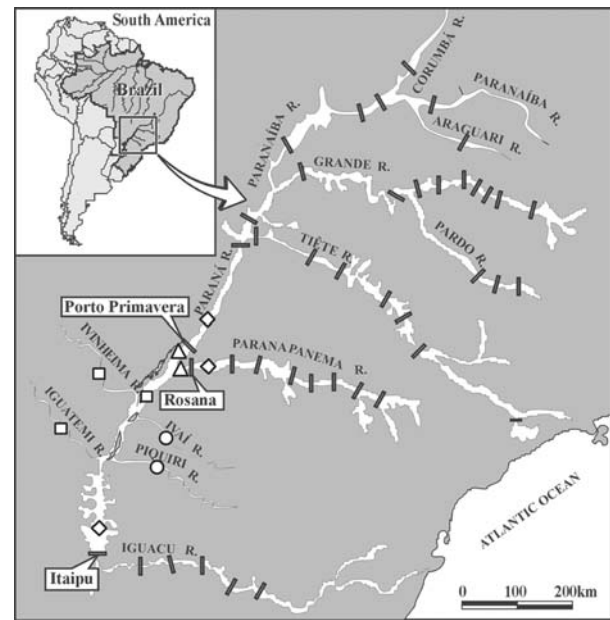


Figure 1. Study locations (white symbols) and reservoirs (black bars) of the Upper Paraná River basin, Brazil. squares = low-gradient rivers; circles = high-gradient rivers; diamonds = reservoirs; triangles = river stretches below reservoirs.

and others 2003). Detailed descriptions of the Upper Paraná River Basin and its flora and fauna, particularly the remaining floodplain stretch, can be found in Thomaz and others (2004a).

### Study Locations

Aquatic food webs were investigated at ten locations in the Upper Paraná Basin, including the remaining natural floodplain and large tributaries. The aquatic food webs analyzed in this study are delimited by fish consumers and the aquatic and riparian prey or organic sources consumed throughout the web leading to those consumers. Parasites and non-aquatic organisms that feed on fish, such as birds and humans, were not included in this study. The ten study locations were chosen to represent four different landscape types: low-gradient rivers, high-gradient rivers, reservoirs, and river reaches just downstream from reservoirs (Figure 1).

**Low-Gradient Rivers.** Food webs of three low-gradient rivers were investigated: the main stem Paraná River and connected water bodies equidistant between Itaipu Reservoir and Porto Primavera Reservoir, the Ivinheima River, and the Iguatemi River. All three have elevational gradients less than  $0.10 \text{ m km}^{-1}$  in this region (Agostinho and others 1995). The Paraná has a wide (approximately

4 km) braided channel, numerous islands and sand bars, and perennially connected lagoons. Both the Ivinheima and Iguatemi Rivers are turbid meandering rivers with numerous backwater habitats. During the rainy season, the Ivinheima and Iguatemi are important in maintaining the flood regime of the Upper Paraná floodplain. All three rivers are characterized by sandy or muddy substrates, dense macrophyte mats (mainly *Eichhornia* spp.) in backwater areas (Thomaz and others 2004b), and riparian forest transitioning to várzea, dry fields and pastures (Souza and others 2004).

**High-Gradient Rivers.** Food webs of the Piquiri River (2.20 m km<sup>-1</sup>) and the Ivaí River (1.30 m km<sup>-1</sup>) were examined. Both rivers are large east-margin tributaries that have their confluence with the Paraná along its remaining free-flowing stretch (Agostinho and others 1995). Both rivers have high water velocities and high turbidities, rocky substrates, and incised channels with restricted floodplains. Few aquatic macrophytes are present and dense gallery forest transitions to pastures or crops (especially sugar cane).

**Reservoirs.** Three reservoirs were sampled, one downriver and two just upriver of the Upper Paraná floodplain. Itaipu Reservoir is located immediately downriver of the Paraná floodplain, and has an area of 1,350 km<sup>2</sup>. Closure of the dam in 1982 inundated the Sete Quedes waterfalls, a biogeographic barrier that formerly separated the faunas of the Middle and Upper Paraná basins, allowing several species to colonize the upper basin. Contrary to the other reservoirs examined, Itaipu is free-flowing in its upstream end, allowing migratory fishes to move between the reservoir and the upstream floodplain and natural tributaries. Dense forest around the reservoir transitions to agricultural and ranch land. Porto Primavera Reservoir and Rosana Reservoir are located just upriver of the floodplain. Porto Primavera is on the Paraná main channel, upriver of the confluence of the Paranapanema River. Closure of Porto Primavera dam in 1998 flooded an area of 2,250 km<sup>2</sup> and reduced the Paraná floodplain from about 480 to 230 km in length. Rosana Reservoir on the Paranapanema River was closed in 1986, flooding an area of 276 km<sup>2</sup>. Both Porto Primavera and Rosana are predominantly lentic, submerged and floating macrophytes are ubiquitous in littoral zones, and gallery forest is limited around both reservoirs due to deforestation for ranch land.

**Rivers Just Downstream of Reservoirs.** Two river food webs were examined just below impoundments: the Paraná River below Porto Primavera Reservoir and the Paranapanema River below Ro-

sana Reservoir. This stretch of the Paraná is the most upstream point of the floodplain, has a gradient of approximately 0.14 m km<sup>-1</sup> (Agostinho and others 1995), sandy substrate and similar riparian characteristics as the other low gradient river sites, with rooted floating and emergent vegetation common on the west bank. The Paranapanema has a gradient of 0.6 m km<sup>-1</sup> (Agostinho and others 1995), mixed rocky and sandy substrate, gallery forest and a restricted floodplain. Both sites experience daily to weekly pulses in water levels due to dam operation for hydroelectric production (Agostinho and others 2004).

### Sampling Methods

Carbon isotopic signatures of dietary items are conserved within 1‰ in consumer tissues (McCutchan and others 2003), and allow evaluation of the relative importance of carbon sources ultimately supporting secondary production when source isotopic values are distinct (Peterson and Fry 1987). Nitrogen isotope ratios of consumer tissues are typically enriched 2–3‰ relative to their diet (Minagawa and Wada 1984; Post 2002b; Vanderkluft and Ponsard 2003), and can be used to determine consumer trophic position (Peterson and Fry 1987). We used C and N isotope ratios of primary producers and consumers to examine relative importance of basal carbon sources to dominant trophic pathways of the metazoan food web at each study location.

Samples for isotopic analysis were collected between September and early December of 2003 (late dry season), prior to seasonally rising water levels and fish migrations. At each location, representative carbon sources and primary and secondary consumers were collected at multiple points along a 2–5 km sample reach to characterize trophic pathways from source to top consumer (except for Itaipu Reservoir, where two sample reaches were sampled and combined to characterize the reservoir). For all samples/species, 3–5 replicates were taken along the sample reach when possible.

Several basal source groups were collected for isotopic analyses: C<sub>3</sub> plants (aquatic macrophytes and riparian vegetation), C<sub>4</sub> plants (aquatic and riparian grasses), fine particulate organic material (FPOM), coarse detritus, periphyton (attached algae, mostly filamentous algae), and seston (a surrogate for phytoplankton, also included trace amounts of suspended fine particulate organic matter). Multiple leaves of dominant species of C<sub>3</sub> and C<sub>4</sub> aquatic and riparian vegetation were clipped directly from the plant. Coarse detritus (mostly

leaf fragments) was collected from the substrate, and periphyton was scraped from submerged surfaces. FPOM was collected by lightly rinsing the flocculated material present on submerged vegetation through a 68  $\mu\text{m}$  plankton net, and retaining the smaller than 68  $\mu\text{m}$  fraction. Seston samples were collected using a gas powered water pump to pass large volumes of water through a 20  $\mu\text{m}$  plankton net. The retained fraction ( $>20 \mu\text{m}$ ) was then passed through a 68  $\mu\text{m}$  plankton net to remove larger zooplankton and organic material, resulting in a 20–68  $\mu\text{m}$  sample. All samples were stored on ice in the field then frozen upon return to the lab, or refrigerated for immediate processing.

Five types of primary consumers were collected: herbivorous fishes (for example, *Schizodon* spp., *Brycon orbignyanus*, *Metynnis* sp.), detritivorous fishes (for example, *P. lineatus*, *Steindachnerina* spp., *Liposarcus anisitsi*, *Loricariichthys platymetopon*), grazing snails (*Pomacea canaliculata*), filter-feeding bivalves (*Corbicula fluminea*), and herbivorous zooplankton (for example, larger-sized cladocerans and copepods, Santos-Silva and others 1989; Elmoor-Loureiro 1997; Santos-Silva 2000). Fishes were collected using multiple gears (seine, cast-net, gill-net and baited lines) to obtain a representative sample of the community at each site. Additional individuals were purchased from local artisanal fishermen when exact location of capture could be determined. For fishes, each individual was weighed (g) and measured (mm SL), and a skinless and boneless tissue sample (approx. 5–10 g) was excised from the dorsum (for armored catfishes, white muscle tissue samples were taken from the elongate base of the caudal fin), placed in a separate sterile bag, and stored on ice until return to the lab. In some instances, whole fish were packed in ice and returned to the lab for processing. Snails were collected by picking through littoral vegetation and by seining in littoral areas. Bivalves were collected by Eckmann dredge or by diving. Snails and bivalves were stored on ice for processing in the lab. As for seston, zooplankton were collected using a gas powered pump to filter a large volume of water, except that mesh sizes used were 68  $\mu\text{m}$  and 125  $\mu\text{m}$ .

Samples of secondary consumers were represented by fishes at all sites. A representative sample of the fish assemblage was collected using multiple gears as for the herbivorous and detritivorous fish species. Because high trophic-level consumers were to be used to estimate food web properties (see *Statistical Analyses*), special effort was given to obtain species potentially occurring at the top of the food web (for example, piscivorous species such as

*P. corruscans*, *S. brasiliensis*, *Plagioscion squamosissimus* and *Cichla* spp.) so that the vertical structure of the web could be estimated with confidence. Individuals were measured and tissue samples collected as described for herbivorous and detritivorous fishes.

### Laboratory Methods

Upon return to the lab, water samples for seston and FPOM were inspected with the aid of a dissecting microscope, and forceps were used to remove any zooplankton. Samples were then filtered onto pre-combusted (450°C for 8 h) glass fiber filters (Schleicher and Schuell GF 52-C,  $47.0 \pm 0.5$  mm pore size). Microscopic inspection verified that seston samples were almost completely phytoplankton, with only trace amounts of suspended detritus. Zooplankton samples were examined microscopically, and target species (herbivorous cladocerans and copepods) were isolated and consolidated onto pre-combusted glass fiber filters using forceps. Filamentous algae samples were rinsed with distilled water, inspected to remove any remaining contaminants, and consolidated onto filters. Leaves of C<sub>3</sub> and C<sub>4</sub> plants were visually inspected and brushed to remove any contaminants (for example, periphyton) and rinsed with distilled water. Coarse detritus samples were visually inspected to remove invertebrates and rinsed with distilled water over a 68  $\mu\text{m}$  filter to remove the fine detritus fraction. Fish tissues were examined to remove skin, scales or small bones. Pure muscle tissue samples were obtained for bivalves by opening the shells and excising the muscular foot from 15–25 individuals collected at the same sampling point within a sampling location. Snails were processed in a similar manner as bivalves.

Following processing, all samples were dried at 60°C for at least 48 hrs. Dried fish, snail, bivalve, vascular plant, and detritus samples were ground to a fine powder using a ball-mill grinder or mortar and pestle. Periphyton, FPOM, seston and zooplankton samples were scraped from the filters using a sterile scalpel. Sub-samples were weighed to the nearest 0.01 mg, or for filtered samples all material retained on the filter was used, and pressed into Ultra-Pure tin capsules (Costech Analytical, Valencia, CA, USA), and sent to the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia, for analysis of carbon and nitrogen isotope ratios. Results are expressed in delta notation (parts per thousand deviation from a standard material):  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ ; where

$R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ . The standard material for carbon is Pee Dee Belemnite (PDB) limestone, and the nitrogen standard is atmospheric nitrogen.

Subsequent analyses are based on carbon and nitrogen isotopic ratios of 838 source and consumer samples. Standard deviations of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses were 0.18 and 0.19‰, respectively for plant replicates, and 0.04 and 0.10‰, respectively for animal replicates. A series of samples, including many algae and seston samples, were inadvertently destroyed due to equipment failure during mass spectrometry analysis of carbon and nitrogen isotope concentrations. Whereas replicate samples of muscle and vascular plant tissue were sent for analysis, replicate samples of algae and seston were not available because all of the sample material was included in the original filtered sample which was destroyed. Resulting lower sample sizes for these carbon sources may have affected the observed mean and standard deviation of carbon and nitrogen isotopic signatures. Importantly, the available data include isotopic signatures of seston and filamentous algae (the two sources with lowest sample sizes) for at least one food web of all landscape types sampled, and source values correspond with values reported in other studies in freshwater systems (for example, Bunn and others 2003; Herwig and others 2004).

### Statistical Analyses

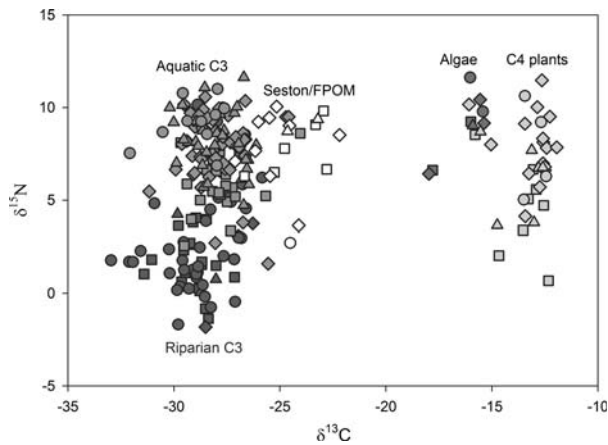
Analysis of variance was used to compare mean carbon and nitrogen isotope signatures among sources (riparian  $\text{C}_3$  plants, aquatic  $\text{C}_3$  plants,  $\text{C}_4$  plants, seston/FPOM, and filamentous algae) for all sites combined, as well as among landscape types for each source group. When significant differences were observed, pairwise comparisons of source means were performed using Tukey's post-hoc procedure. Values for the two size fractions of detritus (coarse detritus and FPOM) were combined with their respective live sources (see Results) in all statistical analyses. Combining sources in this manner is a logical compression of the data that should not affect interpretations of allochthonous versus autochthonous source contributions (see Phillips and others 2005; Delong and Thorp 2006).

Stable isotope ratios provide an integrated measure of assimilated energy of all trophic pathways leading to a consumer (Post 2002a, b). With this in mind, we used isotopic signatures of the highest trophic level consumers in each food web to provide integrated measures (in terms of carbon assimilated) of the dominant trophic pathways reaching upper trophic levels. Due to energetic

inefficiency of trophic transfer and secondary production (approximately 90% of energy consumed is used in metabolic processes, whereas only 10% is applied to growth and reproduction, Humphreys 1979), trophic pathways supporting secondary production of upper level consumers should represent dominant flows of energy in the metazoan component of the food web.

Consumers used to represent each food web were those with mean  $\delta^{15}\text{N}$  values within 1‰ of the highest trophic position species in the web (that is, species within less than 0.5 trophic levels of the apex species). If less than five species had means within 1‰ of the apex species, the five highest trophic level consumers were used to represent the food web to prevent source estimates from being biased by a single or few species. For each food web, an appropriate N baseline was calculated using  $\delta^{15}\text{N}$  signatures of fish species known from prior studies to be primary consumers (for example, *P. lineatus*, *L. anisitsi*, *M. maculatus*, *Schizodon* spp.). Trophic positions of secondary consumers were estimated as the difference in consumer  $\delta^{15}\text{N}$  from the nitrogen baseline (representing trophic level 2), while accounting for +2.54‰ per trophic level fractionation (Vanderklift and Ponsard 2003).

The software package IsoSource (Phillips and Gregg 2003) was used to calculate ranges of proportional contributions of each source to upper trophic level consumers because the number of potential sources in these systems is too large to permit a unique solution (that is,  $n_{\text{sources}} > n_{\text{isotopes}} + 1$ ). This procedure uses mean isotope values of sources and consumers to estimate all possible source contributions from 0 to 100% using small increments, with combinations summing to within a selected mass balance tolerance of the consumer isotope signature retained as feasible solutions (see Phillips and Gregg 2003). Analyses were performed using mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of source groups for each landscape type, with source increments of 1% and mass balance tolerance of 0.5‰. Due to limited samples of seston and filamentous algae for some food webs, mean source values combined across all sites were used for seston/FPOM in high-gradient river analyses, and for filamentous algae in below reservoir analyses. Consumer isotope signatures were corrected for trophic fractionation of carbon (+0.5‰ per trophic level, McCutchan and others 2003) and nitrogen (+2.54‰ per trophic level, Vanderklift and Ponsard 2003) before use in analyses of source contributions. As recommended by Phillips and Gregg (2003), interpretations are based primarily on the 1–99th percentile range (that is, minimum and



**Figure 2.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of sources collected at sampling locations of the Upper Paraná River basin, Brazil. Symbols designate landscape type as in Figure 1, and colors distinguish source groups. Values for coarse detritus and fruits are combined with those for riparian  $\text{C}_3$  plants, and FPOM values are combined with those for seston (see Source and Consumer Isotopic Signatures). Riparian  $\text{C}_3$  plants:  $n = 66$ ; Aquatic  $\text{C}_3$  plants:  $n = 111$ ; Seston/FPOM:  $n = 18$ ; Filamentous algae:  $n = 8$ ;  $\text{C}_4$  plants:  $n = 34$ .

maximum) of feasible contributions of each source. Results are presented as the mean and standard deviation of 1st and 99th percentile estimates for upper trophic level consumers in each food web.

## RESULTS

### Source and Consumer Isotopic Signatures

Mean carbon and nitrogen isotopic ratios of leaf litter ( $\delta^{13}\text{C} = -29.3\text{‰}$ ,  $\delta^{15}\text{N} = 1.2\text{‰}$ ) were similar to those of riparian  $\text{C}_3$  plants ( $\delta^{13}\text{C} = -28.7\text{‰}$ ,  $\delta^{15}\text{N} = 2.8\text{‰}$ ), and FPOM isotopic values ( $\delta^{13}\text{C} = -24.9\text{‰}$ ,  $\delta^{15}\text{N} = 6.9\text{‰}$ ) were similar to those observed for seston ( $\delta^{13}\text{C} = -24.6\text{‰}$ ,  $\delta^{15}\text{N} = 7.8\text{‰}$ ), reflecting the primary sources of these two size fractions of benthic organic material. Fruits had mean values similar to leaves of their parent trees ( $\delta^{13}\text{C} = -29.4\text{‰}$ ,  $\delta^{15}\text{N} = 1.0\text{‰}$  and  $\delta^{13}\text{C} = -30.8\text{‰}$ ,  $\delta^{15}\text{N} = 1.1\text{‰}$ , respectively). In all subsequent analyses, values for leaf litter/coarse detritus and fruits are combined with riparian  $\text{C}_3$  plants, and FPOM and seston values are combined.

Across all landscapes, carbon and nitrogen isotopic signatures differed among source groups (Figure 2). Source groups were well differentiated by carbon isotopic signatures (ANOVA  $P < 0.001$ , all pairwise comparisons  $P \leq 0.005$ ). Filamentous algae and  $\text{C}_4$  grasses had the most enriched mean  $\delta^{13}\text{C}$  values ( $-16.3\text{‰}$  and  $-13.3\text{‰}$ , respectively),

whereas seston/FPOM ( $-24.7\text{‰}$ ) and terrestrial and aquatic  $\text{C}_3$  plants ( $-28.8\text{‰}$  and  $-28.1\text{‰}$ , respectively) were relatively  $^{13}\text{C}$  depleted. Within a source group, no differences in  $\delta^{13}\text{C}$  signatures were observed among landscape types (all ANOVAs  $P > 0.05$ ; Table 1). Mean  $\delta^{15}\text{N}$  values were similar for aquatic  $\text{C}_3$  plants, seston/FPOM and  $\text{C}_4$  plants ( $7.7\text{‰}$ ,  $7.7\text{‰}$  and  $6.8\text{‰}$ , respectively), whereas the mean nitrogen isotopic signature of filamentous algae was slightly higher ( $9.0\text{‰}$ ). Riparian  $\text{C}_3$  plants had the most distinct mean nitrogen isotope signature ( $2.6\text{‰}$ ), at least  $5\text{‰}$  lower than mean signatures of the other sources (Figure 2, all pairwise comparisons  $P < 0.001$ ). Within source groups, some variation in mean source  $\delta^{15}\text{N}$  values was observed among landscape types (Table 1). Low-gradient rivers had lower  $\delta^{15}\text{N}$  values for aquatic  $\text{C}_3$  plants (all pairwise comparisons  $P < 0.001$ , Table 1) than observed for the other landscape types.

The species occupying the highest trophic positions, and used to provide integrated measures of the dominant trophic pathways reaching upper trophic levels, were generally similar across all webs (for example, piranha *Serrasalmus marginatus*, dourado-cachorro *Rhaphiodon vulpinus*, curvina *P. squamosissimus*, tucunaré *Cichla* spp., barbado *Pini-rampus pirinampu*, pintado *P. corruscans*, traíra *Hoplias malabaricus*), although to a lesser degree in the high-gradient rivers which have relatively distinct fish faunas (Agostinho and others 1995, 1997). Carbon isotope signatures of top consumers differed relatively little within food webs, whereas larger differences were observed among landscape types (Table 2). Consumer  $\delta^{13}\text{C}$  values in high-gradient river food webs were enriched compared with all other landscape types, and consumers in low-gradient river food webs had the most depleted  $\delta^{13}\text{C}$  values. Carbon isotope signatures of upper trophic level consumers in reservoir and below reservoir food webs were similar, and slightly more enriched than consumers in low-gradient river food webs (Table 2).

### Relative Source Contributions

Aquatic  $\text{C}_3$  plants and phytoplankton were the principal sources supporting dominant trophic pathways leading to top consumers for all food webs. Relative source contributions differed among landscape types, and to a lesser degree among food webs within landscape types (Figure 3). For all low-gradient river food webs, aquatic  $\text{C}_3$  plants contributed approximately 20–80% of carbon assimilated by top consumers (Figure 3). Seston/FPOM was secondarily important, accounting for

**Table 1.** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Values of Source Groups by Landscape Type

Landscape type	Source means ( $\pm$ 1 SD)				
$\delta^{13}\text{C}$	Riparian C <sub>3</sub> plants	Aquatic C <sub>3</sub> plants	Seston/FPOM	Filamentous algae	C <sub>4</sub> plants
Low-gradient rivers	-29.00 (1.09)	-27.83 (1.27)	-24.30 (1.54)	-17.51 (1.40)	-13.52 (1.16)
High-gradient rivers	-28.79 (1.63)	-29.03 (1.40)	-24.51	-15.73 (0.42)	-13.02 (0.53)
Reservoirs	-27.46 (1.02)	-27.97 (1.26)	-25.47 (1.71)	-16.64 (1.36)	-13.05 (1.07)
Below reservoirs	-28.86 (0.91)	-28.07 (1.19)	-23.92 (1.01)	-15.90	-13.64 (1.21)
$\delta^{15}\text{N}$	Riparian C <sub>3</sub> plants	Aquatic C <sub>3</sub> plants	Seston/FPOM	Filamentous algae	C <sub>4</sub> plants
Low-gradient rivers	2.04 (1.99)	5.78 (1.47) <sub>a</sub>	7.69 (1.47)	7.70 (1.37)	4.58 (2.51) <sub>a</sub>
High-gradient rivers	2.90 (2.91)	9.15 (1.31) <sub>b</sub>	2.72	10.70 (1.30)	7.79 (2.58) <sub>a,b</sub>
Reservoirs	3.02 (3.68)	7.86 (1.84) <sub>b</sub>	7.92 (1.88)	7.98 (2.16)	7.94 (1.85) <sub>b</sub>
Below reservoirs	1.69 (2.24)	8.18 (1.61) <sub>b</sub>	9.04 (0.46)	9.03	6.23 (2.07) <sub>a,b</sub>

*Letters following standard deviations designate significant differences*

**Table 2.** Mean and Standard Deviation of  $\delta^{13}\text{C}$  Values of Consumers used to Provide Integrated Measures of Dominant Trophic Pathways reaching Upper Trophic Levels for each Food Web and Landscape Type

Landscape type Location	$\delta^{13}\text{C}$ mean ( $\pm$ 1 SD)
Low-gradient rivers	-25.25 (0.34)
Iguatemi	-25.58 (0.65)
Ivinheima	-25.27 (0.74)
Paraná	-24.90 (1.77)
High-gradient rivers	-20.88 (0.32)
Piquiri	-20.65 (2.34)
Ivaí	-21.10 (1.97)
Reservoirs	-24.01 (0.49)
Itaipu	-23.80 (1.29)
Rosana	-23.67 (1.43)
Porto Primavera	-24.57 (1.08)
Below reservoirs	-24.15 (0.02)
Below Rosana	-24.13 (0.51)
Below Porto Primavera	-24.16 (1.64)

0–50%. Within low-gradient rivers, the Iguatemi River food web was supported to a greater degree by aquatic C<sub>3</sub> plants (40–90%), whereas carbon derived from riparian C<sub>3</sub> plants potentially contributed up to 40% of carbon assimilated by consumers of the Ivinheima River food web, and seston/FPOM had a higher relative contribution to the Paraná River food web (Figure 3).

Relative contributions of sources supporting high-gradient river food webs differed greatly from source contributions in all other landscape types (Figure 3). Most notably, both filamentous algae and C<sub>4</sub> plants contributed up to 40% of carbon assimilated. All sources had relatively similar 99th percentile contribution estimates, suggesting that

consumers in these food webs rely on multiple carbon sources to a greater degree than food webs of the other landscape types where two sources were dominant (aquatic C<sub>3</sub> plants and seston/FPOM). Standard deviations of carbon isotopic signatures of top consumers were highest in the two high-gradient rivers (Table 2), indicating that the relative importance of carbon sources differed more among species within these food webs than among species in food webs of the other landscape types. Within high-gradient rivers, riparian C<sub>3</sub> plants were relatively more important to the Piquiri River food web, and consumers in the Ivaí River food web assimilated relatively more carbon derived from aquatic C<sub>3</sub> plants (Figure 3).

Source contribution estimates were similar for food webs of reservoirs and river stretches below reservoirs. For both landscape types, aquatic C<sub>3</sub> plants and seston/FPOM were the dominant sources (Figure 3). For reservoir food webs, 99th percentile contribution estimates were approximately 80% for both aquatic C<sub>3</sub> plants and seston/FPOM, although 1<sup>st</sup> percentile contribution estimates were greater for aquatic C<sub>3</sub> plants than for seston/FPOM. The same pattern was observed for relative source contribution estimates to food webs of river stretches below reservoirs, except that 1<sup>st</sup> percentile estimates for aquatic C<sub>3</sub> plants and seston/FPOM were approximately 40 and 20%, respectively, and 99th percentile estimates were approximately 60% for both sources (Figure 3).

## DISCUSSION

### *Isotopic Composition of Sources*

Observed source  $\delta^{13}\text{C}$  values agreed with values reported for other freshwater rivers (for example,



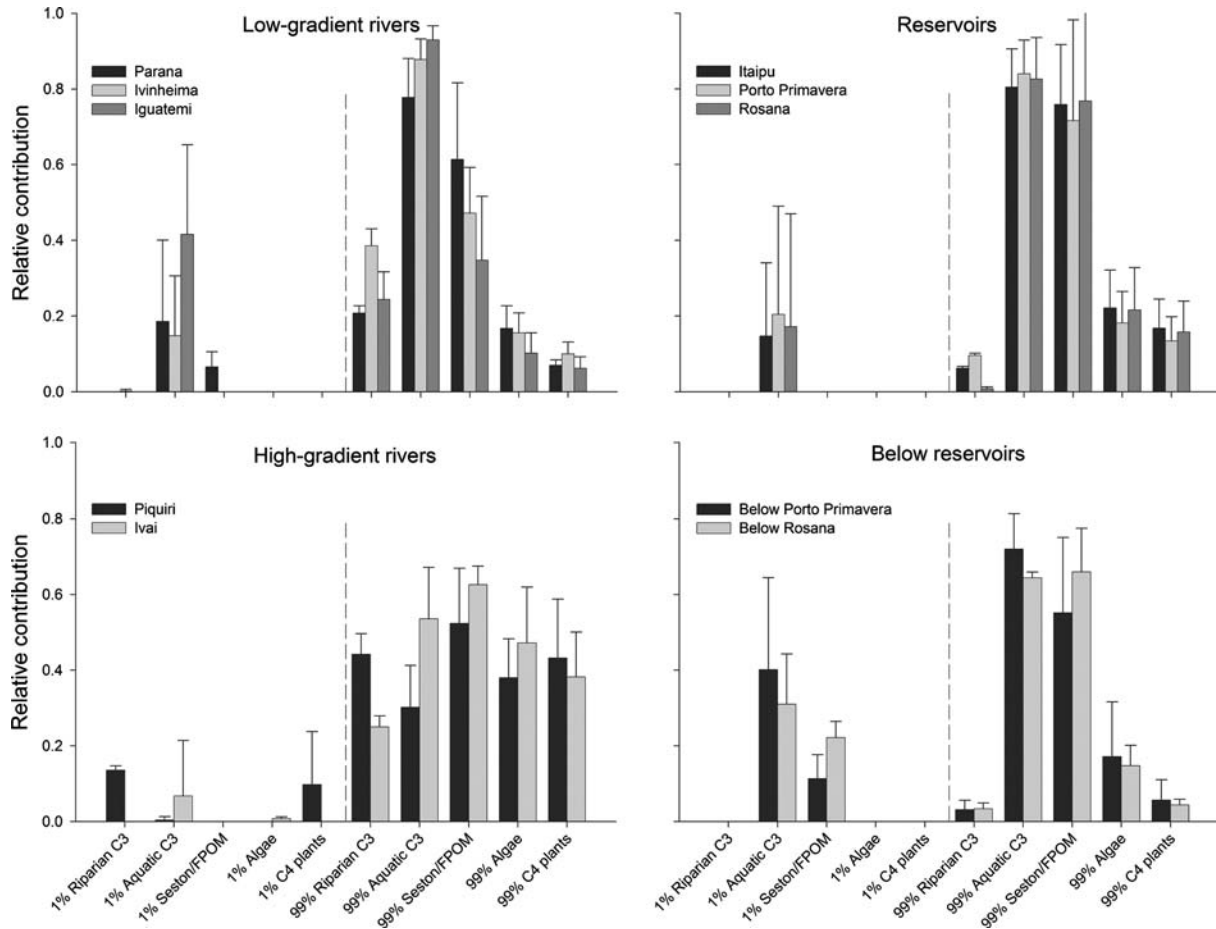


Figure 3. 1st and 99th percentile contribution estimates of sources supporting upper-level consumers in each food web. Bars are means ( $\pm 1$  SD) for each food web of 1st and 99th percentile estimates calculated independently for each consumer species.

Boon and Bunn 1994; Bunn and others 2003; Herwig and others 2004; Pease and others 2006). As in other studies, source groups were well distinguished by carbon isotope ratios. Nitrogen isotope ratios were somewhat less informative, although riparian  $C_3$  plants were clearly distinguished from all other sources, and variation in source  $\delta^{15}N$  among sites, such as lower values for aquatic macrophytes in low-gradient rivers, added additional resolution for some food webs.

Some studies in other basins of South America have observed more depleted  $\delta^{13}C$  values for phytoplankton/seston ( $-35$  to  $-30\%$ ; for example, Araujo-Lima and others 1986; Hamilton and others 1992); this is likely due to differences in watershed geochemistry (Tan and Edmond 1993; Jepsen and Winemiller 2007) and trophic state of the water bodies. Phytoplankton of oligotrophic systems, such as the study region of the Upper Paraná basin (Agostinho and others 1995), are often  $^{13}C$  enriched

compared to more productive systems with similar basin geochemistry (Grey and others 2000). Enriched  $\delta^{13}C$  values also correspond to higher rates of photosynthesis (MacLeod and Barton 1998) and carbon limitation in larger watersheds (Finlay 2001) or during periods of lower rainfall or watershed flushing (Depetris and Kempe 1993). Given that sampling occurred during the late dry season (reduced watershed flushing, high rates of photosynthesis), the oligotrophic nature of the waterbodies and large watershed size, the comparatively enriched  $\delta^{13}C$  values observed for algae may result from relative limitation of dissolved  $CO_2$ .

### *Upper Trophic Level Consumers as Indicators of Food Web Carbon Flow*

Isotopic signatures of the highest trophic level consumers in each food web were used to summarize dominant pathways of carbon flow through

the metazoan component of the food web. This approach is an appealing way to summarize aspects of food web structure, and is particularly applicable to studies of highly connected, species-rich food webs. The choice of which, or how many, consumer species to use to summarize food web carbon flow may potentially affect the resulting source contribution estimates. For this reason, an objective criterion was defined a priori to determine which species would be used to summarize each food web: the top 1‰ based on N stable isotope ratios, with a minimum of five species. This is equal to approximately the upper one-third of a trophic level of each web (considering fractionation between 2.5 and 3.4‰ per trophic level, Post 2002b; Vanderkluft and Ponsard 2003).

For only one food web (Porto Primavera Reservoir) was it necessary to include species outside the top 1‰ of N isotope values to fulfill the minimum of five species requirement set a priori, and this was due to the very high trophic position of the apex species *P. squamosissimus* in relation to the rest of the top predators. Mean  $\delta^{13}\text{C}$  of the top 1‰ and the top five species differed only slightly ( $-24.5$  and  $-24.6$ ‰, respectively), and would have affected estimated source contributions very little. Further illustrating the robustness of upper trophic level consumers to summarize dominant pathways of carbon flow, a piscivorous bird (unidentified species of kingfisher) collected at the Piquiri River had a C isotopic ratio of  $-20.5$ ‰, closely matching the mean value of piscivorous fishes used to summarize the food web ( $-20.7$ ‰). Stable isotope ratios of upper trophic level consumers provide an integrated and comprehensive metric of vertical carbon flow through the metazoan component of food webs, even given the diverse trophic ecologies typified by Neotropical fish faunas (Lowe-McConnell 1987; Winemiller 1990, 1991).

### *Estimates of Relative Source Contributions*

Even though  $\delta^{13}\text{C}$  values for source groups were distinct, and additional resolution was provided by  $\delta^{15}\text{N}$  values, in some cases wide ranges of potential contributions to food webs were observed (that is, contributions to the mixture may vary widely for some sources, yet yield the same signature). This was most evident for the estimated contribution of seston/FPOM to reservoir food webs (approximately 0–80%). As shown in Table 1, nitrogen isotope ratios were relatively less informative for distinguishing sources of reservoir food webs. Due to the intermediate  $\delta^{13}\text{C}$  signature of seston/FPOM,

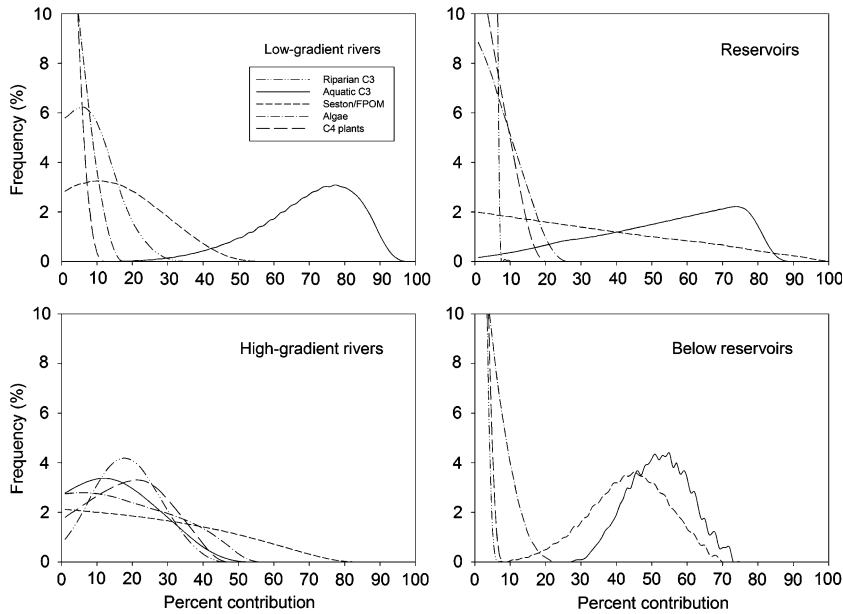
similar mass balance could be reached by a combination of comparatively  $\delta^{13}\text{C}$  depleted (aquatic  $\text{C}_3$  plants) and enriched sources (algae or  $\text{C}_4$  plants). This is a general problem when using stable isotopes to determine trophic relationships in food webs with multiple basal energy sources (Phillips and Gregg 2003; Phillips and others 2005). However, differences in the 1–99 percentile ranges of feasible source contributions among food webs and landscape types reveal key differences in food web structure.

Our estimates of relative source contributions should also be considered conservative, in that we used a fairly broad mass balance tolerance (0.5‰) in our IsoSource analyses. Our chosen mass balance tolerance more adequately accounts for source and consumer isotopic variability, and incorporates potential uncertainty associated with assumptions of trophic fractionation of carbon and nitrogen and correcting isotopic signatures of consumers using their estimated trophic position. Using a broad mass balance tolerance increases the number of feasible solutions generated for each analysis, and may result in slightly wider 1–99th percentile ranges of estimated source contributions (Phillips and Gregg 2003), reflecting uncertainty due to the aforementioned sources of variability.

### *Landscape-Scale Hydrologic Characteristics and Carbon Source Contributions*

Estimated relative importance of carbon sources fueling dominant trophic pathways differed among aquatic metazoan food webs distinguished by landscape-scale hydrologic characteristics. Distributions of feasible source contributions in Figure 4 depict the key differences in the relative importance of carbon sources supporting food webs among landscape types. Differences in the relative contributions of sources appear to reflect differences in the availability of sources among landscape types.

Food webs of lowland floodplain rivers are based primarily on carbon derived from aquatic macrophytes, and to a much lesser degree phytoplankton production. Dense aquatic macrophyte mats, primarily *Eichhornia* spp. are ubiquitous in these rivers. Greatest macrophyte biomass occurs during the low-water period, concomitant with detritus accumulation (Thomaz and others 2004b). Aquatic invertebrates reach highest densities in the littoral areas associated with macrophyte mats, and are probably an important link passing carbon derived from aquatic plants to fish consumers, as few fish



**Figure 4.** Distributions of feasible source contributions by landscape type. Distributions were calculated using mean adjusted  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of upper trophic level consumers and sources for each landscape type. The y-axis is scaled to focus on distributions of sources with the greatest percent contributions to the food web.

species directly consume aquatic plants other than in the form of detritus. Dense macrophyte mats, especially in the Ivinheima and Iguatemi Rivers, may also limit phytoplankton production.

The potential importance of phytoplankton as a carbon source was greater in reservoirs and rivers just below reservoirs than in lowland rivers. This may be a function of greater water clarity as a result of sedimentation, as well as longer water residence times. Although aquatic macrophytes are common in littoral areas, the ratio of pelagic versus littoral zones in these landscape types is comparatively much higher than low-gradient and high-gradient rivers. This may also account for the lower 99th percentile contribution estimates of riparian  $\text{C}_3$  plants observed for reservoir and below reservoir food webs relative to low-gradient and high-gradient rivers.

Only in high-gradient rivers did filamentous algae or  $\text{C}_4$  plants potentially contribute a substantial amount of carbon flowing through the metazoan component of the food webs. Aquatic macrophytes that are abundant in the other landscape types are comparatively rare in these large high-gradient rivers, which may account for the reduced importance of this source compared to other landscape types. At the same time, the rocky substrate of the Piquiri and Ivaí Rivers provides ample opportunities for the attachment of filamentous algae, and emergent grasses are common in the littoral zone. *S. nasutus*, a fish species belonging to a herbivorous genus known to preferentially graze aquatic  $\text{C}_4$  grasses (Forsberg and others 1993; Jepsen and Winemiller 2002), accounted for most of the biomass collected in gill-nets in the Piquiri River, and

the benthic grazing *P. lineatus* collected in the Piquiri had a mean  $\delta^{13}\text{C}$  signature of  $-19.0\text{‰}$  (corresponding with filamentous algae) compared to  $-28.2\text{‰}$  (corresponding with aquatic  $\text{C}_3$  plants, likely in the form of detritus) for the same species collected in the lowland Iguatemi River.

Compared to differences among landscape types, relatively little variation in the estimated importance of carbon sources was observed within landscape types. This result emphasizes that the trends observed are associated with the landscape-scale hydrological characteristics distinguishing these landscapes. Variation in source contributions within landscape types may be attributable to differences in local characteristics. For example, the greater density of gallery forest along the Ivinheima River compared to the Paraná and Iguatemi Rivers corresponds with the higher contribution of carbon derived from riparian  $\text{C}_3$  plants, and greater water velocity of the Piquiri River compared to the Ivaí River may reduce the availability and contribution of phytoplankton and aquatic macrophytes to the food web.

### *Landscape-Scale Hydrologic Characteristics and Large-River Ecosystem Concepts*

Three general concepts of ecosystem functioning widely applied to large rivers, namely the River Continuum Concept (Vannote and others 1980), the Flood Pulse Concept (Junk and others 1989) and the Riverine Productivity Model (Thorpe and Delong 1994, 2002), each stress the importance of different principal energy sources supporting large-

river food webs. Differences in the relative importance of carbon sources supporting food webs among landscape types in the present study differentially support predictions of the these large-river ecosystem concepts.

The metazoan food webs of the low-gradient floodplain rivers (Paraná, Ivinheima and Iguatemi) were fueled primarily by aquatic macrophyte production, in fitting with the FPC (Junk and others 1989) and some earlier floodplain food web studies (for example, Bayley 1989). Phytoplankton was secondarily important, contributing between 0 and 50%. The importance of phytoplankton and benthic algae to floodplain river food webs has been observed for the Orinoco River floodplain in Venezuela (Hamilton and others 1992) and the central Amazon River floodplain in Brazil (Araujo-Lima and others 1986; Forsberg and others 1993), and was influential in development of the RPM (Thorp and Delong 1994, 2002). Although phytoplankton may be important to some food web compartments, for example, some species of large detritivorous fishes (Araujo-Lima and others 1986) and invertebrates associated with floating meadows (Hamilton and others 1992), and was considered the dominant source supporting secondary production (Lewis and others 2001), isotope signatures of piscivores from the same studies (Araujo-Lima and others 1986; Forsberg and others 1993) show that other sources, such as  $C_3$  and  $C_4$  plants, also make their way through the food web to higher order consumers in those rivers.

The RPM differs from the FPC in the predicted relative importance of algae to the food web. The RPM predicts plankton and algae should be the dominant energy sources fueling secondary production (Thorp and Delong 1994, 2002), and has been supported by stable isotope studies in the Upper Mississippi River basin, USA (Thorp and others 1998; Delong and Thorp 2006), and Cooper Creek floodplain of Australia (Bunn and others 2003) in addition to the floodplain river studies cited previously. In the present study, the highest estimated relative importance of the phytoplankton pathway was observed for food webs of reservoirs and river stretches just below reservoirs, although  $C_3$  plants may still contribute a large amount of the primary production fueling the food web. Findings for the reservoir and below reservoir food webs generally support the RPM.

In the high-gradient Piquiri and Ivaí Rivers, most sources had similar 99th percentile contribution estimates, with phytoplankton slightly higher. The estimated contribution of phytoplankton to the food web was comparable to estimates for flood-

plain rivers, however carbon derived from aquatic  $C_3$  macrophytes was much lower. Concomitant with the lower importance of  $C_3$  plants was a greater relative importance of filamentous algae and  $C_4$  plants. Although the relative source contributions differed from reservoir and below reservoir food webs, estimates for high-gradient river food webs support the RPM to some degree. This is due primarily to the high relative importance of phytoplankton and filamentous algae. However, the RPM underestimates the relative importance of direct riparian inputs to these food webs, especially for the higher gradient Piquiri River.

It is difficult to evaluate the RCC due to the overlap of source signatures along the river gradient and separation of FPOM derived from upriver versus lateral inputs (see Thorp and others 1998), however the data presented here do not suggest that terrestrially derived particulate organic matter transported from upriver is an important carbon source supporting secondary macroconsumers in these food webs. Coarse detritus was shown to be derived primarily from riparian  $C_3$  plant production; however, organic material transported downriver at the scale suggested by the RCC would not arrive at downstream sites in this size fraction. For upriver-derived organic material to be considered a potentially important source to these food webs, FPOM at our sites would need to have a carbon isotopic signature aligned with either  $C_3$  or  $C_4$  terrestrial vegetation. Instead, FPOM at our sites was derived primarily from phytoplankton. Interruption of the continuum by river impoundment could be a consideration for the reservoir and below reservoir food webs, but even food webs of free-flowing lowland and high-gradient rivers did not support predictions of the RCC. For all of the landscape types examined here, the principal carbon sources supporting the metazoan component of the food web appear to be those that were readily accessible and locally produced, such as aquatic  $C_3$  macrophytes in lowland rivers and phytoplankton in reservoirs. Although food webs of high-gradient rivers were supported to some degree by riparian sources, these were in the form of direct lateral inputs rather than downstream transport. It is important to note that transported terrestrial organic material may be an important energy source for the microbial loop, which was not directly examined here.

Relative abundance of invertebrate functional feeding groups (FFG; for example, gatherers, scrapers) along the river continuum was given in support of predictions of the RCC (Vannote and others 1980). However, FFG's are defined based on

feeding mode or particle sizes ingested (Cummins 1973), which do not necessarily separate sources of allochthonous or autochthonous origins, and calls into question the suitability of FFG's to examine ecosystem models such as the RCC (Mihuc 1997). Studies using gut content analyses and stable isotopes to examine food webs across a range of systems suggest that terrestrially derived organic matter may be directly important to secondary consumers in small upstream stretches or during winter months when aquatic primary production is lower (for example, Huryñ and others 2001, 2002; Rosi-Marshall and Wallace 2002; England and Rosemond 2004), but support is lacking for the importance of terrestrially derived transported organic matter to secondary production of macroconsumers such as fish in large-river food webs (Thorp and Delong 2002; Delong and Thorp 2006).

## CONCLUSIONS

Incorporation of landscape-scale hydrologic features, such as river slope or floodplain width (see Sedell and others 1989) and the presence of impoundments, may help reconcile distinctions among ecosystem concepts applied to large rivers (RCC, FPC and RPM) and lead to a more holistic understanding of ecosystem processes in these systems. An advancement in this regard is the River Ecosystem Synthesis (Thorp and others 2006). The differences in relative importance of carbon sources supporting dominant metazoan trophic pathways among hydrologic landscape types observed in this study appear to qualitatively support the description of the river basin as a series of large functional process zones determined in part by hydrogeomorphology (although specific predictions about which energy sources are most important to macroconsumer food webs in different zones were not completely supported by our results). Additional research is needed in other tropical and temperate river systems to further evaluate the roles of hydrogeomorphology and river impoundment on the structure and function of large-river food webs.

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