FOOD WEB ARCHITECTURE IN NATURAL AND IMPOUNDED RIVERS OF THE UPPER PARANÁ DRAINAGE BASIN, BRAZIL

A Dissertation

by

DAVID JOSEPH HOEINGHAUS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2006

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Kirk O. Winemiller
Committee Members,	Stephen E. Davis, III
	Robert A. Wharton
	Daniel L. Roelke
Head of Department,	Delbert M. Gatlin, III

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ABSTRACT

Food Web Architecture in Natural and Impounded Rivers of the Upper Paraná
Drainage Basin, Brazil. (December 2006)
David Joseph Hoeinghaus, B.S., Texas A&M University
Chair of Advisory Committee: Dr. Kirk O. Winemiller

Freshwater ecosystems are some of the most threatened on the planet. 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. In this study I use natural abundances of carbon and nitrogen isotopes to examine patterns of energy flow and food-chain length of large-river food webs characterized by different landscape-scale hydrologic features. Ten locations along an approximately 500 km stretch of the Upper Paraná River Basin, Brazil, provided the setting for this work. Carbon derived from C_3 plants and phytoplankton were the dominant energy sources across all webs, but relative contributions differed among landscape types (low-gradient river, high-gradient river, river stretches downstream of reservoirs, and reservoirs). Increases in food chain length corresponded with higher relative importance of phytoplankton derived carbon, likely due to size-structured effects of the phytoplankton-zooplankton-secondary consumer trophic link. River impoundment corresponded with decreased ecological and economic efficiency of fisheries production, an important ecosystem service provided by many tropical rivers.

ACKNOWLEDGEMENTS

My dissertation research was supported in part by grants from the Society of Wetland Scientists, Texas A&M Office of Graduate Studies, and a Mills Scholarship from the Texas Water Resources Institute. Kirk Winemiller kindly contributed funds to cover partial costs of isotope analyses, and assisted with travel expenses to Brazil in 2003. Angelo Agostinho and the Research Nucleus in Limnology Ichthyology and Aquaculture (Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura – Nupélia) generously provided all of the logistics in Brazil for completion of my project.

Special thanks are due to my graduate committee: Drs. Kirk Winemiller (advisor), Steve Davis, Bob Wharton and Dan Roelke. Each member challenged me to think in different ways, and provided excellent feedback and suggestions (often on short notice). In particular, this last year has been a mad dash for the finish line. I am very grateful for your suggestions, guidance, and patience throughout this process. In addition to being a member of my graduate committee, I also benefited from research collaborations with Steve Davis.

This project would not have come to fruition without the insights, motivation, mentorship, field and lab assistance, experiences, pass-times and laughs provided by many friends and colleagues. Without a doubt, Kirk Winemiller has had the most singular influence on my scientific development. As an undergraduate I began working in Kirk’s lab and got my first taste of research – it was all downhill (or downriver) from there. My Winemiller Lab colleagues as an undergrad, Albrey Arrington, Archis Grubh,

Craig Layman, Hernán Lopez, José Vicente Montoya and Stuart Willis also played a part in my early scientific development, especially through several collaborations on the Rio Cinaruco in Venezuela. During my undergrad days, I also had the opportunity to meet and interact with other researchers who have influenced me both professionally and personally. In particular, Alexandre "Sensei" Garcia has been a great friend, colleague and mentor over the last few years. Our initial meeting in the Winemiller Lab has spawned a series of research collaborations, exchanges of English and Portuguese slang, and mass consumption of sushi when possible.

As a graduate student, Kirk allowed me the freedom to explore my curiosity while at the same time providing timely nudges. One important nudge was to contact Angelo Agostinho when political issues in Venezuela torpedoed my original research plans. Angelo graciously agreed to collaborate on my research and was my host while in Brazil. Without the logistical support and insights provided by Angelo and many others at Nupélia, this work would not have been possible. Although space prevents me from naming everyone who contributed in some way or another, Claudia Bonecker, Luiz Gomes, Horácio Júlio Jr., João Latini, Edson Okada, Rosi Ribeiro, and Sidinei Thomaz are deserving of special mention because of their extensive discussion, logistical assistance, and help in the field and lab. João and Tato participated in almost all of my field collections. Several graduate students at Nupélia also helped in many ways. I especially would like to thank Rodrigo Costa, Elaine Kashiwaqui, Fernando Pelicice, Ana Petry, and Pitágoras Piana for their hospitality, discussions, help in the field and lab, and friendship. Collaborating with the group at Nupélia was a great experience that I cannot acknowledge enough.

Although leaving Brazil was more difficult after each trip, I had great lab mates and colleagues at TAMU to welcome me back. The collection of personalities in the lab created a unique dynamic that was a highlight of my time at TAMU. Jenny Birnbaum, Bibiana Correa, Gage “Full House” Dayton, José Vicente “Casa Llena” Montoya, Allison “2000 Flushes” Pease, Clint “Hollywood” Robertson, Virginia Shervette and Steve “KGB” Zeug not only made College Station more bearable, but also provided great ecological, philosophical and sometimes delusional discussions (not to mention the extra income from our weekly poker night!). I consider myself fortunate to have been a member of such an active and motivated lab, and acknowledge the contributions of side projects conducted with Jenny Birnbaum, Virginia Shervette and Steve Zeug.

My family has been the foundation on which all of this was built. I especially want to thank my mother for always fueling my curiosity, fostering my education and instilling the belief that I could achieve anything I put my mind to. Thank you. My brothers also helped in many ways. Geoff cared for all of my effects in the U.S. while I spent half of the last four years in Brazil and Venezuela. My greatest discovery while in Brazil happened at a friend’s house rather than in the field or lab - I met my future wife while she was on an internship at Nupélia in 2003. Ana Paula has given new context to my life and work, and fuller meaning to the word “motivation”. She was a constant source of encouragement, support and patience while completing this dissertation, for which I am deeply grateful.

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CHAPTER I

INTRODUCTION:

HYDROLOGIC MODIFICATION AND LARGE-RIVER FOOD WEBS

Freshwater ecosystems are some of the most threatened on the planet (Allan & Flecker 1993; Jackson *et al.* 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 *et al.* 1996; Rosenberg *et al.* 2000; Bunn & Arthington 2002; Foley *et al.* 2005). At the global scale, few large rivers remain in relatively natural states (Gore & Shields 1995; Rosenberg *et al.* 2000; Nilsson *et al.* 2005). The vast majority of all temperate rivers are heavily regulated (Dynesius & 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 *et al.* 2000; Agostinho *et al.* 2005b). 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 (Johnson *et al.* 1995; Delong & Thorp 2006).

Food webs provide a general framework for studying the complexities of ecosystems (Pimm 2002), and appropriate ecological scales for investigating impacts of species introductions/extirpations (Moyle & Light 1996a; Olden & Poff 2003) and managing some ecosystem services (Kremen 2005). Complexity within food webs and

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This dissertation follows the style of *Ecology Letters*.

aggregate ecosystem-level effects of anthropogenic impacts may be summarized by emergent properties (sensu Salt 1979) of food webs, such as food-chain length or the relative importance of carbon sources supporting dominant feeding pathways. However, difficulty in compiling high quality food webs that can be compared across systems has restricted generalizations about determinants of web structure (Paine 1988; Hall & Raffaelli 1993; de Ruiter *et al.* 2005; Winemiller & Layman 2005).

Analysis of stable isotope ratios, especially of carbon and nitrogen, have important applications to studies of energy flow in food webs (e.g. Araujo-Lima *et al.* 1986; Peterson & Fry 1987; Kling *et al.* 1992; France 1995; Vander Zanden *et al.* 1999a; Lewis *et al.* 2001b; Post 2002b) and provide a standardized metric for comparison among webs. Isotopic signatures in tissues of slow growing or long-lived organisms may require several weeks to months to turn-over, thereby describing long-term trophic relationships (Cabana & Rasmussen 1996; Vander Zanden & Rasmussen 1999; MacAvoy *et al.* 2001). Most importantly, stable isotope ratios provide a common currency for comparisons of food web attributes. In this study I use natural abundances of carbon and nitrogen isotopes in basal sources and aquatic consumers to describe energy flow through large-river food webs.

The general objective of this study is to examine landscape-scale effects on emergent properties of large-river food webs and an important service these ecosystems provide (fisheries production). An approximately 500 km stretch of the Upper Paraná River Basin, Brazil, provided the setting for this work and was chosen based on the presence of sites that differ in several landscape-scale characteristics. Rivers on the west margin of the Paraná River have low gradients and wide floodplains, whereas east-margin rivers have higher gradients and narrow floodplains. In addition to free-flowing rivers, large reservoirs are also present. The general hydrological characteristics that distinguish these sites are known to determine aquatic community structure and function (Poff & Allan 1995; Lamouroux *et al.* 2002; Hoeinghaus *et al.* In Press-a), and may also determine food web structure. In addition to landscape type, other large-scale characteristics such as climatic regimes and terrestrial vegetation zones also vary across the study region.

Food-chain length and the relative contributions of basal carbon sources to dominant trophic pathways were determined for 10 aquatic food webs that differ in landscape type (low-gradient rivers, high gradient rivers, reservoirs, and river stretches just below reservoirs) and other landscape characteristics. Because these webs share a regional species pool (species present at any location may potentially colonize other locations), differences in constituent communities should be predominantly determined by characteristics of the habitats rather than historical factors (see Ricklefs 1987; Ricklefs & Schluter 1993; Ricklefs 2004). Variation in food web attributes observed across these landscape types therefore reveal landscape-scale influences on local food web structure, as mediated by attributes of the constituent species.

Food webs have aspects of horizontal, vertical and internal structure. I begin this study at the base of the webs, estimating the relative importance of various carbon sources to dominant trophic pathways. The relative importance of principal energy sources driving river food webs are addressed in three widely-cited models of large-river ecosystem functioning: the River Continuum Concept (Vannote *et al.* 1980), the Flood Pulse Concept (Junk *et al.* 1989) and the Riverine Productivity Model (Thorp & Delong 1994, 2002). Each model makes specific predictions about the dominant sources of energy supporting river food webs, but studies testing the trophic predictions of these models are rare (Thorp *et al.* 1998) and typically address only a single river or river type. River impoundment has been addressed only to a limited degree (Ward & Stanford 1983, 1995), even though the above models have explicit longitudinal and lateral contexts that are disrupted by reservoirs in most large river systems. Chapter II describes fundamental differences in the relative importance of production sources supporting dominant pathways of energy flow through food webs distinguished by landscape-scale hydrological characteristics and reconciles the above-mentioned models of large-river ecosystem function.

Food web height or food-chain length is an important property of biological communities that affects ecosystem processes and community structure (Paine 1980; Rasmussen *et al.* 1990; Schindler *et al.* 1997; Pace *et al.* 1999; Duffy *et al.* 2005). The models discussed in Chapter II do not address issues of vertical web structure, and at present there is no consensus on what factors determine the length of food-chains across ecological systems in general (Post 2002a). Previously popular theories which suggested dynamic stability (Pimm & Lawton 1977) or resource availability (Hutchinson 1959; Schoener 1989) limit the length of food-chains have been called into question (e.g. Briand & Cohen 1987; Spencer & Warren 1996; Sterner *et al.* 1997; Post *et al.* 2000), and recent studies emphasize a variety of environmental factors ranging from local to regional scales (reviewed in Post 2002a). In Chapter III, I compare food-chain length across the study region, and identify landscape-scale determinants of vertical web structure for these large-river landscape types.

River impoundment may affect local communities through selection for native species pre-adapted for lentic conditions, blockage of migration routes, and facilitation of species invasions (Moyle & Light 1996a). Changes in the structure of the food web may directly affect the ability of the ecosystem to provide services valued by humans. One such ecosystem service provided by many large rivers of the tropics is fisheries production (Welcomme 1985; Allan *et al.* 2005). In Chapter IV, I focus on trophic characteristics of commercially important fish species, and demonstrate anthropogenic impacts on the ecological and economic efficiency of these exploited food webs. In Chapter V, I summarize my findings from previous chapters, present a holistic conceptual model of energy flow and food-web structure of large rivers, and highlight areas requiring further investigation.

CHAPTER II

LANDSCAPE-SCALE HYDROLOGIC FEATURES DETERMINE ENERGY FLOW IN LARGE-RIVER FOOD WEBS

INTRODUCTION

It is difficult to overstate the importance of large river ecosystems. Some of the world's highest levels of biodiversity occur in large tropical rivers (Lowe-McConnell 1987). Most large rivers of the tropics also support substantial fisheries (Welcomme 1985; Allan *et al.* 2005) in addition to providing other ecosystem services. At the same time, freshwater ecosystems are some of the most threatened on the planet (Allan & Flecker 1993; Jackson *et al.* 2001). Perhaps the greatest impact to the functioning of large river ecosystems is alterations to the global water cycle through water diversion and impoundment (Postel *et al.* 1996; Rosenberg *et al.* 2000; Bunn & Arthington 2002; Foley *et al.* 2005). At the global scale, few large rivers remain in relatively natural states (Gore & Shields 1995; Rosenberg *et al.* 2000; Nilsson *et al.* 2005). The vast majority of all temperate rivers are heavily regulated (Dynesius & 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 *et al.* 2000).

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, especially with regard to energy flow (Johnson *et al.* 1995; Delong & Thorp 2006). Despite the relative paucity of food web studies in large rivers, three general models of ecosystem functioning are widely cited, each stressing the importance of a different principal energy source driving river food webs: the River Continuum Concept (RCC - Vannote *et al.* 1980), the Flood Pulse Concept (FPC - Junk *et al.* 1989) and the Riverine Productivity Model (RPM - Thorp & Delong 1994; Thorp & Delong 2002). The RCC attributes secondary production in large river food webs to the assimilation of terrestrially derived organic carbon "leaked" downstream due to inefficient processing by consumers in headwaters and intermediate reaches. According to the FPC, seasonal floodplain inundation drives ecosystem dynamics, with most secondary production directly or indirectly attributed to floodplain vegetation and aquatic macrophytes that thrive during inundation. The RPM emphasizes the refractory nature of transported organic material, and suggests that lowland river food webs are based primarily on autochthonous production of microalgae.

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

In the present study I used stable isotopes of carbon and nitrogen to trace energy flow through dominant metazoan trophic pathways of 10 aquatic food webs of natural and hydrologically impacted river stretches (low-gradient rivers, high-gradient rivers, reservoirs, and rivers just below reservoirs) of a large Neotropical river basin, and determine the relative importance of different carbon sources supporting each species-rich food web. Estimated source contributions for each food web are used to evaluate the suitability of the above-mentioned models of energy flow for these ecosystems, and to describe potential effects of landscape-scale hydrological characteristics and river impoundment on energy flow in large-river food webs.

METHODS

Regional description and study locations

The Paraná River is the tenth largest river in the world in annual discharge (5.0×10^8 m^3yr^{-1}) and fourth in drainage area (2.8×10^6 km^2). The upper third of the Paraná River Basin (891,000 km^2) is almost completely in Brazilian territory, including the most densely populated region of Brazil (Agostinho *et al.* 1995). The Upper Paraná is one of the most intensively dammed river basins in the world (Figure 1), with over 130 major reservoirs (dam height ≥ 10 m) on the eastern side among which 20% are larger than 10,000 ha (Agostinho *et al.* 2000; Gomes & Miranda 2001a). 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 (≤ 20 km) on the west margin and experiences a relatively predictable seasonal flood pulse in part due to several important tributaries that flow into the Paraná in this stretch. Floodplain inundation is of shorter duration and lower magnitude than historically observed (Agostinho *et al.* 2004b). Eastern margin tributaries (e.g. 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 (e.g. Ivinheima and Iguatemi) from December through April, with large-scale reproductive migrations of several fish species (e.g. *Prochilodus lineatus, Pseudoplatystoma corruscans, Salminus maxillosus*) coinciding with rising water levels and wet season flooding (Agostinho *et al.* 2003). Greater 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 *et al.* 1997). Detailed descriptions of the Upper Paraná River Basin, particularly the remaining floodplain stretch, can be found in Thomaz *et al.* (2004a).

Aquatic food webs were investigated at 10 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 all of the aquatic and riparian prey or organic sources consumed throughout the web leading to those consumers. Parasites and non-aquatic organisms which feed on fish, such as birds and humans, were not included in this study. The 10 study locations were chosen to represent 4 different landscape types: low-gradient rivers, high-gradient rivers, reservoirs, and river reaches just downstream from reservoirs (Figure 1).

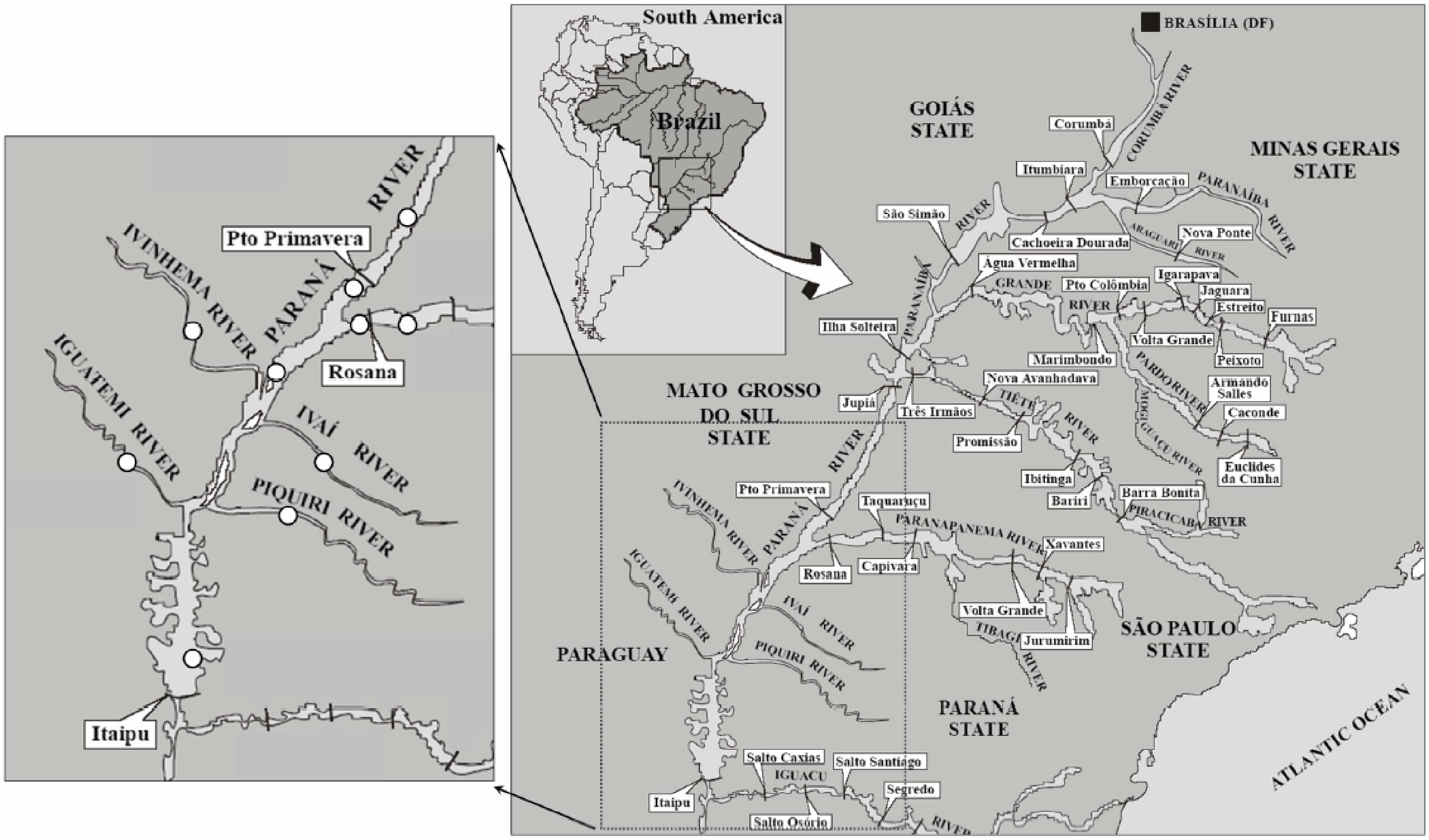

Figure 1 Study locations (white circles in left panel) and large reservoirs of the Upper Paraná River basin, Brazil. Modified from Agostinho *et al.* (2004b).

Low-gradient rivers – Food webs of three low gradient rivers were investigated: the main stem Paraná and connected water bodies equidistant between Itaipu Reservoir and Porto Primavera Reservoir, the Ivinheima River, and the Iguatemi River. All three have gradients < 0.10 m km^{-1} in this region (Agostinho *et al.* 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., Figure 2a) in backwater areas (Thomaz *et al.* 2004b), and riparian forest transitioning to várzea, dry fields and pastures (Souza *et al.* 2004).

High-gradient rivers – Food webs of the Piquiri River (2.20 m km^{-1}) and the Ivaí River (1.30 m km^{-1}) were examined. Both rivers are large east-margin tributaries that have their confluence with the Paraná along its remaining free-flowing stretch (Agostinho *et al.* 1995). Both rivers have high water velocities and high turbidities, rocky substrates, and incised channels with restricted floodplains (Figure 2b). Few aquatic macrophytes are present and dense gallery forest transitions to pastures or crops.

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^2. Closure of the reservoir in 1982 inundated the Sete Quedes waterfalls, a biogeographic barrier that formerly separated the faunas of the Middle and Upper Paraná basins, allowing many 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^2 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^2. 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 (Figure 2c).

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 Rosana Reservoir. This stretch of the Paraná is the most upstream point of the floodplain, has a gradient of approximately 0.14 $m\ km^{-1}$ (Agostinho *et al.* 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 (Figure 2d). The Paranapanema has a gradient of 0.6 $m\ km^{-1}$ (Agostinho *et al.* 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 *et al.* 2004b).

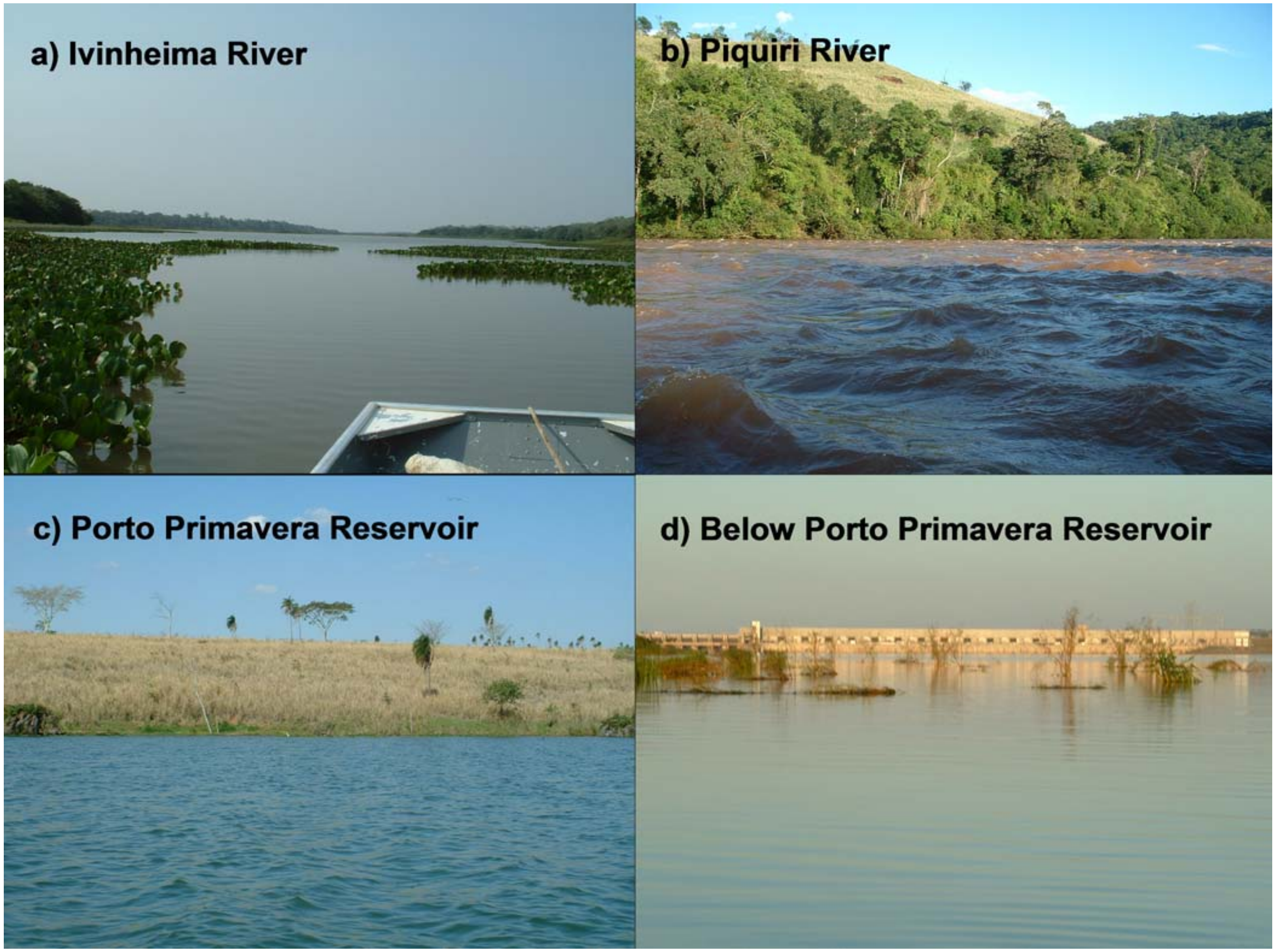

Figure 2 Characteristic habitats of a) low-gradient rivers, b) high-gradient rivers, c) reservoirs, and d) river stretches below reservoirs.

Sampling methodology

Carbon isotopic signatures of dietary items are conserved (within 1‰) in consumer tissues, and allow determination of carbon sources ultimately supporting secondary production when source isotopic values are distinct (Peterson & Fry 1987). Nitrogen isotope ratios of consumer tissues are enriched 2 – 3‰ relative to their diet (Minagawa & Wada 1984; Post 2002b; Vanderklift & Ponsard 2003), and can be used to determine consumer trophic position (Peterson & Fry 1987). I used C and N isotope ratios of primary producers and consumers to examine relative importance of basal carbon sources to dominant trophic pathways 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. Colleagues at the Research Nucleus in Limnology, Ichthyology and Aquaculture (Nupelia) at the State University of Maringá (UEM), Brazil, aided in field collections and identification of species.

Isotopic signatures of carbon sources were used to trace their importance to secondary consumers. Several basal source groups were collected for isotopic analyses: C_3 plants (aquatic macrophytes and riparian vegetation), C_4 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 a small fraction of suspended fine particulate organic matter). Multiple leaves of dominant species of C_3 and C_4 aquatic and riparian vegetation were clipped directly from the plant. 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 μm plankton net, and retaining the < 68 μm fraction. Seston samples were collected using a gas powered water pump to pass large volumes of water through a 20 μm plankton net. The retained fraction (>20 μm) was then passed through a 68 μm plankton net to remove larger zooplankton and organic material, resulting in a 20 – 68 μm sample. All samples were stored on ice in the field then frozen upon return to the lab (except water samples, which were refrigerated and processed first).

Primary consumers were used to determine the base of each food-web. Five types of primary consumers were collected: grazing snails (*Pomacea canaliculata*), filter-feeding bivalves (*Corbicula fluminea*), herbivorous fishes (e.g. *Schizodon* spp., *Brycon orbignyanus*, *Metynnis* sp.), detritivorous fishes (e.g. *Prochilodus lineatus*, *Steindachnerina* spp., *Liposarcus anisitsi*, *Loricariichthys platymetopon*), and herbivorous zooplankton (e.g. larger-sized cladocerans and copepods, Santos-Silva *et al.* 1989; Elmoor-Loureiro 1997; Santos-Silva 2000). 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. 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 bags, 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. 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 µm and 125 µm.

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 Analyses in this chapter and Chapter IV), special effort was given to obtain species potentially occurring at the top of the food web (e.g. piscivorous species such as *Pseudoplatystoma corruscans*, *Salminus maxillosus*, *Plagioscion squamosissimus* and *Cichla* spp.) so that the entire vertical structure of the web could be estimated with confidence. Additional specimens were purchased from local fishermen at some locations. Individuals were measured and tissue samples collected as described for herbivorous and detritivorous fishes. A list of the species collected at each sampling location is provided as Appendix A.

Laboratory methodology

Upon return to the lab, water samples for seston and FPOM were inspected with the aid of a dissecting microscope, and tweezers were used to remove any zooplankton. Samples were then filtered onto pre-combusted (450˚C for 8 hrs) glass fiber filters (Schleicher & Schuell GF 52-C, 47.0±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 tweezers. Filamentous algae samples were rinsed with distilled water, inspected to remove any remaining contaminants, and consolidated onto filters. Leaves of C_3 and C_4 plants were visually inspected and brushed to remove any contaminants (e.g. periphyton) and rinsed with distilled water. Coarse detritus samples were visually inspected to remove invertebrates and rinsed with distilled water over a 68 µm filter to remove the fine detritus fraction. Fish tissues were examined to remove skin, scales or small bones, and rinsed with distilled water. 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 60ºC 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 10^{-6} g, or for filtered samples all material retained on the filter was used, and pressed into Ultra-Pure tin capsules (Costech Analytical), 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): $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) -1] *1000$; where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material for carbon is Pee Dee Belemnite (PDB) limestone, and the nitrogen standard is atmospheric nitrogen.

Analyses

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, I used $\delta^{13}C$ signatures of the highest trophic level fish species in each web to provide an integrated measure of the carbon sources fueling dominant trophic pathways of the metazoan component of the food web. The species with the highest trophic position was determined using $\delta^{15}N$ values, and the $\delta^{13}C$ signatures of all consumers with mean $\delta^{15}N$ values within 1‰ of the highest trophic position species (or the top five trophic level consumers if less than five species had means within 1‰ of the apex species) were averaged. This method provides a $\delta^{13}C$ value for each web which is an integrated estimate (in terms of energy assimilated) of the dominant trophic pathways leading to top predators in the web. Mean carbon isotope signatures were compared among source groups using analysis of variance (ANOVA), and pairwise comparisons of source means were performed using Tukey's post-hoc procedure and the harmonic mean sample size (Gotelli & Ellison 2004). Integrated food web $\delta^{13}C$ values were compared among landscape types (low-gradient rivers, high-gradient rivers, reservoirs, river stretches downstream of reservoirs) using ANOVA, and post-hoc comparisons were made using Tukey's procedure as above.

The software package IsoSource (Phillips & Gregg 2003) was used to calculate ranges of proportional contributions of each source to integrated food web $\delta^{13}C$ signatures because the number of potential sources in these systems is too large to permit a unique solution (i.e. $n_{sources} > n_{isotopes}+1$). This procedure uses mean isotope values 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 & Gregg 2003; Hoeinghaus & Davis III In Press). Analyses were performed using mean $\delta^{13}C$ signatures of source groups, with source increments of 1% and mass balance tolerance of 0.05‰. As recommended by Phillips & Gregg (2003), distributions of feasible contributions and the 1 – 99th percentile range are reported along with the mean contribution for each source.

RESULTS

Source isotopic signatures

A total of 748 basal source and consumer samples were analyzed for carbon and nitrogen isotopic ratios. Carbon isotopic signatures were significantly different among source groups (Figure 3; $p < 0.001$, $df = 3$, $F = 1141.86$, all pairwise comparisons p <

0.001). No differences in $\delta^{13}C$ signatures of source groups were observed among sites, so source values were combined for all webs for subsequent analyses. Filamentous algae and C_4 grasses had the most enriched mean values (-15.72‰ and -13.11‰, respectively), whereas seston and C_3 plants were relatively ^{13}C depleted (-24.54‰ and -28.42‰, respectively). Carbon isotopic ratios of coarse detritus (-29.97‰) overlapped with those of C_3 plants, and FPOM $\delta^{13}C$ (-24.30‰) did not differ from seston, reflecting the ultimate sources of these two size fractions of benthic organic material. Values of these two detrital components were combined with their respective live sources for all subsequent comparisons. Combining fractions in this manner is a logical compression of the data that should not affect interpretations of allochthonous vs. autochthonous source contributions (see Phillips *et al.* 2005; Delong & Thorp 2006). A series of samples, including several algae and seston samples, were inadvertently destroyed due to equipment failure during laboratory analysis of carbon and nitrogen isotope concentrations. Whereas new samples of muscle or vascular plant tissue could be sent for analysis, replicate algae and seston samples could not be analyzed because all of the 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 includes 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 (e.g. Bunn *et al.* 2003; Herwig *et al.* 2004).

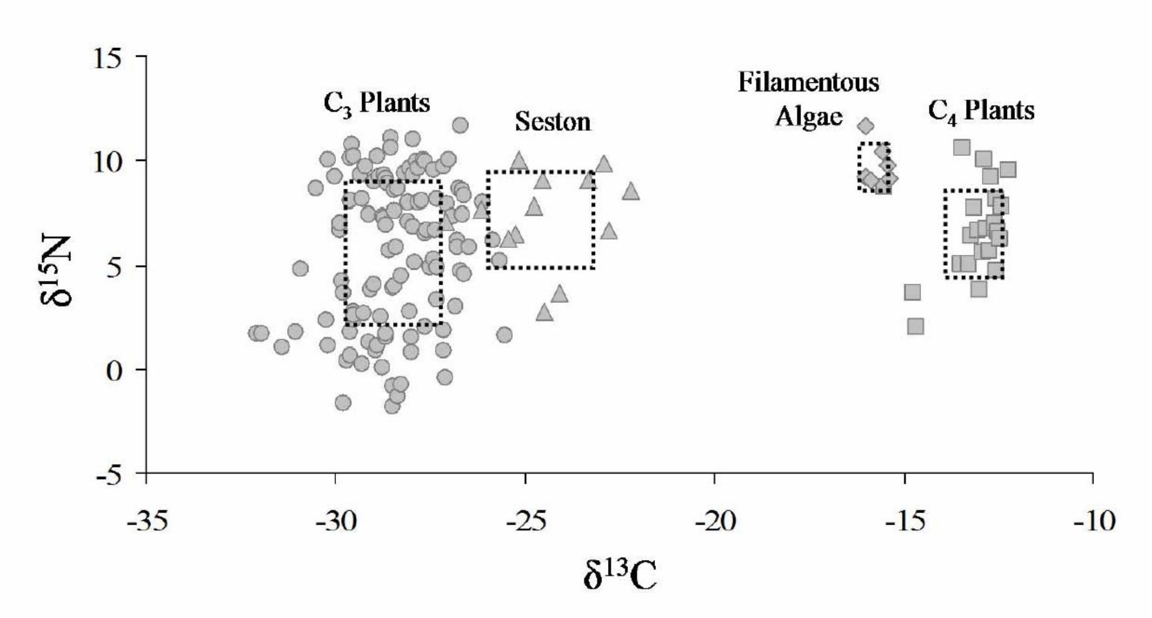

Figure 3 δ^{13}C and δ^{15}N values of source groups combined across sampling locations of the Upper Paraná River basin, Brazil. Boxes depict means ± 1 SD. Values for coarse detritus are combined with those for C_3 plants, and FPOM values are combined with those for seston (see *Source isotopic signatures*). C_3 plants: n=113; Seston: n=13; Filamentous algae: n=6; C_4 plants: n=23.

Integrated food web $\delta^{13}C$ signatures and source contributions

The species occupying the highest trophic positions and used to provide integrated food web $\delta^{13}C$ signatures were generally similar across all webs (e.g. *Serrasalmus marginatus, Rhaphiodon vulpinus, Plagioscion squamosissimus, Cichla* spp., *Pinirampus pirinampu, Pseudoplatystoma corruscans*, Appendix A), although to a lesser degree in the high-gradient rivers which have relatively distinct fish faunas (Agostinho *et al.* 1995; Agostinho *et al.* 1997). Carbon isotope signatures of the top consumers used to calculate integrated food web $\delta^{13}C$ values differed little within food webs (see standard deviations of integrated $\delta^{13}C$ in Table 1), but integrated food web signatures differed significantly among habitats (Figure 4; $p < 0.001$, $df = 3$, $F = 58.98$), with high-gradient rivers significantly more enriched in $\delta^{13}C$ than all other habitats ($p < 0.01$ for all pairwise comparisons), and low-gradient rivers the most depleted. Carbon isotope ratios for reservoir food webs were different from both river types, and overlapped with values for food webs just below reservoirs (Figure 4). Integrated carbon signatures of food webs below reservoirs were marginally significantly different in pairwise comparison with values observed for food webs of low-gradient rivers ($p = 0.06$).

Differences in food web $\delta^{13}C$ signatures are due to differences in the relative contributions of carbon sources to dominant trophic pathways. Ranges of source contributions were broad (especially for seston, Table 1), potentially limiting inferences within webs (i.e. contributions to the mixture may vary widely for some sources, yet provide the same $\delta^{13}C$ signature). This is a general problem when using stable isotopes to determine trophic relationships in complex systems (Phillips & Gregg 2003; Phillips *et al.* 2005), and was part of the motivation for combining coarse detritus and FPOM samples with their live sources. However, variation in estimated mean source contributions (and range of potential contributions) across habitats reveals key differences in food web structure.

Across all webs, C_3 vegetation and phytoplankton appear to fuel the dominant trophic pathways leading to top consumers (Table 1). Mean percent contributions of C_3 vegetation and phytoplankton (seston) ranged from 23-62% and 25-37% respectively across all webs. C_3 vegetation and phytoplankton together account for almost 90% of the mean source contribution to all three low-gradient rivers, with C_3 plants contributing a mean of 53-62% (Table 1, Figure 5). Contributions of filamentous algae and C_4 grasses were conspicuously higher in the high-gradient Piquiri and Ivaí food webs than other landscape types. Higher relative importance of filamentous algae and C_4 grasses in high-gradient food webs is concomitant with a large reduction in the contribution of C_3 vegetation (Table 1, Figure 6). Integrated $\delta^{13}C$ signatures of reservoir and below-reservoir food webs fall within 1 SD of the mean $\delta^{13}C$ value for seston (Table 1, Figure 3), and source ranges suggest that phytoplankton production is the dominant autotrophic energy source for these habitats, although C_3 vegetation may contribute significant amounts as well (Figures 7 & 8).

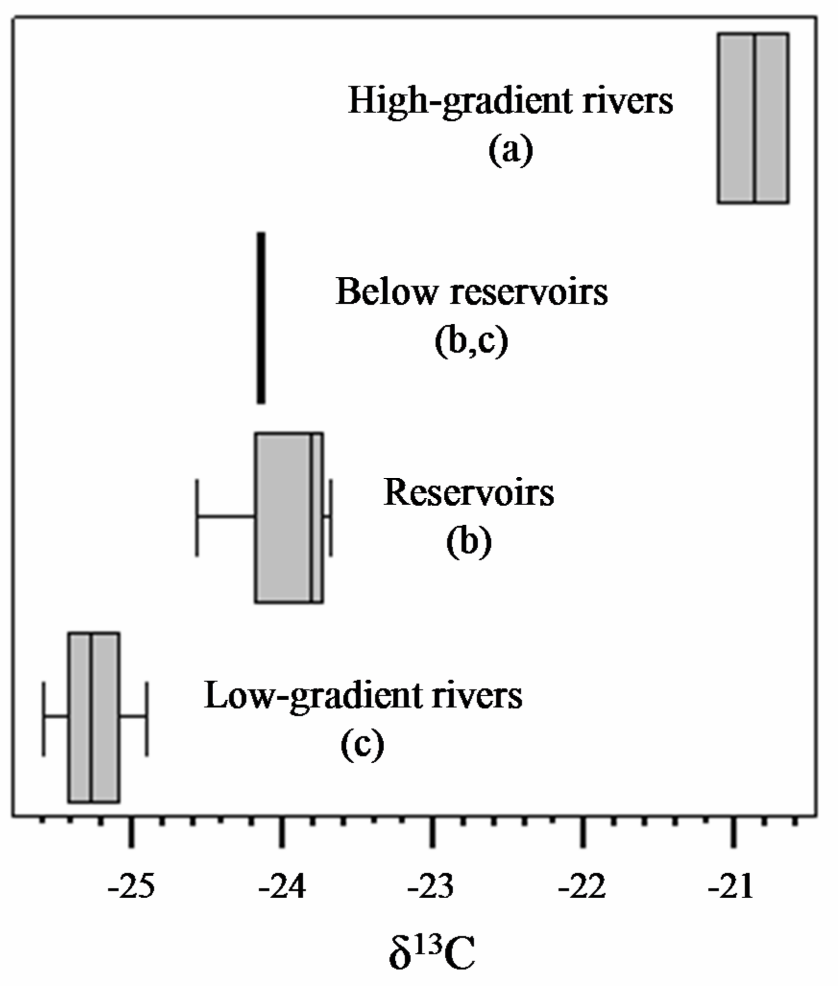

Figure 4 Mean (solid line within box), quartiles (box) and range (whiskers) of integrated food web $\delta^{13}C$ signatures among landscape types. Food web $\delta^{13}C$ signatures are significantly different among habitats ($p < 0.001$), with significantly different subsets denoted by letters in parentheses). Below reservoirs and low-gradient food webs were only marginally not significantly different ($p = 0.06$).

Table 1 Integrated $\delta^{13}C$ values for each food web, mean $\delta^{13}C$ values by habitat, and mean percent contribution and 1-99th percentile of sources to the dominant trophic pathways of each web. Standard deviations for each location are calculated from the consumer species mean $\delta^{13}C$ values used to calculate the integrated food web value.

Habitats	Integrated δ13C		Mean % contribution				1 - 99th percentile			
	mean	(± 1 SD)	C_3 veg	C_4 veg	Seston	Algae	C_3 veg	C_4 veg	Seston	Algae
Low-gradient rivers	-25.25	(0.34)								
Iguatemi	-25.58	(0.65)	62	6	25	7	30 - 80	0 - 17	0 - 68	0 - 21
Ivinheima	-25.27	(0.74)	58	7	28	8	23 - 78	0 - 19	0 - 76	0 - 23
Paraná	-24.90	(1.77)	53	8	31	9	15 - 76	0 - 21	0 - 83	0 - 25
High-gradient rivers	-20.88	(0.32)								
Piquiri	-20.65	(2.34)	23	22	29	26	0 - 47	0 - 47	0 - 63	0 - 57
Ivaí	-21.10	(1.97)	25	20	31	24	0 - 50	0 - 45	0 - 67	0 - 54
Reservoirs	-24.01	(0.49)								
Itaipu	-23.80	(1.29)	40	10	37	13	1 - 68	0 - 28	0 - 91	0 - 33
Rosana	-23.67	(1.43)	39	11	37	13	1 - 67	0 - 28	0 - 90	0 - 34
Porto Primavera	-24.57	(1.08)	48	8	34	10	6 - 73	0 - 23	0 - 91	0 - 28
Below reservoirs	-24.15	(0.02)								
Paranapanema below Rosana	-24.13	(0.51)	43	9	36	11	2 - 70	0 - 26	0 - 93	0 - 31
Paraná below Porto Primavera	-24.16	(1.64)	44	9	36	11	2 - 70	0 - 26	0 - 93	0 - 31

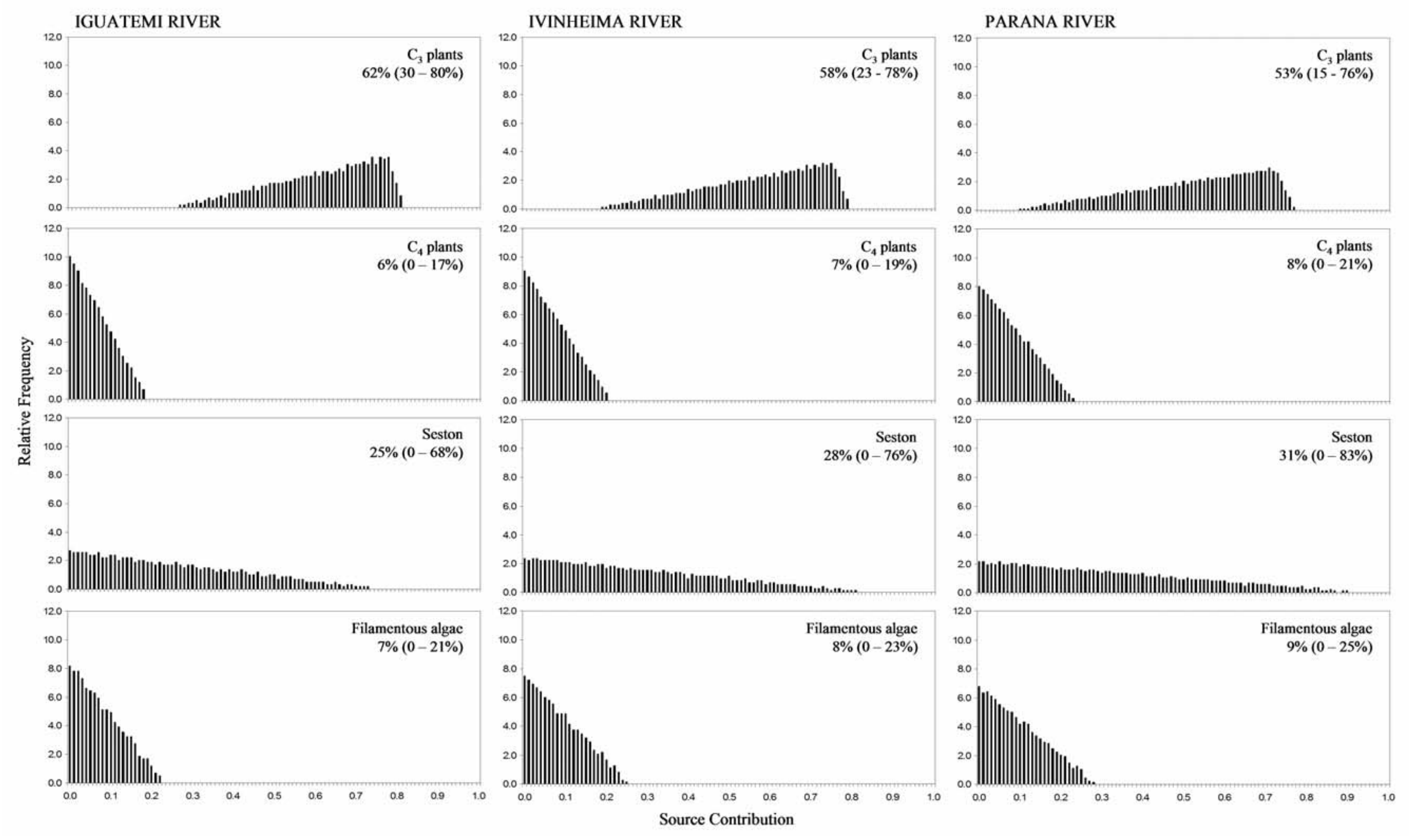

Figure 5 Distributions of feasible source contributions to low-gradient river food webs. Mean percent contribution and the 1-99th percentile range (in parentheses) are given for each source.

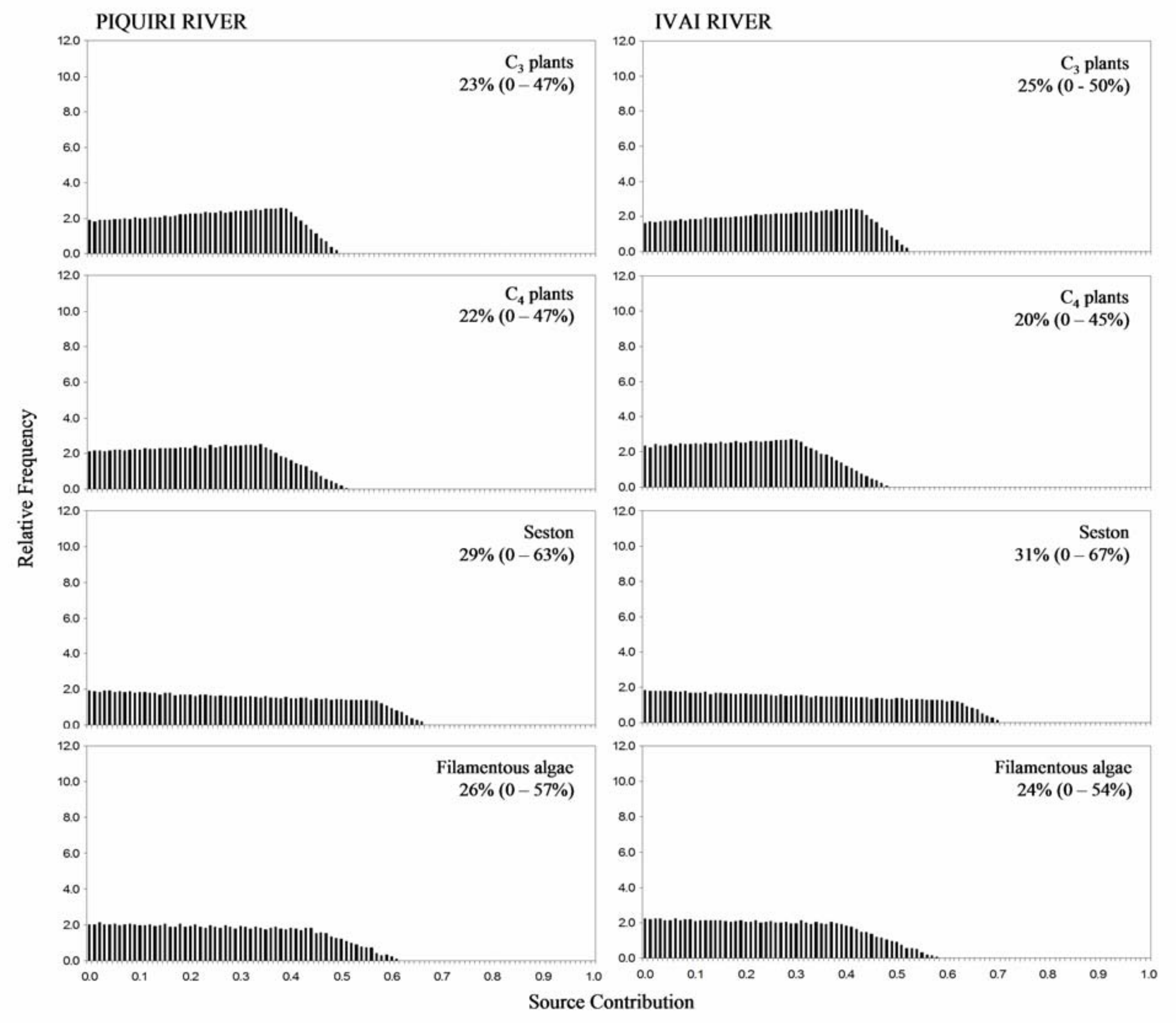

Figure 6 Distributions of feasible source contributions to high-gradient river food webs. Mean percent contribution and the 1-99th percentile range (in parentheses) are given for each source.

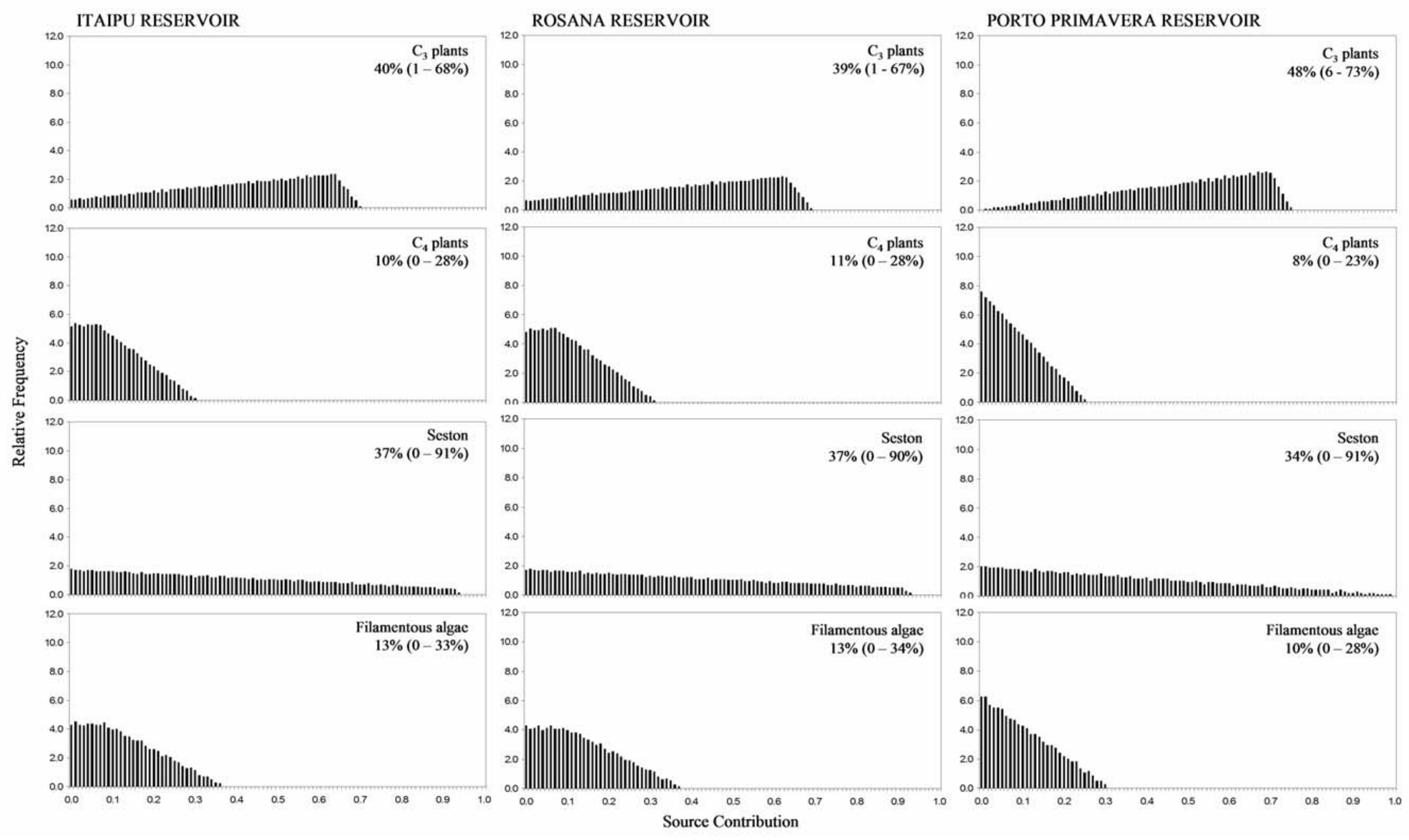

Figure 7 Distributions of feasible source contributions to reservoir food webs. Mean percent contribution and the 1-99th percentile range (in parentheses) are given for each source.

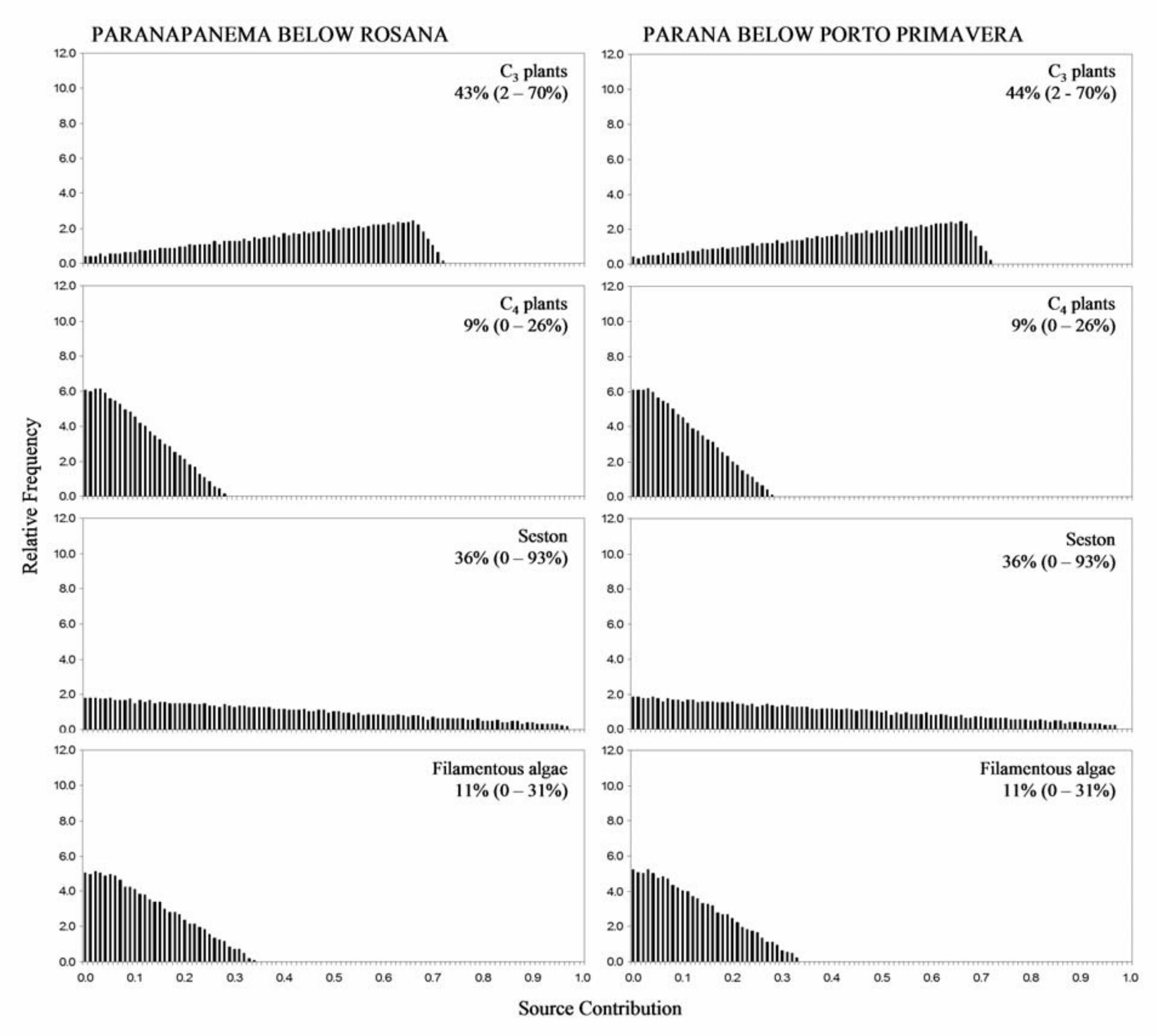

Figure 8 Distributions of feasible source contributions to below-reservoir food webs. Mean percent contribution and the 1-99th percentile range (in parentheses) are given for each source.

DISCUSSION

Isotopic composition of sources and integrated food web $\delta^{13}C$

Observed source $\delta^{13}C$ values corresponded with reported values for other freshwater rivers (e.g. Boon & Bunn 1994; Bunn *et al.* 2003; Herwig *et al.* 2004; Pease *et al.* 2006). Some studies in other basins of South America have observed more depleted $\delta^{13}C$ values for phytoplankton/seston (-35 to -30‰, e.g. Araujo-Lima *et al.* 1986; Hamilton *et al.* 1992; Jepsen & Winemiller In Review); this is likely due to differences in watershed geochemistry and trophic state of the water bodies. Basin geochemistry determines C isotope ratios of dissolved inorganic carbon, which is assimilated in tissues of autotrophs (Tan & Edmond 1993; Jepsen & Winemiller In Review). Phytoplankton of oligotrophic systems, such as the study region of the Upper Paraná basin (Agostinho *et al.* 1995), are often ^{13}C enriched compared to more productive systems with similar basin geochemistry (Grey *et al.* 2000). Additionally, carbon isotope signatures of algae are affected by photosynthesis rate (largely influenced by water temperature and light intensity) and availability of dissolved CO_2, with more enriched $\delta^{13}C$ values corresponding to higher rates of photosynthesis (MacLeod & Barton 1998) and carbon limitation in larger watersheds (Finlay 2001) or during periods of lower rainfall or watershed flushing (Depetris & Kempe 1993). Given that sampling occurred during the late dry season (reduced watershed flushing) from the end of spring to early summer (presumably high rates of photosynthesis), the oligotrophic nature of the waterbodies and large watershed size, the enriched $\delta^{13}C$ values observed for algae may result from relative limitation of dissolved CO_2.

Even though $\delta^{13}C$ values for source groups were distinct, wide ranges of potential contributions to food webs were observed. In many cases, inclusion of a second isotope such as N or S can improve resolution of source contributions (Phillips & Gregg 2003; Phillips *et al.* 2005). However, inclusion of N isotopic ratios in our IsoSource analyses was not feasible due to the integrated approach whereby all dominant pathways in the food web were summarized by C isotope ratios of its top consumers. Even if N ratios of sources and consumers were included in the models, mean $\delta^{15}N$ values differed only slightly across source groups, and likely would not have proven as useful in constraining source contributions as in other systems where $\delta^{15}N$ values of sources were more distinct (e.g. Hoeinghaus & Davis III In Press).

Integrated food web $\delta^{13}C$ signatures were calculated to summarize the dominant pathways of energy flow from primary producers to top consumers. These signatures are a useful metric of web structure in highly connected, species-rich food webs. The choice of which, or how many, consumer species to use to summarize food web $\delta^{13}C$ may potentially affect the resulting integrated food web values. For this reason, an objective criterion was defined *a priori* to determine which species would be included to summarize each web: the top 1‰ based on N stable isotope ratios, with a minimum of five species. This is equal to approximately the top one third of a trophic level of each web (considering fractionation between 2.54 and 3.4‰ per trophic level, Post 2002b; Vanderklift & Ponsard 2003).

In only one instance (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 *Plagioscion squamosissimus* in relation to the rest of the top predators. Integrated $\delta^{13}C$ values calculated based on the top 1‰ and the top five species differed only slightly (-24.48‰ and -24.57‰, respectively), and would not have affected estimated source contributions. Further illustrating the robustness of this method 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 -20.49‰, closely matching the integrated value calculated for the aquatic food web (-20.65‰) using piscivorous fishes. Calculating integrated $\delta^{13}C$ values based on the above criterion provides a comprehensive metric of vertical carbon flow through food webs, even given the diverse trophic ecologies typified by Neotropical fish faunas (Lowe-McConnell 1987; Winemiller 1990, 1991).

Carbon isotope signatures of the top consumers used to estimate food web $\delta^{13}C$ were generally very similar. However, standard deviations of carbon signatures of top consumers were higher in the two high-gradient rivers. At these sites, the relative contributions of all sources were also similar (20-30% mean contribution). These results suggest that top predators may be supported by relatively more trophic pathways at these sites than in the other habitats where carbon flow was dominated by one source-consumer pathway (e.g. C_3 plants in lowland rivers).

Hydrological characteristics and energy flow in large-river food webs

Significant differences in the relative importance of carbon sources fueling dominant trophic pathways were observed among aquatic food webs distinguished by landscape-scale hydrologic characteristics. Lowland floodplain river food webs were primarily based on C_3 plants and to a lesser degree phytoplankton (seston) production. The potential importance of phytoplankton as an energy source was greater in reservoirs and rivers just below reservoirs than in lowland rivers. Only in high-gradient rivers did filamentous algae and C_4 plants contribute a substantial amount of energy flowing through the web. Little variation in the relative importance of carbon sources was observed within landscape types, emphasizing that the trends observed are related to phenomenon associated with the landscape-scale hydrological characteristics distinguishing these landscapes. Incorporation of landscape-scale hydrologic features may help reconcile distinctions among the currently popular models of energy flow through river food webs (RCC, FPC and RPM) and provide a more holistic basis to the understanding of ecosystem processes in large-river systems.

Key distinctions of the FPC and RPM were observed in different habitats in the present study. Food webs of the low-gradient floodplain rivers (Paraná, Ivinheima and Iguatemi) were fueled primarily by C_3 plant production, in fitting with the FPC (Junk *et al.* 1989) and some earlier floodplain food web studies (e.g. Bayley 1989). The assimilated C_3 production is most likely derived from the abundant aquatic macrophytes present at these sites, as terrestrial C_3 plants have lower nutritional value (i.e. lower protein content and higher fiber content, Forsberg *et al.* 1993). Phytoplankton was secondarily important, contributing an estimated 30% of the energy to the food web on average. The importance of phytoplankton and benthic algae to floodplain river food webs has been observed for the Orinoco River floodplain in Venezuela (Hamilton *et al.* 1992) and the central Amazon River floodplain in Brazil (Araujo-Lima *et al.* 1986; Forsberg *et al.* 1993), and was influential in development of the RPM (Thorp & Delong 1994, 2002). While phytoplankton may be important to some food web compartments, e.g. some species of large detritivorous fishes (Araujo-Lima *et al.* 1986) and invertebrates associated with floating meadows (Hamilton *et al.* 1992), and was considered the dominant source supporting secondary production (Lewis *et al.* 2001a), isotope signatures of piscivores from the same studies (Araujo-Lima *et al.* 1986; Forsberg *et al.* 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 relative importance of phytoplankton to the food web. The RPM suggests that plankton and algae should be the dominant energy sources fueling secondary production (Thorp & Delong 1994, 2002), and has been supported by studies in the Upper Mississippi River basin, USA (Thorp *et al.* 1998; Delong & Thorp 2006), and Cooper Creek floodplain of Australia (Bunn *et al.* 2003) in addition to the floodplain river studies cited previously. In the present study, the highest relative importance of the phytoplankton pathway was observed for food webs of reservoirs and rivers just below reservoirs, although C_3 plants may still contribute a large fraction of the primary production fueling the food web (especially in the former floodplain stretch which is now Porto Primavera Reservoir). The increase in the relative importance of phytoplankton in comparison with the other habitats may be due to the increased water residence time and water clarity of the reservoirs.

Only in the high-gradient Piquiri and Ivaí Rivers were both the mean contribution and 99th percentiles of phytoplankton production assimilated in the food web higher than those for C_3 plants, but this was due to a dramatic decrease in the relative importance of C_3 plants rather than increased importance of the phytoplankton pathway. The estimated mean contribution of phytoplankton to the food web was similar to estimates for floodplain rivers. Concomitant with the reduced importance of C_3 plants was an increase in the relative importance of filamentous algae and C_4 plants. Floating aquatic macrophytes that are abundant in the other habitats are comparatively rare in these high-gradient sites which, combined with the lower energetic value of leaves from riparian trees (Forsberg *et al.* 1993), may explain the decrease in the importance of C_3 plants to these food webs. 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. *Schizodon nasutus*, a species belonging to a herbivorous genus known to preferentially graze aquatic C_4 grasses (Forsberg *et al.* 1993; Jepsen & Winemiller 2002), accounted for most of the biomass collected in gill-nets in the Piquiri River, and the benthic grazing *Prochilodus lineatus* collected in the Piquiri had a mean $\delta^{13}C$ signature of -18.98‰ (corresponding with filamentous algae) compared to -28.22‰ (C_3 plants, likely in the form of detritus) for the same species collected in the lowland Iguatemi River. The combined importance of phytoplankton and filamentous algae in these food webs support the RPM.

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 vs. lateral inputs (see Thorp *et al.* 1998), however the data presented here do not suggest that terrestrially derived particulate organic matter transported from upriver is an important primary production source supporting secondary macroconsumers in these food webs. Coarse detritus was shown to be derived from C_3 plant production; however, organic material transported down river 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 should have a C isotopic signature aligned with either C_3 or C_4 terrestrial vegetation. Instead, fine particulate organic matter at our sites was derived mostly from phytoplankton. Interruption of the continuum by river impoundment could be a consideration for the reservoir food webs, but even free-flowing lowland and high-gradient rivers did not support predictions of the RCC for these food webs. For all of the landscape types examined here, the principal energy sources supporting the macroconsumer food web appear to be those that were readily accessible and locally produced in each landscape type, such as C_3 vegetation in lowland rivers and phytoplankton in reservoirs. Transported terrestrial organic material may be an important source of other food web compartments not examined here (e.g. the microbial loop).

Relative abundance of invertebrate functional feeding groups (FFG, e.g. gatherers, scrapers) along the river continuum was given in support of predictions of the RCC (Vannote *et al.* 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). Recent studies using stable isotopes to examine food webs across a range of systems suggest that terrestrially derived organic matter may be important in small headwater streams or during winter months when aquatic production is lower (e.g. Huryn *et al.* 2001; Huryn *et al.* 2002; England & 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 & Delong 2002; Delong & Thorp 2006).

Conclusion

The relative importance of different carbon sources to the dominant trophic pathways in 10 large river food webs were shown to differ in relation to landscape-scale hydrologic characteristics. Macroconsumer food webs of the low-gradient rivers Paraná, Ivinheima and Iguatemi were consistent with predictions of the Flood Pulse Concept, namely that dominant trophic pathways were based on C_3 macrophyte production. Reservoirs, rivers below reservoirs and high-gradient rivers, all habitats with restricted floodplains, followed predictions of the Riverine Productivity Model, with phytoplankton and filamentous algae (especially in the high-gradient sites) supporting secondary production. Terrestrial production does not appear to contribute significant amounts of energy to any of the large-river macroconsumer webs examined here. Incorporation of landscape-scale hydrologic or geomorphic characteristics such as river slope or floodplain width (see Sedell *et al.* 1989) may resolve discrepancies between the Flood Pulse Concept, Riverine Productivity Model and River Continuum Concept, and lead to a more holistic model of ecosystem function in large rivers (see Thorp *et al.* 2006).

CHAPTER III

FOOD-CHAIN LENGTH OF LARGE RIVERS DETERMINED AT THE LANDSCAPE-SCALE

INTRODUCTION

The number of trophic transfers from the base to the top of a food web is called food-chain length. This aspect of vertical web structure strongly affects community structure (Paine 1980; Pace *et al.* 1999) and ecosystem function (Rasmussen *et al.* 1990; Schindler *et al.* 1997; Duffy *et al.* 2005). For this reason, food-chain length is considered a central characteristic of ecological communities (Post 2002a), and identifying what factors determine food-chain length is a fundamental issue of ecology (Fretwell 1987; Pimm 2002). Even with its auspicious beginnings (e.g. Elton 1927; Lindeman 1942; Hutchinson 1959; Hairston *et al.* 1960), the study of what limits or otherwise determines the length of food-chains has seen limited progress.

Theoretical, experimental and observational studies have suggested a number of potential determinants of food-chain length (reviewed in Post 2002a). Previously popular theories that suggested dynamic stability (Pimm & Lawton 1977) or resource availability (Hutchinson 1959; Schoener 1989) limit the length of food-chains have been called into question by recent studies (e.g. Briand & Cohen 1987; Spencer & Warren 1996; Sterner *et al.* 1997; Post *et al.* 2000). Food-chain length may only be limited when resource availability is <10 g C m^{-2} yr^{-1} (Moore *et al.* 1993; Post 2002a) as in experimental microbial or treehole communities (Jenkins *et al.* 1992; Kaunzinger &

Morin 1998). The history of community organization (Kitching 2001), size-structure of predator-prey interactions (Hastings & Conrad 1979), and human induced changes to communities (Pauly *et al.* 1998) may also affect food-chain length, but these hypotheses are difficult to measure or are oftentimes correlated with one another. Ecosystem size has been shown to determine food-chain length in some systems (e.g. temperate lakes, Vander Zanden *et al.* 1999b; Post *et al.* 2000), but the functional aspects of this relationship are unclear and ecosystem size is not readily determinable for many natural ecosystems (e.g. rivers).

Perhaps the greatest roadblock to progress has been the inherent difficulty of compiling accurate and comparable food webs, and an oversimplified approach to food webs as static arrangements of discrete trophic levels (Paine 1988; Hall & Raffaelli 1993; de Ruiter *et al.* 2005; Winemiller & Layman 2005). Studies of highly-resolved webs suggest that patterns emerging from early comparisons of food web structure may merely be artifacts of methodology or scale (Winemiller 1990; Hall & Raffaelli 1991; Goldwasser & Roughgarden 1997). Developments in the use of natural abundances of stable isotopes (particularly of nitrogen and carbon) in ecological studies over the last couple decades have had a profound impact on the way ecologists study energy flow and trophic structure (Peterson & Fry 1987; Post 2002b; Thompson *et al.* 2005). Importantly, stable isotopes provide a continuous measure of trophic position that integrates energy assimilated along all pathways leading to the consumer. Continuous measures of trophic position allow detection of the subtle differences in food-chain length that typify natural ecosystems (e.g. Vander Zanden *et al.* 1999b; Post *et al.* 2000).

Ecosystem characteristics have also limited our understanding of food-chain length. Most advances have been made in non-natural experimental assemblages or systems characterized by easily definable boundaries and low species richness such as water-filled tree holes and temperate lakes (e.g. Jenkins *et al.* 1992; Vander Zanden *et al.* 1999b; Kitching 2000; Post *et al.* 2000). Studies investigating anthropogenic impacts on aspects of food web structure have been limited to the same types of systems, with few exceptions (e.g. Zaret & Paine 1973; Ogutu-Ohwayo 1990; Layman *et al.* 2005a). Species-rich tropical webs and ecosystems with poorly defined boundaries have received inadequate attention. Post (2002a), in his review of the determinants of food-chain length, suggests broadening the search for a single determinant to when and where a suite of potentially interacting factors affect the length of food-chains. Diverse food webs with diffuse boundaries need to play a role in this search. In this chapter, I examine the role of landscape characteristics in determining food-chain lengths of species-rich Neotropical rivers, and impacts of river impoundment on vertical web structure.

METHODS

Study design and estimates of food-chain length

Stable isotopes were used to examine patterns of energy flow through 10 species-rich food webs of the Upper Paraná River basin, Brazil. Site descriptions and sampling methodology are described in Chapter II. I used a natural experiment approach to test for differences in food-chain length attributable to landscape-scale characteristics of each web. Each food web was classified according to landscape type following designations in Chapter II, and climatic zone, temperature regime and terrestrial landscape (Table 2) as determined using scale maps produced by the Instituto Brasileiro de Geografia e Estatística (publicly accessible at www.ibge.gov.br). Climate zones are determined based on combined annual patterns of monthly rainfall and temperatures. Temperature regimes are classified as hot (> 18°C during all months) or warm (between 15 and 18°C in at least one month). Terrestrial landscapes are either savanna or seasonal semi-deciduous forest (SSF).

Food-chain length was the maximum trophic position (MTP) observed for each web (see Post *et al.* 2000; Post 2002b). Trophic positions were calculated for species in each food web using the following equation:

$$TP = \lambda + (\delta^{15}N_{predator} - \delta^{15}N_{baseline})/F,$$

where λ is the trophic level of consumers estimating the food web base (in this case $\lambda = 2$ because primary consumers were used, see below), $\delta^{15}N_{predator}$ is the nitrogen isotopic signature of the predator being evaluated, $\delta^{15}N_{baseline}$ is the average nitrogen isotope signature of the consumers used to estimate the base of the food web, and F is the per trophic level fractionation of nitrogen. I used a $\delta^{15}N$ fractionation of 2.54‰ following the meta-analysis of Vanderklift and Ponsard (2003). An appropriate N baseline was calculated independently for each web using $\delta^{15}N$ signatures of fish species known from prior studies to be primary consumers (e.g. *Prochilodus lineatus, Liposarcus anisitsi, Metynnis maculatus, Schizodon* spp.). Other studies have used $\delta^{15}N$ signatures of bivalves and snails to estimate the pelagic and littoral base of the food web, respectively (e.g. Post 2002b). These approaches are fundamentally similar, as both use long-lived consumers to integrate temporal variability in source isotopic signatures. I chose to estimate the N baseline using fishes because they are larger, more mobile consumers than either snails or bivalves, and therefore provide greater temporal and spatial integration of source variability. Tissue turnover rates of these species are also more comparable to those of top-consumers because of their similar body size. In diverse tropical systems with high habitat heterogeneity, numerous sources potentially support secondary consumers (see Chapter II); in these systems fishes likely provide a more robust estimate of the baseline nitrogen signature.

Statistical analyses

Food-chain length (MTP) was compared among categories of each landscape characteristic independently using ANOVA. Landscape characteristics significant in independent tests were included in a multiple regression analysis to determine their relative contribution in determining food-chain length. In the multiple regression analysis, MTP was the dependent variable, and independent variables were coded as dummy variables. I tested for multicollinearity of independent variables using variance inflation factors (VIF). Stepwise selection was used to include independent variables significant at $P = 0.05$. Significant variables were only retained if they increased the adjusted R^2 by 0.1 or more, otherwise the reduced model was selected. All analyses were performed using SPSS v12.

Table 2 Food-chain length (FCL) and landscape-scale classifications for each food web. Category descriptions are provided in the text.

Food web	FCL	Landscape type	Climate Zone	Temperature Regime	Terrestrial Landscape
Iguatemi	4.12	Low-gradient river	Tropical central	Warm	Savanna
Ivinheima	4.19	Low-gradient river	Tropical central	Warm	Savanna
Paraná	4.09	Low-gradient river	Tropical central	Warm	Savanna
Piquiri	4.00	High-gradient river	Temperate	Warm	SSF
Ivaí	4.02	High-gradient river	Tropical central	Warm	SSF
Itaipu	4.25	Reservoir	Temperate	Warm	SSF
Rosana	4.34	Reservoir	Tropical central	Hot	SSF
Porto Primavera	4.35	Reservoir	Tropical central	Hot	Savanna
Paranapanema below Rosana	4.09	Below reservoir	Tropical central	Hot	SSF
Parana below Porto Primavera	4.30	Below reservoir	Tropical central	Hot	Savanna

RESULTS

Food-chain lengths ranged from 4.00 to 4.35 (Table 2), and were within ranges reported elsewhere in the literature (typically between 3 and 5 trophic levels, Pimm 2002). In independent comparisons, temperature regime ($F_{1,9} = 5.27$; $P = 0.051$) and landscape type ($F_{3,9} = 7.02$; $P = 0.022$) significantly affected food-chain length (Figure 9). Post-hoc comparisons found reservoir food-chains to be significantly longer than those of high-gradient rivers ($P = 0.017$), and only marginally not significantly longer than those of low-gradient rivers ($P = 0.092$). Within-habitat variation in food-chain length was greater for river stretches below reservoirs than the other landscape types (Table 2, Figure 9).

In the multiple regression analysis, the habitats 'reservoir' (β_1) and 'high-gradient river' (β_2) together explained 74.8% of the variation in food-chain length ($y = 0.155\beta_1 - 0.148\beta_2 + 4.16$; $F_{2,9} = 10.40$, $P = 0.008$), and 'reservoir' accounted for 54.2% of the variation in a reduced model. Inclusion of the dummy variable 'high-gradient river' in the model increased the adjusted R^2 from 0.48 to 0.68. The habitat category 'reservoir' was positively correlated with food-chain length, whereas 'high-gradient river' was negatively correlated.

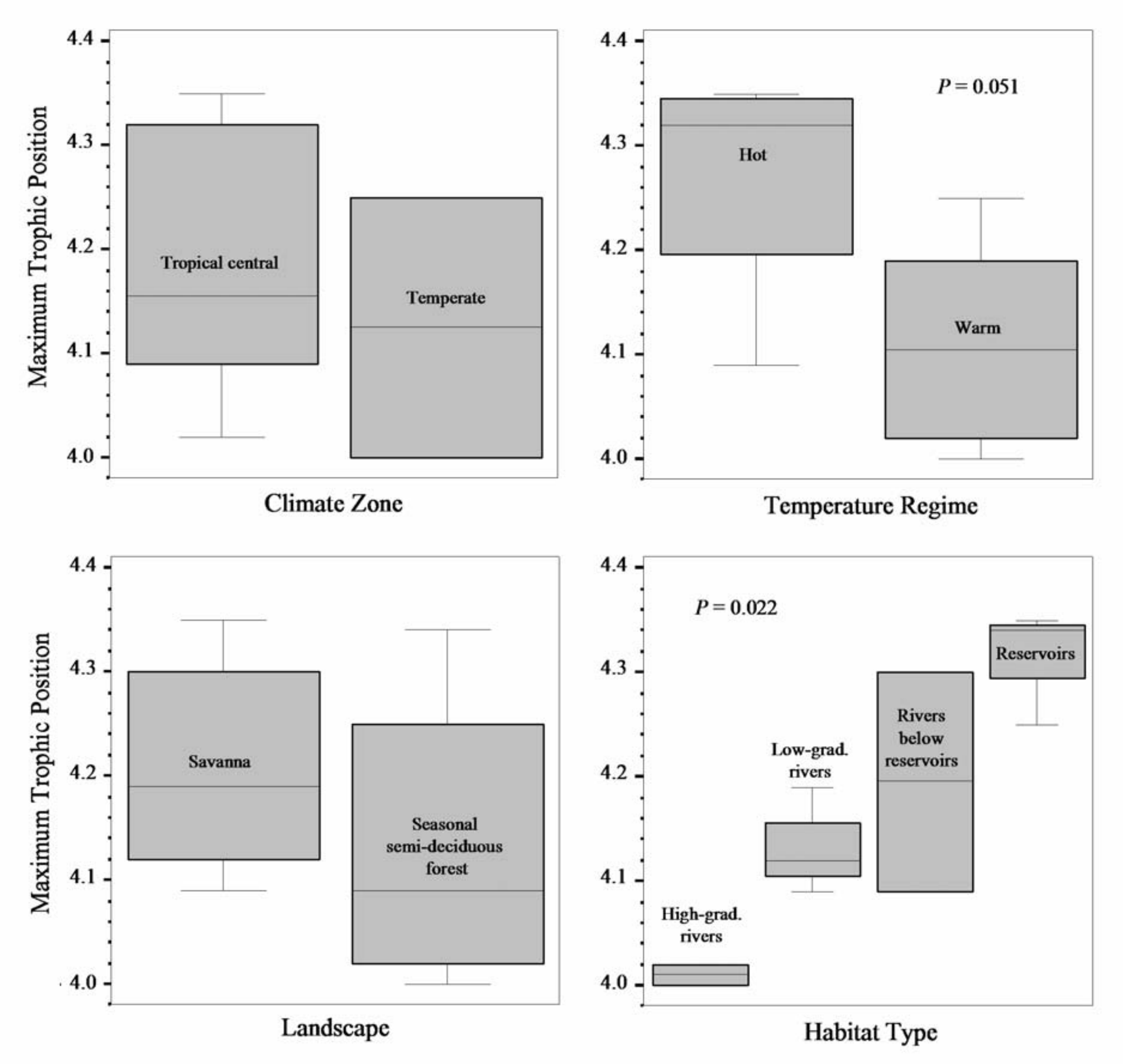

Figure 9 Boxplots depicting independent comparisons of food-chain lengths among different categories of landscape characteristics. Mean (solid line within box), quartiles (box) and range (whiskers) are present for each category.

DISCUSSION

Food-chain lengths of 10 species-rich food webs were found to differ significantly among landscape types. Temperature regime, which was correlated with food-chain length in independent analysis, did not significantly contribute to the explained variation in food-chain length after taking into account 'reservoir' and 'high-gradient river' landscape types in the multiple regression. The multiple regression model explained almost 75% of the variation in the length of food-chains across all sites, and can be interpreted as follows: food-chain lengths of low-gradient rivers and rivers below reservoirs are average or typical (although it is interesting that food-chain lengths of river stretches below reservoirs varied more widely), increasing the river elevational gradient decreases food-chain length, whereas impounding a river increases food-chain length.

The observed differences among food-chain lengths may initially appear slight (maximum difference of 0.35 trophic "levels"). A simplified representation of the 0.35 difference in food-chain length observed between high-gradient rivers and reservoirs is that approximately 35% of the energy reaching the top consumer in reservoirs compared to high-gradient rivers flowed through pathways with an additional trophic step. Several features of these food webs and other studies suggest that the differences in food-chain length observed in this study are actually quite substantial. First, the food webs examined in this study are extremely diverse. There are over 200 species of fishes (not to mention invertebrates) known to occur in the sampling region. Second, the trophic ecology of Neotropical fishes is also extremely diverse (Winemiller 1991). Aquatic food webs of Neotropical rivers are highly connected and omnivory is commonplace (see Winemiller 1990). Additionally, the observed difference in food-chain length is somewhat comparable to other non-experimental studies in less diverse aquatic environments discussed previously, i.e. the temperate lakes of Vander Zanden et al. (1999) and Post et al. (2000).

A larger difference was observed in Post et al. (2000) after ecosystem size increased enough to include a different piscivore (lake trout) that was not present in smaller lakes (similar to adding a trophic level as in experimental studies). Post et al. (2000) also attributed longer food-chains in larger lakes to decreased trophic omnivory. Like aquatic food webs of other Neotropical systems, the ones studied here are relatively more complex (including a greater frequency of omnivory) than those of temperate lakes, and relatively smaller differences in food-chain lengths across landscape types may therefore be expected. It is important to note that comparing different landscape types in this study did not “add” trophic levels, similar piscivore assemblages occurred at all study locations. What changed among webs was the relative number of links on the diverse and highly connected trophic pathways leading to top consumers. Longer food-chains correspond to a greater number of trophic transfers *within* the web, not by adding species to the top of it.

A problem with many studies investigating determinants of food-chain length is that mechanistic explanations are difficult to tease out of correlations. For example, both Post et al. (2000) and Vander Zanden et al. (1999b) found ecosystem size to correlate with food-chain length in north-temperate lakes. But what functional aspect of ecosystem size is important? As noted above, a combination of increased functional diversity and reduced trophic omnivory was suggested as the potential mechanism determining food-chain length in these systems (Post *et al.* 2000).

I suggest that the mechanism determining food-chain length in the present study is the relative importance of the pelagic trophic pathway to higher consumers. Fish faunas of tropical rivers are characterized by great niche diversification (Winemiller 1991), with a diversity of species that graze detritus, algae, plants and fruits/seeds (Goulding 1980; Lowe-McConnell 1987). These primary consumer species range in body size from some of the smallest to largest species in the food web, including optimally-sized prey for larger piscivorous species (Layman *et al.* 2005c; Hoeinghaus *et al.* In Press-b). On the other hand, zooplankton are the dominant primary consumers of the phytoplankton-based trophic pathway. Zooplankton are most efficiently consumed by small-sized fish species capable of plucking them from the water column. These small fishes are in turn consumed by larger pisicivores. The pelagic phytoplankton-based pathway may therefore include an added size-based trophic step skipped in other pathways in which fishes are primary consumers.

To test this hypothesis, I performed a linear regression of food-chain length against the mean and 99th percentile contribution estimates of phytoplankton (seston) to dominant trophic pathways of each web (from Chapter II). Food-chain length was positively correlated with the relative contribution of the phytoplankton based trophic pathway (Figure 10). The relationship between food-chain length and the 99th percentile estimate was highly significant ($F_{1,9} = 9.41$, $R^2 = 0.54$, $P = 0.015$), and the relationship was marginally significant for mean phytoplankton contribution ($F_{1,9} = 3.81$, $R^2 = 0.32$, $P = 0.087$). These results suggest that the added size-based trophic step of zooplankton associated with the relative importance of the phytoplankton-based pelagic pathway may be the mechanism behind landscape differences in food-chain length observed in this study. Study locations were selected based on landscape-scale hydrologic characteristics, which affected the relative importance of source contributions to consumers (Chapter II).

This mechanism may also apply to the Post et al. (2000) and Vander Zanden et al. (1999b) studies in temperate lakes. Increasing ecosystem size for lakes increases the relative proportion of pelagic vs. littoral zones. Contribution of zoobenthos to lake trout (top consumers in both of these studies) diets in northern lakes decreases dramatically with lake area, approaching zero for lakes >100 km^2 (Vadeboncoeur *et al.* 2002). A concomitant increase in the relative importance of the pelagic trophic pathway is observed. Differences in the size-structured nature of pelagic vs. littoral pathways may be a general determinant of food-chain length in aquatic systems. This hypothesis is more readily testable than the ecosystem size hypothesis, because pelagic vs. littoral contributions can easily be determined whereas an objective manner to determine ecosystem size is lacking for most natural systems (but see Cousins 1990).

Part of the mechanism proposed above is similar to the hypothesis of Hastings and Conrad (1979). In the absence of size-structuring, they argue that the evolutionary stable food-chain length should be near three. They reasoned that there is little evolutionary advantage to feeding on other carnivores, as herbivores are generally more

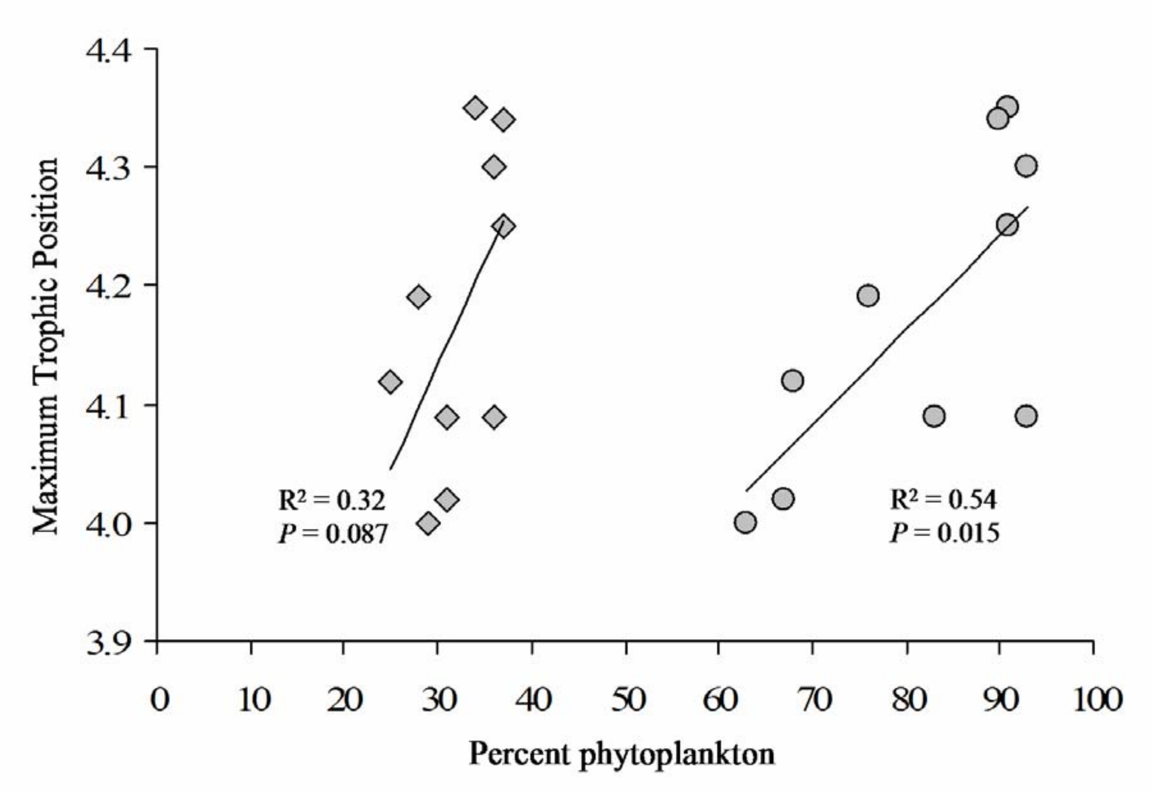

Figure 10 Relationships between the mean (diamonds) and 99th percentile (circles) contributions of the phytoplankton-based trophic pathway and food-chain length. Percent contribution data are from Chapter II.

abundant, less well protected, and provide similar nutritional value. However, later work suggested that the majority of food webs are size-structured with trophic level positively correlated with body size (Cohen *et al.* 1993). Most fishes engulf their prey whole, so predator-prey sizes in aquatic food webs are necessarily correlated. However, the great ecomorphological diversity of tropical fishes (i.e. wide range in body size of primary consumers) may allow piscivores to feed on optimally-sized prey while at the same time feeding low in the food web (Layman *et al.* 2005c). Differences in the relative importance of basal carbon sources to the food webs presented in Chapter II do not determine whether or not the food webs are size-structured – they all are. What changes is the ratio of body size between predators and primary consumers. Most large predators cannot efficiently feed on zooplankton, so an additional consumer species is needed to complete the chain. Like terrestrial mammal communities (which are generally not size-structured, Hairston & Hairston 1993), tropical fish communities may be expected to exhibit short food-chains when phytoplankton carbon is a minor contributor to the food web.

Productivity probably does not limit food-chain length of the webs studied here. Although productivity data are not available for all sites, the chain of reservoirs along the Paranapanema River and mainstem Paraná River are known to sequentially reduce aquatic primary productivity by retaining large amounts of phosphorous through sedimentation (Agostinho *et al.* 1995). Low-gradient and high-gradient rivers are assumed to have higher productivities because they drain similar landscapes but lack reservoirs. Contrary to expectations of the energetic hypothesis, food-chain lengths were longer in the least productive habitats (reservoirs).

Human alteration of communities may also affect food-chain length, both directly through over-harvest or species introductions, and indirectly by affecting other factors that may determine food-chain length (e.g. hydrology, connectivity). Several fish species have been introduced to the Upper Paraná Basin (Thomaz *et al.* 2004a), but their role in the food web differs among habitats (discussed in Chapter IV). For example, the curvina *Plagioscion squamosissimus* (purposefully introduced from the Amazon Basin to reservoirs of southern Brazil) is found throughout the basin, except the high-gradient rivers. It is especially well adapted for reservoirs, and is the top-consumer of both the Porto Primavera and Rosana Reservoir food webs. However, longer food-chains of reservoirs are probably not attributable to the addition of the curvina, as this species is also found in low-gradient rivers and below reservoirs, where it does not occupy the highest trophic positions.

Direct exploitation of commercial species may also affect food-chain length. Contrary to "fishing down" marine food webs (Pauly *et al.* 1998), over-exploitation of large primary consumers important in tropical river fisheries (Welcomme 1985) may "fish up" these webs as large piscivores shift their diet to include prey occurring higher in the food web (Layman *et al.* 2005a). Additionally, many of the large primary consumer species occurring in the Upper Paraná Basin are migratory, and have experienced population declines due to disruption of migration routes and flood height and timing caused by river impoundment (Agostinho *et al.* 2004b). The roles of predator-prey body size ratios (Jennings & Warr 2003) and differences in abundance of size-classes within and across trophic levels in size-structured webs needs to be evaluated further.

Faunas of all the food webs examined here are part of the same regional species pool, so differences among communities are predominantly determined by environmental factors that distinguish the landscapes (i.e. hydrology). Hydrology has been shown to strongly affect the functional characteristics of fish communities (Poff & Allan 1995; Lamouroux *et al.* 2002; Hoeinghaus *et al.* In Press-a), and the relative contributions of sources supporting secondary production in the food webs examined here (Chapter II). Landscape-scale hydrologic characteristics (i.e. river gradient or water residence time) also affected food-chain length at the study locations. High-gradient rivers had the shortest food-chains and reservoirs the longest. The relative importance of pelagic trophic pathways to the food web, corresponding to the size-structured aspect of the phytoplankton – zooplankton trophic link, appears to be the mechanism driving this pattern. The functional relationship between hydrology, species attributes and food-chain length deserves more attention.

CHAPTER IV

EFFECTS OF RIVER IMPOUNDMENT AND INTRODUCED SPECIES ON ECOLOGIC AND ECONOMIC EFFICIENCY OF FISHERIES PRODUCTION

INTRODUCTION

Natural ecosystems provide numerous goods and services that are the life-support systems of our planet (Daily 1997). Ecosystems can be considered renewable natural capital in that they may be renewed using a portion of the original stock and solar energy (Costanza & Daly 1992). This renewable natural capital produces a flow of natural income that may be harvested as ecosystem goods (e.g. fisheries) and yield a flow of ecosystem services (e.g. nutrient cycling, climate regulation) when left in place. These goods and services contribute directly and indirectly to human welfare, representing a significant component of our global economic value (Costanza *et al.* 1997; Balmford *et al.* 2002). Production of manufactured capital (e.g. buildings) and human capital (e.g. education and culture) requires reorganization of energy bound in renewable and non-renewable natural capital (Costanza & Daly 1992). Therefore, available energy and its use govern the structure of our societies and global economy (Costanza 1980).

Food webs can describe the flow of energy through the complex trophic structure of biological systems, and therefore provide an appropriate ecological scale for investigating some aspects of ecosystem services (Kremen 2005). Additionally, food web structure may determine population abundances (Pace *et al.* 1999) and the ecological efficiency of secondary production (Humphreys 1979), i.e. the availability and direct energetic cost of ecosystem goods. Indirect or direct changes to the biological structure, including food web structure, of an ecosystem may affect its ability to provide important services valued by humans (e.g. Bunker *et al.* 2005; Larsen *et al.* 2005).

One such ecosystem service common to many large tropical rivers is fisheries production (Welcomme 1985, 1990; Holmlund & Hammer 1999; Allan *et al.* 2005; Winemiller 2005). In developing countries, fisheries may provide the majority of dietary protein consumed by local and regional communities, and economic opportunities of last resort for many low-income families in rural areas (Allan *et al.* 2005). In a human-dominated world (Vitousek *et al.* 1997), managing ecosystem services, such as fisheries production, requires understanding how human impacts affect the ecology of the key species or functional groups providing the services (Kremen 2005; Farber *et al.* 2006); only a handful of services have been investigated in this manner (Kremen & Ostfeld 2005).

Hydrologic impoundment is a common impact to large-river ecosystems that affects aquatic community structure and function through ecosystem fragmentation and isolation, selection for native species pre-adapted for lentic conditions, facilitation of species invasions (Allan & Flecker 1993; Moyle & Light 1996a), and modification of patterns of energy flow and trophic structure (Chapters II and III). In this chapter, I use fisheries landings data from before and after closure of Itaipu Reservoir and trophic characteristics of the fishery to provide a unique assessment of effects of river impoundment on this important ecosystem service. I assessed impoundment effects in two ways, the energetic costs of fisheries production, and the commercial market value of the dominant species in the fishery.

METHODS

The aspect of trophic structure important to the present analysis are the relative trophic positions (internal web structure) of species captured in artisanal fisheries of Itaipu Reservoir. Because energetic assimilation efficiency is around 10% (Humphreys 1979), a consumer feeding at tropic level four is approximately 10 times more energetically costly for the ecosystem to produce than a consumer of the same biomass feeding at trophic level three, and 100 times more costly than a primary consumer. Comparisons of species trophic positions depict relative efficiency of production, where lower trophic position consumers are more ecologically efficient in terms of energy assimilation than higher trophic level consumers.

Relative trophic positions reflect energy directly assimilated in the biological production process. This is only half of the story, because fisheries production is an ecosystem good which requires additional energy associated with harvesting before it can be appreciated by human society. The total amount of energy associated with the harvesting component of fisheries (e.g. energy bound in the fisherman's labor, boat, fuel, materials, knowledge, etc.) is extremely difficult to estimate. However, trends in catch per unit effort (CPUE) may be used as a surrogate for the energy expended to harvest a given biomass of fish. The combined direct plus indirect energy required to produce an ecosystem good or service is its embodied energy (Costanza 1980), and is fundamentally equivalent to the *emergy* concept as described in Odum (1988).

Because fisheries production is an ecosystem good that is captured by the commercial market (unlike many other ecosystem services), effects of river impoundment on fisheries can also be assessed in terms of the actual market value of dominant species comprising the fishery. Species were separated into locally used commercial classes (Table 3), and the relative proportion of fisheries landings of each class before and after impoundment was evaluated. Class groupings are based on such factors as quality of the flesh, fish size, and traditional acceptance in the market. Smaller individuals of high-value species are sold in lower commercial classes; for this reason, some species are separated into size-classes in our analyses to correspond with sizes represented in different commercial classes.

Long-term data on annual fisheries landings are available for Itaipu Reservoir before and after closure (Agostinho *et al.* 2005a; Okada *et al.* 2005), and are presented here for the years 1977 (five years before impoundment), 1987 (five years after impoundment) and 1997 (15 years following impoundment). Species trophic positions (determined following methodology in Chapters II and III) are not available for earlier periods, and trophic position estimates were not extended to earlier years as diets may have changed somewhat over time with changes in species relative abundances. However, trophic classifications (e.g. piscivore, omnivore, detritivore) are possible, allowing discussion of general trends in ecological efficiency. Fishery CPUE is only available for the period following dam closure (1987-2004), limiting evaluation of

Table 3 Commercial classification of fish species captured in artisanal fisheries of the Upper Paraná River basin, Brazil (modified from Agostinho *et al.* 2005a). Highest market values (by weight) are for fishes in Class I, and decrease with increasing Class number.

Class	Description
I	"Pescado de primeira" - large fishes with high-quality flesh traditionally consumed in the region, especially several long-distance migratory species (e.g. *Pseudoplatystoma corruscans, Salminus brasiliensis*)
II	medium to large migratory species with high fat content "carne remosa" (e.g. *Paulicea luetkeni*, large *Pinirampus pirinampu*); smaller individuals of Class I species; largest individuals of species not historically accepted in the market (e.g. *Cichla* sp., *Plagioscion squamosissimus*) are occasionally sold in this category
III	larger armado *Pterodoras granulosus* and "cascudo" (armored catfishes), which have high palatability yet consumer restrictions because of their appearance (even when filleted); large individuals of *Prochilodus lineatus*; most individuals of *P. pirinampu*
IV	constitutes the majority of captures - small to medium-sized individuals of various species which are sold together under the term "misto" (mixed); includes almost all *P. squamosissimus*, and three of the other top species in the commercial catch (*Hypopthalmus edentatus, Hoplias malabaricus, Pimelodus maculatus*); also individuals < 30 cm of species sold in higher classes
Other (*)	many species of small size which are generally discarded, fed to domestic animals or used as bait; also medium to large species with numerous bones (e.g. *Rhaphiodon vulpinus*) and culturally unaccepted species such as piranhas (Serrasalmus spp.) and stingrays (*Potamotrygon motoro*); some may be sold as Class IV after being filleted, or donated to low-income households during certain times of year associated with religious observations (e.g. Lent)

embodied energy before and after impoundment. However, it is known that start-up and operational costs of the fishery were less prior to closure of the reservoir (Agostinho *et al*. 2005). Some species currently important in the fishery were not present or targeted before impoundment, and thus were not part of the market. We assume that general market classifications remained roughly the same throughout the period. Although largely qualitative, this study provides a unique assessment of potential impacts of river impoundment on fisheries production by identifying trends in ecological and economic aspects of the fishery over time.

RESULTS

Fisheries landings of Itaipu Reservoir (and the Paraná River prior to impoundment) have changed dramatically over the last 30 years. In 1977, five years prior to closure of the reservoir, over 90% of the landings were comprised by eight large migratory species (Figure 11, Agostinho *et al.* 1999). Three of the eight species (approximately 35% of landings) feed low in the food web: *Piaractus mesopotamicus* (~20% of landings) consumes plants, fruits, and insects; *Prochilodus lineatus* (~10%) grazes detritus/sediment; *Brycon orbignyanus* (5%) feeds on fruits and some insects. The top four species (*Paulicea luetkeni, P. mesopotamicus, S. brasiliensis,* and *P. corruscans*), which represented approximately 75% of the landings, are all sold in local markets in the highest commercial classes (Class I or II). All of the species important in the artisanal fishery were native.

By 1987, five years following impoundment, the high-value species that dominated the fishery in 1977 contributed a combined 5% to fisheries landings (Figure 11). Lentic conditions of the reservoir and the pulse of production in the first few years following impoundment led to increases in the fishery yield of *P. lineatus*, *H. edentatus*, *P. squamosissimus*, and *P. granulosus* (Figure 11). *Prochilodus lineatus* and *H. edentatus* both feed low in the food web (detritivorous and planktivorous, respectively), whereas *P. squamosissimus* and *P. granulosus* feed higher in the food web (piscivorous and omnivorous, respectively). These species all have relatively low market values (Table 3).

The relative fishery yield of *P. lineatus* had fallen back to pre-impoundment levels by 1997, whereas *P. granulosus* and *P. squamosissimus* increased greatly (Figure 11). Decreases in stocks of *H. edentatus* to present day conditions (8.3% total landings; Figure 12) correspond with increased abundance of *P. squamosissimus* (14.4%), which preys heavily on young *H. edentatus* in the pelagic zone (Ambrósio *et al.* 2001). With the decreased importance of *P. lineatus* and *H. edentatus*, the fishery is dominated by higher trophic position (ecologically inefficient) species. The species are also of low commercial value (Table 3).

Total fisheries yield of Itaipu Reservoir followed a general decreasing trend from 1987 to 2004 (from 1600 to 530 tons, Agostinho *et al.* 2005a; Okada *et al.* 2005). During the same period, CPUE decreased by almost 65%, from a mean of 23.2 kg $\text{fisher}^{-1}\text{day}^{-1}$ in 1987 to 8.7 kg $\text{fisher}^{-1}\text{day}^{-1}$ in 2004 (Agostinho *et al.* 2005a; Okada *et al.* 2005). This decline in CPUE represents an increase in the relative harvest cost (indirect

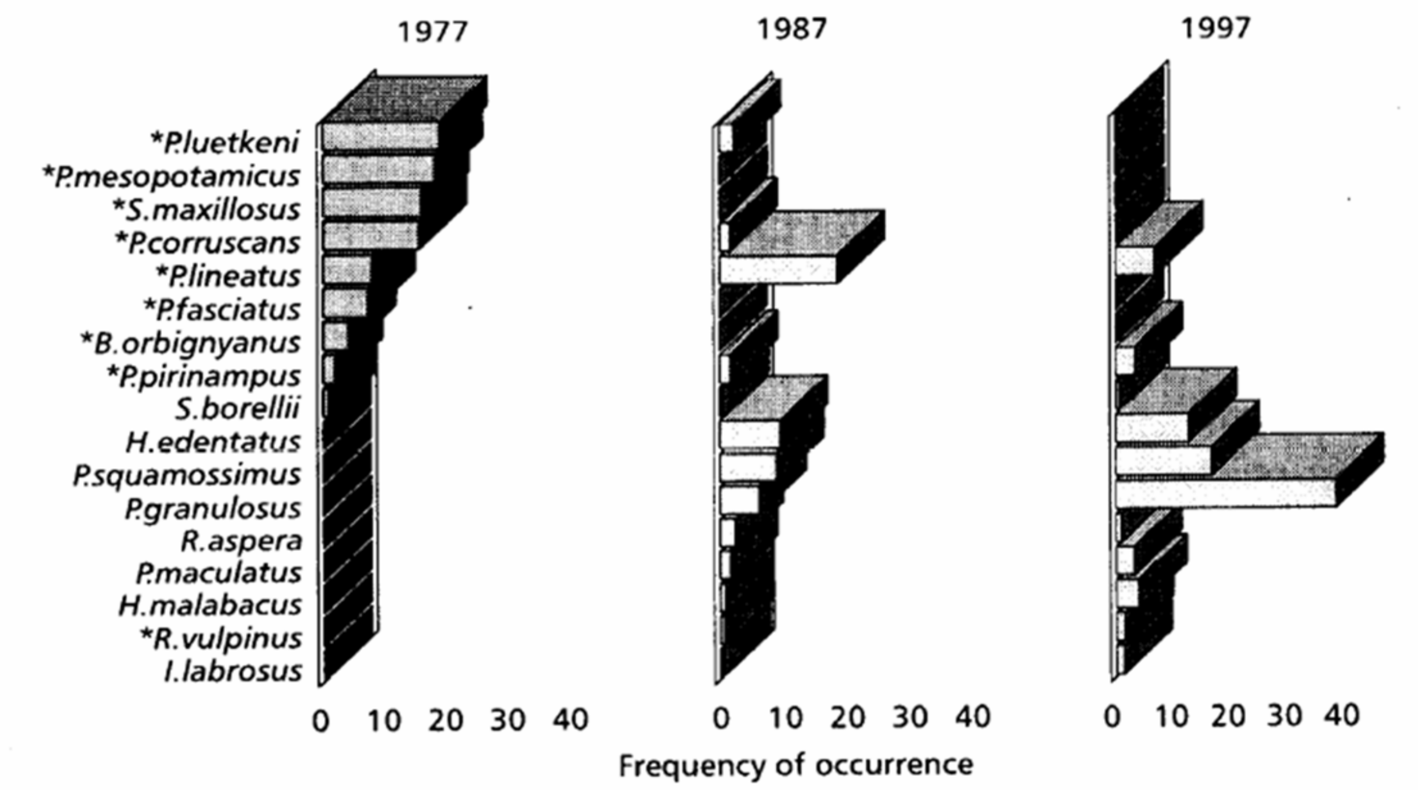

Figure 11 Species frequency of occurrence in commercial fishery landings before (1977) and after impoundment of Itaipu Reservoir (1987 and 1997). Species denoted with an * attain lengths > 60 cm. From Agostinho et al. (1999). [*S. maxillosus* = *S. brasiliensis*]

energetic cost) per kg of the fishery. When combined with the increase in direct energetic cost of production (decreased ecological efficiency) shown above, the embodied energy per kg of the fishery increased greatly from 1987 to 1997. Embodied energy of the fishery prior to closure of the reservoir cannot be put on the same scale because CPUE is not available. However, indirect energetic costs of harvest infrastructure were lower than after dam closure (Agostinho *et al.* 2005a). Added to the relatively moderate direct energetic cost of production, the low indirect energetic costs yield a low to moderate embodied energy for the fishery prior to impoundment. Relative direct and indirect costs of production, embodied energy, and commercial classification of the fishery for 1977, 1987 and 1997 are summarized in Table 4.

Trophic position estimates are available for the most recent year, and allow a more quantitative evaluation of the energetic efficiency of the fishery. In 2004, five species accounted for almost 75% of the total landings (Figure 12): *Pterodoras granulosus* (43.33%), *Plagioscion squamosissimus* (14.41%), *Hypopthalmus edentatus* (8.30%), *Pinirampus pirinampu* (5.63%), and *Hoplias malabaricus* (3.17%). All of these species occupy relatively high trophic positions, except *H. edentatus* which is planktivorous (Figure 12a). Trophic position followed an increasing trend with increasing importance in the landings, reaching an asymptote at an approximate trophic position of 4 (Figure 12a). Approximately 80% of the fishery catch was comprised of high trophic-position species. Based on a 10% efficiency of energy assimilation, these species are 10-100 times more energetically costly to produce per kg than low trophic position species such

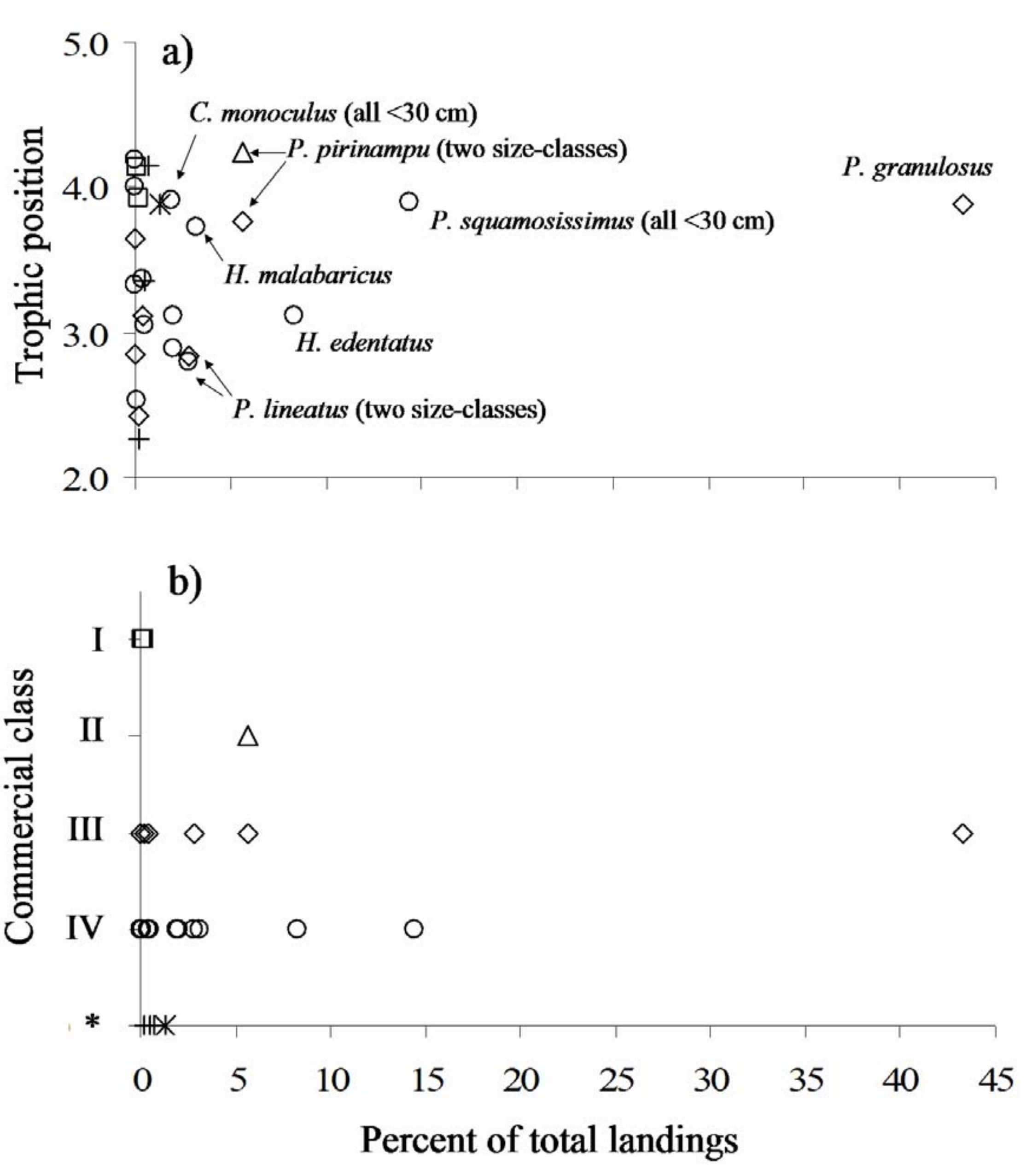

Figure 12 Trophic position (a) and commercial classification (b) of dominant species in fishery landings from Itaipu Reservoir in 2004. Landings data from Agostinho et al. (2005), classifications follow Table 3. Commercial class I = □, class II = △, class III = ◇, class IV = ○, other = *. The class "other" is further subdivided into species with no market value (+) and species which may be sold in class IV following additional preparation of the filet (✳).

as *H. edentatus* and *P. lineatus* which dominated the fishery in the early stages of reservoir development.

At the same time, commercial classification of the species decreased with increased importance in the landings (Figure 12b). Approximately 95% of the landings are categorized in the lower two commercial classes (large barbado *P. pirinampu* are the only exception). Species with high trophic positions that also command high market values, such as the class I species dourado *Salminus brasiliensis* and pintado *Pseudoplatystoma corruscans*, contributed little to fisheries landings in 2004 (0.12 and 0.21% respectively, Figure 12). Low trophic-position (ecologically efficient) species sold in the lowest commercial classes (especially Class IV, Table 3) composed approximately 15% of the total landings (Figure 12).

Table 4 Relative embodied energy and market value of the Itaipu fishery before and after closure of the reservoir in 1982. Embodied energy is divided into the direct energetic cost of production and the indirect cost associated with harvesting (see text).

	1977 (5 yr before)	1987 (5 yr after)	1997 (15 yr after)
Embodied energy	Low-Med	Low-Med	Very High
Direct cost	Med	Low	High
Indirect cost	Low	Med	High
Market value	High	Low	Low

DISCUSSION

Sustainability requires that a certain quantity and quality of natural capital be maintained to provide the flow of ecosystem goods and services on which our society depends (Costanza & Daly 1992). Because many ecosystem services are not captured by commercial markets or are not quantified in comparable terms with economic services, they are generally undervalued in decisions regarding the use of natural capital (Costanza & Daly 1992; Rapport *et al.* 1998; Farber *et al.* 2002; Farber *et al.* 2006). This undervaluation threatens sustainability. To remedy this shortcoming, numerous methods of valuing ecosystem services relative to other forms of capital have been developed (Bingham *et al.* 1995; Alexander *et al.* 1998; Costanza *et al.* 1998; Heal 2000; Pritchard *et al.* 2000; Farber *et al.* 2002; Howarth & Farber 2002; Turner *et al.* 2003; Farber *et al.* 2006; Hein *et al.* 2006). One such method is the energetic value of capital, i.e. the total amount of energy utilized directly and indirectly in the production of that capital (Costanza 1980; Odum 1988; Odum & Odum 2000). Comparisons between methods of valuation, such as energetic value and market value presented here, may be especially informative (e.g. Costanza 1980; Cleveland *et al.* 1984).

In general, the combined impacts of river impoundment appear to have initially increased the ecological efficiency of fisheries production. Five years following closure of the reservoir, the relative contribution of species that feed low in the food web (i.e. relatively more ecologically efficient) was greater than before dam closure, most notably the algivore/detritivore *P. lineatus*. This is likely the result of the pulse of production and decomposition that occurs in early stages of reservoir ecosystem development

(Agostinho *et al.* 1999). Although the ecological efficiency of production increased, the relative market value of the fishery decreased greatly due to reduced catches of high-value species such as dourado and pintado.

Ten years later, fisheries landings were dominated by the omnivore *P. granulosus* and piscivore *P. squamosissimus*, reflecting a large decrease in the ecological efficiency of fisheries production (i.e. greater direct energetic cost of production). Fishery CPUE also decreased, representing increased indirect cost of production (harvest costs). The embodied energy of the fishery increased markedly during this period. Although the energetic cost of the fishery increased, the market value remained low. To obtain the same income as before impoundment, present-day fishermen generally need to sell at least four times the biomass of fish (Agostinho *et al.* 2005a).

Contemporary fisheries of the reservoir are energetically costly and commercially undervalued. This mismatch is further exacerbated by interactions, such as reduction of *H. edentatus* populations through predation by *P. squamosissimus* (Ambrósio *et al.* 2001; Gomes & Miranda 2001b). These species have similar market values, but *H. edentatus* is more than 10 times less energetically costly per kg to produce than *P. squamosissimus* because of its lower trophic position. A similar trend is observed in Porto Primavera and Rosana Reservoirs. In both, *P. squamosissimus* dominates the pelagic zone, as few native species of the Upper Paraná basin are pre-adapted for lentic environments of reservoirs (Gomes & Miranda 2001b). *Hypopthalmus edentatus* is also well adapted for lacustrine conditions, but as in Itaipu Reservoir, populations of this species may remain low through predation by *P.*

squamosissimus. Ironically, *P. squamosissimus* was introduced from the Amazon Basin into reservoirs of the Paraná basin to increase fishery yields.

River impoundment facilitates species introductions by altering biotic interactions and abiotic conditions (Moyle & Light 1996a). Several of the species that dominate fishery landings following impoundment are non-native. *Pterodoras granulosus* and *H. edentatus*, along with more than 20 other species, colonized the Upper Paraná following inundation of Sete Quedes waterfalls (a former biogeographic barrier) upon closure of Itaipu Reservoir (Bonetto 1986; Agostinho *et al.* 2004a). The curvina *P. squamosissimus* was stocked in several reservoirs of southern Brazil, and is now widespread.

Colonization by non-native species may have affected reservoir food webs in many ways. Longer food chains are observed in reservoirs of the Upper Paraná basin, but this is likely not the cause of species introductions, but appears to result from a shift in the relative importance of phytoplankton to trophic pathways leading to top consumers, and associated predator-prey body size ratios (Chapters II and III). On the other hand, introduced species greatly affected the market value of the fishery. With the reduction in stocks of migratory species of high commercial value due to blockage of migration routes and impacts of dam operations on the hydrologic regime (Agostinho *et al.* 2003; Agostinho *et al.* 2004b), non-native species increased in importance to the fishery. Although several of these species are highly palatable, they have low market values due to consumer preferences for species traditionally consumed in the region.

Small-scale artisanal fisheries and subsistence- and sport-fisheries of free-flowing rivers of the Upper Paraná basin target large native species such as catfishes (*P. corruscans, P. pirinampu*), curimba *P. lineatus*, piaparas *Leporinus* spp., dourado *S. brasiliensis*, traíra *H. malabaricus*, and only more recently the non-native armado *P. granulosus* (Petrere Jr. *et al.* 2002). Large migratory species are especially important to local fisheries during the piracema (seasonal migration), as upper reaches of these rivers are important spawning sites for migratory fish populations between Itaipu Reservoir and the reservoirs upstream (Agostinho *et al.* 1993; Vazzoler *et al.* 1997). The trophic and economic characteristics of these fisheries are similar to those described above for the Itaipu region before impoundment: both high- and low-value species feeding at a variety of trophic positions are present in fisheries catches. Introduced species, i.e. *P. squamosissimus* and *Cichla* spp., appear in catches from low-gradient rivers, but they do not dominate fisheries. High-gradient rivers of the basin are essentially free of exotic and dispersed species (Agostinho *et al.* 2004a), as high water velocities appear to limit colonization by some invasive species (Moyle & Light 1996b). For the Upper Paraná basin in general, species harvested by fisheries of free-flowing rivers are characterized by greater ecological efficiency and higher commercial value in comparison with species caught in reservoir fisheries.

Large alterations in the fish communities of both impounded and free-flowing stretches of the Upper Paraná basin have resulted from, or been facilitated by, river impoundment (Agostinho *et al.* 1995; Agostinho *et al.* 2000; Agostinho *et al.* 2004b; Thomaz *et al.* 2004a). Aquatic communities of sites that are now reservoirs experienced local extirpations of some species and increases in abundances of others (generally omnivores and piscivores) as the aquatic habitat abruptly changed from lotic to lentic (Agostinho *et al.* 1999). Lower numbers of long-distance migrants (e.g. *P. luetkeni, S. brasiliensis, B. orbignyanus*) utilize free-flowing rivers for seasonal spawning as populations have declined due to blockage of upstream migration routes, reduction of floodplain area and alteration of flood height and duration (Gomes & Agostinho 1997; Agostinho *et al.* 2003; Agostinho *et al.* 2004b). The effects of migratory species on their recipient communities may be large and varied, as aquatic communities respond to the transport of biomass and nutrients into the system (Polis *et al.* 1997; Winemiller & Jepsen 1998; Vanni *et al.* 2002). For example, migratory fishes of other tropical and temperate river basins have been shown to provide important nutritional subsidies to resident piscivores (e.g. MacAvoy *et al.* 2000; Winemiller & Jepsen 2004; Hoeinghaus *et al.* In Press-b), and may affect food web structure and ecosystem processes such as the relative importance of bottom-up vs. top-down control (e.g. Flecker *et al.* 2002; Winemiller *et al.* 2006). Further studies are needed to address these aspects of fish migration on food webs of the Upper Paraná basin and ecosystem services.

River impoundment significantly reorganized the commercial fishery of Itaipu Reservoir. The contemporary fishery yields lower biomass, at greatly higher per kg direct and indirect energetic cost, and lower market value. This ecological inefficiency may contribute to further declining yields. At the same time, because of the role of species identity in determining market value, the declining catches may continue to bring low commercial values to artisanal fishermen. These trends raise important social considerations, especially since the people most directly affected (the fishermen) have already been forced to the margin of society and in many cases have no legal economic alternatives (Allan *et al.* 2005; Okada *et al.* 2005).

Improvement in human welfare generally results from economic growth or development. Growth is an increase in the flow of energy through the economy (increased harvest of natural capital), whereas development is an increase in the economic yield of a given amount of energy (i.e. increased efficiency) utilized in the economy (Costanza & Daly 1992). Development does not occur at additional expense of natural capital and may be sustainable, whereas growth is ultimately not. The present evaluation shows that over the last few decades, the Itaipu fishery has experienced both negative growth (decreased yield) and perhaps even more importantly negative development (greatly increased embodied energy per kg harvested). Without outside assistance (e.g. state or federal aid or policy) or feasible economic alternatives (e.g. development of a fishery for ornamental species, see Pelicice & Agostinho 2005), the economic welfare and social condition of the fishermen and their families is not likely to increase by sustainable or even non-sustainable means.

CHAPTER V

SUMMARY AND FUTURE DIRECTIONS

Determinants of food web structure are poorly understood in general, and even more so for species-rich large-river systems. Limited understanding of the functional dynamics of large-rivers hinders our ability to manage, conserve and restore these important ecosystems. In this study, I described differences in emergent food web characteristics of several large tropical rivers distinguished at the landscape-scale. My results suggest that hydrologic characteristics may be a dominant structuring mechanism of freshwater food webs. The relative importance of carbon sources fueling dominant trophic pathways (Chapter II) and food-chain length (Chapter III) were significantly affected by hydrologic characteristics which defined landscape types (low-gradient river, high-gradient river, river stretches immediately downstream of reservoirs, and reservoirs). Figure 13 illustrates landscape-scale hydrologic effects on emergent properties of the food webs studied. Size-structured trophic relationships associated with the relative importance of phytoplankton to the food web appear to be the mechanism driving differences in food-chain length across habitats (Chapter III). Longer food-chains of reservoirs result in decreased ecological efficiency of fisheries production, which is dominated by non-native species of low commercial value that are better adapted for lentic environments of reservoirs than high-value native species (Chapter IV). The differences observed among landscape types portray substantial impacts of hydrologic modification such as river impoundment on aquatic food web structure and function.

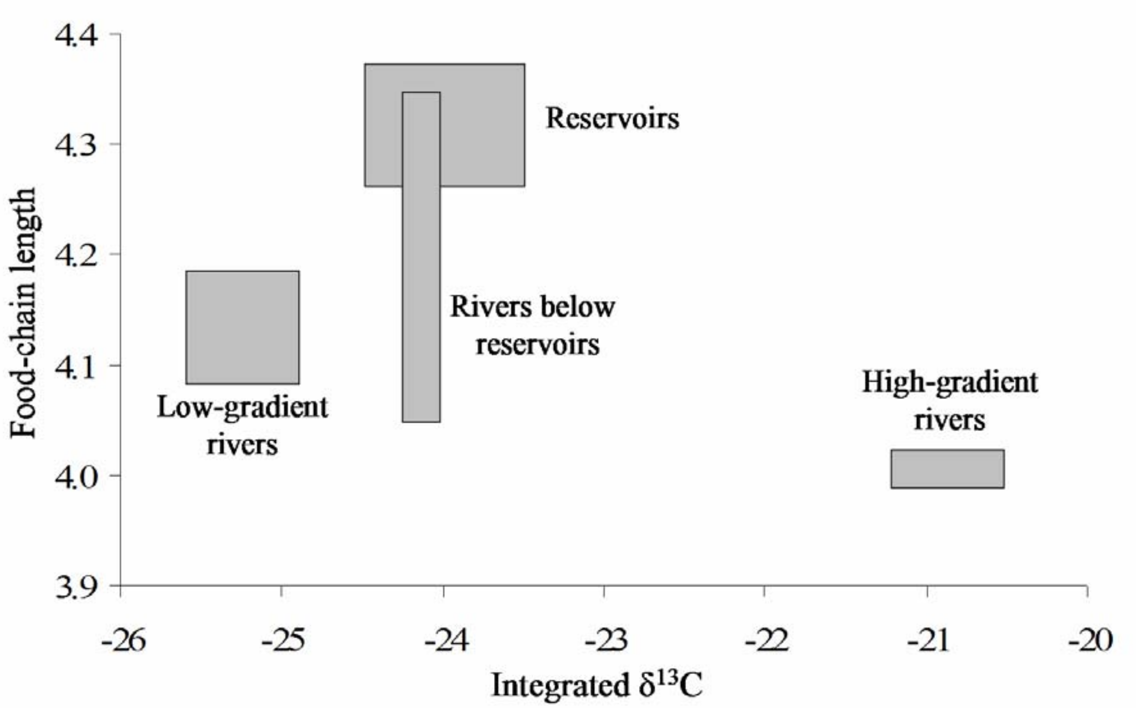

Figure 13 Divergent food web properties of rivers with different hydrologic characteristics (see Chapters II and III). Integrated $\delta^{13}C$ represents the relative importance of carbon sources to dominant trophic pathways. Boxes are means ± 1 S.D. Landscapes are significantly different (MANOVA: $F_{6,10} = 16.11$, $P < 0.001$; DFA: 100% correct classification).

TOWARDS A HOLISTIC MODEL OF ENERGY FLOW FOR LARGE-RIVER FOOD WEBS

Among habitat differences in the relative importance of carbon sources to aquatic food webs observed in Chapter II may represent hydrological-based generalities applicable to other river systems. In the present study, metazoan food webs of low-gradient rivers with intact floodplains followed predictions of the Flood Pulse Concept (Junk *et al.* 1989), whereas other habitats agreed better with predictions of the Riverine Productivity Model (Thorp & Delong 1994, 2002). Predictions of the River Continuum Concept (Vannote *et al.* 1980) were not supported for the large-river metazoan food webs examined, even in free-flowing rivers, and may be more applicable to lower-order river segments or during winter months in temperate climates (see Sedell *et al.* 1989; Huryn *et al.* 2001).

These generalizations reconcile competing models of energy flow in large-river food webs, especially in regards to hydrologically impacted river systems, and provide insights towards a more holistic model of energy flow for riverine food webs. While viewing rivers as a longitudinal continuum is important, segments with distinct geomorphology and hydrology can also be identified (e.g. as in Thorp *et al.* 2006). Food webs of low-order streams in the upper reaches of a river basin are expected to derive a large portion of their energy from allocthonous sources, as in the RCC. In larger rivers, consumers in higher-gradient segments with narrow floodplains (or river segments isolated from the floodplain through channelization) are expected to derive most of their energy from algae and secondarily from vascular plant production in the littoral zone. In lowland segments with well-developed floodplains, aquatic food webs are expected to be based heavily on floodplain production (with the importance relative to flood pulse predictability and seasonal synchronization). Impounded river segments, and those just below reservoirs, are expected to be driven largely by phytoplankton production.

Future work is needed to address temporal variation in a landscape framework, especially seasonal variation in the relative importance of carbon sources to aquatic consumers in different hydrologic segments. In addition to seasonal comparisons among segments within the same river, subsequent studies should also compare energy flow among river segments of systems typified by different temperature-rainfall regimes (e.g. temperate-aseasonal, temperate-seasonal, tropical-seasonal, see Winemiller 2005). The role of long-distance migratory species on food web dynamics also need to be addressed further, especially in the context of nutrient and biomass transport between river segments. More detailed trophic relationships of key species (e.g. migratory species and their consumers) may be examined using a combined dietary/stable isotope approach (e.g. as in Winemiller & Jepsen 2004; Hoeinghaus *et al.* In Press-b).

DETERMINANTS OF FOOD-CHAIN LENGTH

At present there is no consensus on which factors determine the length of food-chains; classic theories have been called into question, and new hypotheses (e.g. ecosystem size) lack mechanisms. In his review of the determinants of food-chain length, Post (2002a) called for a broader investigation of when and where a variety of factors may contribute to determine the length of food-chains. In Chapter III, I demonstrated the importance of hydrology in determining the length of food-chains in different aquatic landscapes. Shortest food-chains were observed in high-gradient and low-gradient rivers, and longest food-chains were observed in reservoirs. The mechanism that appears to drive this pattern is the relative importance of the phytoplankton-based pelagic trophic pathway that includes a size-based trophic step of zooplankton that may be bypassed in other pathways. Fish faunas of the tropics are characterized by high ecomorphological diversity (Winemiller 1991), including many medium to large-bodied species that consume detritus, filamentous algae, vascular plants and fruits/seeds. Contrary to the phytoplankton-based pathway, trophic pathways based on these sources may be shorter as large piscivores are able to consume optimally-sized prey that feed low in the food web (Layman *et al.* 2005b).

The mechanism proposed above may apply to earlier studies of food-chain length in north temperate lakes (i.e. Vander Zanden *et al.* 1999b; Post *et al.* 2000). This hypothesis is more readily testable than the ecosystem size hypothesis, because pelagic vs. littoral contributions can easily be determined whereas an objective manner to determine ecosystem size is lacking for most natural systems. The proposed mechanism needs to be evaluated in other aquatic habitats with faunas of different levels of ecomorphological diversity. More generally, the roles of predator-prey body size ratios and differences in abundance of size-classes within and across trophic levels in size-structured food-webs requires further evaluation.

EFFECTS OF RIVER IMPOUNDMENT ON ECOSYSTEM SERVICES

Natural ecosystems provide numerous goods and services that are the life-support systems of our planet (Daily 1997). In a finite world of natural capital, how we harvest or reorganize that capital directly affects the life-support function of ecosystems. Sustainability requires that a certain quantity and quality of natural capital be maintained to provide the flow of ecosystem goods and services on which our society depends (Costanza & Daly 1992). Managing ecosystem services requires understanding how human impacts affect the ecology of the key species or functional groups providing the services (Kremen 2005; Farber *et al.* 2006). To date, only a handful of services have been investigated in this manner (Kremen & Ostfeld 2005).

An ecosystem service common to many large tropical rivers is fisheries production (Welcomme 1985, 1990; Holmlund & Hammer 1999; Allan *et al.* 2005; Winemiller 2005). In developing countries, fisheries may provide the majority of dietary protein consumed by local and regional communities, and economic opportunities of last resort for many low-income families in rural areas (Allan *et al.* 2005). In Chapter IV, I used two valuation methods (energetic and market value) to evaluate how closure of Itaipu Reservoir affected local fisheries. This study provides a unique assessment of potential impacts of river impoundment on fisheries production. Impoundment appeared to increase the energetic cost (per kg) of fisheries production, whereas the market value of the fishery fell sharply due to changes in the dominant species comprising the landings. Because fisheries yield also declined over the study period, these trends reflect both negative growth and negative development.

Fisheries production is just one ecosystem service provided by fish populations (Holmlund & Hammer 1999) and rivers in general (Daily 1997). Additional studies are needed to assess impacts of river impoundment on other services provided by naturally flowing rivers, and to characterize these impacts in similar units (e.g. embodied energy, Costanza 1980) as the tradeoffs provided by impoundment. For goods captured in commercial markets, comparisons of energetic cost of production with actual market value can help point out where ecosystem services may be undervalued (as in the case of the Itaipu fishery). Combined, this suite of studies on the relative impacts of river impoundment on ecosystem services should facilitate responsible stewardship of our ecosystems, and the life-support services they provide.

CONCLUSION

Perhaps the greatest impact to the functioning of large-river ecosystems is alteration to the global water cycle through water diversion and impoundment (Allan & Flecker 1993; Postel *et al.* 1996; Rosenberg *et al.* 2000; Jackson *et al.* 2001; Bunn & Arthington 2002; Foley *et al.* 2005). The present work and many other studies highlight the central role of hydrology in determining river ecosystem structure and function (e.g. Poff & Allan 1995; Poff 1997; Lamouroux *et al.* 2002; Agostinho *et al.* 2004b; Hoeinghaus *et al.* In Press-a). Hydrologic alterations, such as river impoundment or reduced flows, greatly impact aquatic ecosystems and the services they provide (Chapters II, III, and IV). Maintaining natural flow regimes should therefore be a priority of riverine conservation and management plans, and additional research is needed to predict functional responses of ecosystems to hydrological alterations across spatial scales.

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Appendix A Fish species collected for isotopic analyses (shaded cells) by landscape type and location (see Methodology in Chapter II). Species used to estimate the integrated $\delta^{13}C$ signature for each food web are denoted with an "X". IGU = Iguatemi River; IVI = Ivinheima River; PAR = Paraná River; PIQ = Piquiri River; IVA = Ivaí River; ITA = Itaipu Reservoir; ROS = Rosana Reservoir; PTP = Porto Primavera; BRS = Paranapanema River below Rosana Reservoir; BPP = Paraná River below Porto Primavera Reservoir.

Species	Low-gradient rivers			High-gradient rivers		Reservoirs			Below reservoirs	
	IGU	IVI	PAR	PIQ	IVA	ITA	ROS	PTP	BRS	BPP
MYLIOBATIFORMES										
Potamotrygonidae										
Potamotrygon motoro	▨	▨								
CHARACIFORMES										
Characidae										
Acestrorhynchus lacustris			▨	▨ X		▨ X	▨ X			
Astyanax altiparanae				▨						
Astyanax schuburti				▨						
Brycon orbignianus									▨	
Galeocharax knerii				▨ X						
Metynnis maculatus			▨						▨	
Myloplus sp. 1				▨						
Mylossoma sp. 1				▨						
Salminus brasiliensis			▨	▨	▨ X	▨ X		▨		▨ X
Serrasalmus maculatus			▨ X			▨	▨		▨ X	
Serrasalmus marginatus	▨ X	▨ X	▨ X			▨ X	▨ X	▨ X		▨
Anostomidae										
Leporinus friderici	▨	▨			▨		▨		▨	
Leporinus lacustris							▨			
Leporinus obtusidens									▨	

Leporinus octofasciatus				▨						
Leporinus sp.						▨				
Schizodon altoparanae								▨		
Schizodon borellii		▨	▨			▨	▨	▨	▨	▨
Schizodon nasutus				▨	▨		▨		▨	
Curimatidae										
Steindachnerina brevipinna			▨				▨			
Steindachnerina insculpta			▨	▨						
Prochilodontidae										
Prochilodus lineatus	▨	▨	▨	▨	▨	▨		▨	▨	▨
Erythrinidae										
Hoplias malabaricus	▨	X	▨	▨	X	▨	X	▨	▨	▨
Cynodontidae										
Rhaphiodon vulpinus	X	▨	X			X	X		X	X
GYMNOTIFORMES										
Sternopygidae										
Sternopygus macrurus				▨						
Rhamphichthyidae										
Rhamphichthys hahni						▨				
SILURIFORMES										
Doradidae										
Pterodoras granulosus	X					▨	▨			
Auchenipteridae										
Auchenipterus osteomystax				▨						
Parauchenipterus galeatus		▨	▨			▨				
Pimelodidae										
Hemisorubim platyrhynchos								X		
Hypophthalmus edentatus	▨					▨				
Iheringichthys labrosus				▨	X			▨	▨	
Pimelodus heraldoi					▨	▨				
Pimelodus maculatus			▨			▨	▨	▨		

Pimelodus ornatus				X	X				X	
Pinirampus pirinampu	X		X			X		▨	X	X
Pseudopimelodus mangunus					X					
Pseudopimelodus zungaru				X						
Pseudoplatystoma corruscans		X				X		X	X	▨
Rhamdia quelen				X						
Sorubim cf. *lima*								▨		▨
Callichthyidae										
Hoplosternum littorale	▨									
Loricariidae										
Hypostomus albapunctatus					▨					
Hypostomus regani					▨	▨				
Hypostomus sp. 1	▨									
Hypostomus sp. 2				▨						
Hypostomus sp. 3				▨						
Hypostomus sp. 4				▨						
Hypostomus sp. 5										▨
Hypostomus sp. 6										▨
Hypostomus sp. 7										▨
Liposarcus anisitsi		▨	▨			▨		▨	▨	▨
Rhinelepis aspera						▨				
Loricaria prolixa					▨					
Loricariia sp. 1	▨									
Loricariichthys platymetopon		▨	▨				▨			
Loricariichthys rostratus		▨								
PERCIFORMES										
Sciaenidae										
Plagioscion squamosissimus	X					X	X	X		X
Cichlidae										
Astronotus ocellatus		▨								
Cichla monoculus		X	▨			X		▨		X
Cichla sp. "azul"		X	▨					X		X

Cichla sp. 1									▨
Crenicichla britskii	▨	▨ X			▨				
Crenicichla jenynsii					▨ X				
Crenicichla sp. 1									▨
Satanoperca pappaterra			▨						
PLEURONECTIFORMES									
Achiridae									
Catathyridium nienderlaine					▨				

VITA

Name: David Joseph Hoeinghaus

Address: Division of Biology, Kansas State University,
104 Ackert Hall, Manhattan, KS 66506

Education: Ph.D., Ecology, Evolutionary Biology and Systematics, Department of Wildlife and Fisheries Sciences, Texas A&M University, 2006

B.S., Conservation Biology and Biodiversity, Department of Wildlife and Fisheries Sciences, Texas A&M University, 2002

Selected Publications:

Hoeinghaus D.J., Winemiller K.O. & Birnbaum J.S. (In Press) Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *Journal of Biogeography*

Hoeinghaus D.J. & Davis III S.E. (In Press) Size-based trophic shifts of salt-marsh dwelling blue crabs elucidated by dual stable C and N isotope analyses. *Marine Ecology Progress Series*

Hoeinghaus D.J., Winemiller K.O., Layman C.A., Arrington D.A. & Jepsen D.B. (In Press) Effects of seasonality and migratory prey on body condition of *Cichla* species in a tropical floodplain river. *Ecology of Freshwater Fish*

Zeug S.C., Shervette V.R., Hoeinghaus D.J. & Davis III S.E. (In Press) Nekton assemblage structure in created and natural marsh habitats of the Guadalupe Estuary, Texas. *Estuarine Coastal and Shelf Science*

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Hoeinghaus D.J., Layman C.A., Arrington D.A. & Winemiller K.O. (2003) Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes*, 67, 379-387