

Migratory Neotropical Fish Subsidize Food Webs of Oligotrophic Blackwater Rivers

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Keywords: Amazon, detritus, diversity (bio-, species), ecosystem, eutrophic, fish(es), fecundity, floodplain, food web, migration, nutrients, oligotrophic, Orinoco, predation (predator-prey interaction), production (primary, secondary), South America, subsidy, isotopes (stable), Venezuela

Introduction

Motivated in part by growing interest in the role of biodiversity for ecosystem health, ecologists have turned their attention to the influence of population dynamics and species interactions on ecosystem processes (Jones and Lawton 1995, Vanni and DeRuiter 1996). This issue also has been stimulated by recent studies showing that consumers can have pronounced direct and indirect effects on energy and nutrient fluxes, which in turn influence productivity and trophic dynamics in other portions of the food web. For example, detritivorous fish feeding in the littoral zone of lakes have been shown to transport and release nutrients (via excretion) to pelagic areas, which then promotes phytoplankton growth in support of the grazer food web (Carpenter et al. 1992, Vanni 1996). Similarly, caiman of the Amazon River feed in productive lagoons then move to unproductive lagoons where their excretion imports nutrients (Fittkau 1973). Reviews of consumer regulation of nutrient dynamics can be found in Kitchell et al. (1979) and Polis et al. (1997). Researchers have demonstrated top-down (consumer) and bottom-up

(producer) control in grazer food webs of aquatic systems, without addressing how phytoplankton production and upper-level trophic dynamics are linked to longer-term nutrient cycling in detrital food webs (Carpenter et al. 1992). Additionally, there may be energy and nutrient conduits into food webs that have gone undetected using traditional research paradigms.

Such pathways that import energy and nutrients from one ecosystem to another have been called "foodweb spatial subsidies" (Polis and Hurd 1996). Foodweb subsidies can be crucial to understand community and ecosystem dynamics and processes (Polis et al. 1996, 1997). Ecosystems can be linked by foodweb subsidies resulting from animal migration. For example, anadromous salmon import nutrients from the ocean into oligotrophic streams of Alaska and the Pacific Northwest (Northcote 1988, Kline et al. 1990, Deegan 1993, Schuldt and Hershey 1995, Willson and Halupka 1995, Bilby et al. 1996, Willson et al. 1998). Marine-derived production assimilated by salmon is consumed directly by a variety of terrestrial carnivores, and decomposition of salmon carcasses enriches riparian landscapes (Willson et al. this volume).

This chapter examines how migratory fish transfer production from nutrient-rich, whitewater river ecosystems to predators of nutrient-poor, blackwater systems in South America. Blackwater rivers of the Amazon and Orinoco Basins have high fish species richness, low primary production, and high piscivore abundance. During the wet season, large schools of algivorous/detritivorous fish (*Semaprochilodus* species) migrate downstream and exit the river to spawn and feed on the productive floodplains of the Amazon and Orinoco. During the early dry season, massive schools of juvenile detritivores enter and ascend blackwater rivers. During their long upstream migrations, these fish are consumed by resident blackwater piscivores. Stomach contents data from a population of *Cichla temensis* in Venezuela revealed heavy feeding on detritivores during

the period of their upstream migration. Reproduction by *Cichla* follows this period of intense feeding on *Semaprochilodus*, and fecundity is undoubtedly influenced by this nutritional source. Preliminary estimation of this nutritional subsidy in a Venezuelan blackwater river suggests that migratory detritivorous fishes of the family Prochilodontidae create trophic linkages between river ecosystems throughout South America.

Tropical Floodplain Rivers and Landscape Heterogeneity

Neotropical floodplain rivers are dynamic ecosystems that support high species richness and important fisheries (Lowe-McConnell 1987, Welcomme 1989). In contrast to the regulated rivers common in temperate regions, most neotropical rivers still retain their natural flow so that floodplains are periodically inundated (Junk et al. 1989, Sparks 1995). Increased demand for animal protein has impacted fish populations and community structure in many tropical areas (Welcomme 1989), and fisheries management must deal with socioeconomic pressures to alter river discharge and exploit natural resources. We are only beginning to understand how tropical river food webs and primary and secondary production are influenced by changes in producer and consumer biomass, and the relative importance of alternative producer pools to fish production and biodiversity (Winemiller 1996).

Tropical rivers are classified based on optical qualities, reflecting the combined influence of geochemistry, soils, and vegetation characteristics (Sioli 1975). Whitewater systems are turbid, nutrient-rich rivers that carry large loads of suspended material (mostly clays), and have low transparencies in the range of 0.1–0.5 m (Secchi-disk) with pH readings from 6.2–7.2 (Sioli 1975). The abundant inorganic nutrients and lentic conditions in marginal habitats promotes extensive development of aquatic macrophytes

(Forsberg et al. 1988). The ecology of these "floating meadows" and their role in fish production in the Amazon was described by Howard-Williams and Junk (1977).

Clearwater rivers are colorless and more or less transparent with Secchi readings of 1.1–4.3 m and pH in the range of 4.5–7.8. The high transparency of clearwater rivers is due to a small suspended sediment load and a lack of humic compounds that stain other systems. Rivers with this profile usually drain latosols (Sioli 1975).

Blackwater rivers are nutrient-poor with few suspended solids and low pH (4.0–5.5). These nutrient-poor systems represent the other end of a continuum that contrasts productive whitewater systems. Transparency is reduced in black waters by the high levels of humic acids that stain the water (1.3–2.3 m). Blackwater rivers usually originate in bleached sand soils where podzolization occurs. Sioli (1975) noted that the absence of suspended matter is explained by the almost complete lack of clay particles in the top horizon of sandy catchment areas. In South America, blackwater and whitewater river drainages may be present in the same region, reflecting the irregular distribution of podzols (Lewis et al. 1995). In contrast to whitewater and clearwater rivers, blackwater rivers typically support very little macrophyte growth, presumably due to low nutrient availability.

Net primary productivity of a whitewater floodplain lake in the Central Amazon was estimated at about $0.8 \text{ g C m}^{-2} \text{ d}^{-1}$ (Schmidt 1973). Aquatic macrophytes dominate the producer biomass in white waters (Sioli 1975), and consumers have been shown to accumulate carbon from C_3 plants (*Eicchornia* spp. and a diverse array of plants from other families) but very little from C_4 macrophytes (mostly *Paspalum repens* and other Gramineae) which presumably passes through the microbial loop. Phytoplankton and C_3 macrophytes are the most nutritious primary production sources in the Amazon

floodplain, and are more important in supporting fish biomass than their standing biomass would indicate. Although C₄ macrophytes comprise a major portion of the primary producer biomass in many systems, they seem to be a minor source of energy for aquatic consumers (Hamilton et al. 1992, Forsberg et al. 1993). There is little information on production rates of attached algae (periphyton) in tropical rivers, but their importance as a source of carbon for aquatic fauna has been demonstrated in stable isotope studies (Hamilton et al. 1992).

Systems with little apparent *in situ* primary production can nevertheless support impressive fish biomass. Many nutrient-poor, blackwater rivers in South America support important fisheries, but the basal production supporting this secondary and tertiary production is not apparent. Model simulations have shown that, even at low light intensities, small standing crops of periphyton can support a relatively large consumer biomass (McIntire 1973). Consumer webs of these oligotrophic systems often are augmented, to varying degrees, by terrestrial allochthonous sources (Goulding et al. 1988).

Foodweb Subsidies from Migratory Fishes

Fishes of the of the neotropical characiform family Prochilodontidae have complex feeding and spawning migrations that coincide with seasonal changes in water levels in the tropics (Goulding 1980, Ribeiro and Petrere 1990, Barbarino et al. 1997, Winemiller and Jepsen 1998). Prochilodontids support major commercial and subsistence fisheries throughout the Amazon, Orinoco, and Paraná river basins. Prior research has shown that *Semaprochilodus* species, abundant algivore/detritivores of blackwater rivers of the Amazon and Orinoco Basins, migrate downstream to the floodplains of the whitewater Amazon or Orinoco Rivers where they spawn during the high-water period (Ribeiro

1983, Goulding et al. 1988, Vazzoler et al. 1989). The productive floodplain habitats of whitewater systems are nursery areas for young *Semaprochilodus*. During the period of falling water, spawned-out adults and young-of-the-year (YOY) *Semaprochilodus* migrate up to several hundred kilometers back into blackwater rivers, where YOY detritivores are preyed upon by large predatory fishes, especially *Cichla temensis* (Perciformes, Cichlidae), an important diurnal piscivore of neotropical blackwater rivers (Jepsen et al. 1997, Winemiller et al. 1997). The period from zygote to first migration to blackwater is 3–6 months, and most adults probably spend 3–4 months feeding on the Orinoco floodplain and live 2–3 years (based on data for the better-studied *Prochilodus mariae*; Lilyestrom 1983, Barbarino et al. 1998). *Semaprochilodus* spawning migrations are an ecological strategy that exploits the high productivity of flooded whitewater ecosystems to enhance survival and growth of early life stages (Ribeiro 1983, Vazzoler et al. 1989). Presumably, YOY and adults migrate to blackwater tributaries during the falling-water period in order to avoid stranding in drying floodplain pools and the extremely high densities of competitors and predators in the channels and permanent lagoons of the whitewater system.

The Río Cinaruco is a blackwater tributary (ca. 400 km) of the Orinoco in Venezuela's llanos region (Fig. 1) with high fish species richness (>250 species), low aquatic primary production and invertebrate abundance, but high piscivore abundance. The Cinaruco has lower pH, alkalinity, turbidity and dissolved nutrient concentrations than whitewater tributaries of the Orinoco (Lewis 1988, Winemiller et al. 1997). Primary production and aquatic macrophyte and phytoplankton densities are much lower in the blackwater Cinaruco compared with the whitewater Orinoco (Lewis 1988). Terrestrial leaf litter tends to be high in refractory organic matter and extremely slow to decompose in the acidic environment of blackwater rivers (information summarized by Goulding et al. 1988). In the lower Río Negro in Brazil (blackwater tributary of the Amazon),

Semaprochilodus species have been observed feeding on fine detritus from the surface of submerged vegetation in the flooded forest. This fine detritus is believed to be derived from decomposition of terrestrial litter during the annual flood period. Stomach contents of Río Cinaruco *Semaprochilodus* collected during the low-water period indicate that diatoms growing over the sand substrate was a more important food resource than fine detritus.

[Fig. 1 Map of Cinaruco]

Juvenile *Semaprochilodus kneri* were estimated to provide nearly 50% of the annual biomass ingested by large *Cichla temensis* (>40 cm) of the Cinaruco (Fig. 2). These large *Cichla* comprise about 60% of the adult population during the falling and low-water period (Jepsen et al. 1997, Winemiller et al. 1997), constituting a much greater percentage in terms of population biomass. Gonadal maturation in *Cichla* follows the falling-water period when feeding on *Semaprochilodus* and other fishes is most intense. Body condition and fat stores of *Cichla* increase significantly during this falling-water period (Jepsen et al. 1997). The migratory detritivores probably provide *Cichla* and other large piscivores (other large piscivores are the piranha, *Serrasalmus manueli*, payara, *Hydrolycus scomberoides*, and river dolphin, *Inia geoffrensis*) of nutrient-poor rivers with a significant nutritional subsidy that allows them to achieve significantly greater growth, fecundity, recruitment, and population densities than those that would be supported by *in situ* production alone. Based on the mark-recapture method, Taphorn and Barbarino (1993) conservatively estimated *C. temensis* density at approximately 71 adults ha⁻¹ in a lagoon of the Cinaruco.

[Figure 2. Cichla diet data.]

As the low-water season progresses, the density of YOY fishes declines and the frequency of *Semaprochilodus* in *Cichla* diets declines markedly (Fig. 2). During the

latter phase of the low-water period, virtually all *Cichla* have empty stomachs, and gonadal maturation occurs in preparation for spawning just prior to the beginning of the annual floods (Jepsen et al. 1997, Jepsen and Winemiller unpublished data).

No other fishes of the Cinaruco undertake seasonal movements of the great size, regularity, and spatial scale (several hundred kilometers each year) of the *Semaprochilodus* migrations (there are two species in the Cinaruco, with *S. kneri* far more abundant than *S. laticeps*). When these abundant fish migrate back into nutrient-poor, blackwater rivers they provide blackwater piscivores with a significant nutritional subsidy that should permit greater growth, fecundity, and stock densities than would be supported by production from the local ecosystem alone (Fig. 3).

Using preliminary data from the Cinaruco, we now explore how stable isotopes can complement stomach contents data to estimate the nutritional subsidy of migratory fishes for resident piscivores of the blackwater river. Young *Semaprochilodus* that immigrate into the blackwater river have previously assimilated food resources with carbon isotopic signatures different than the resources in the blackwater river. This stable isotope signature permits estimation of the percent assimilation of whitewater-derived biomass relative to blackwater-derived biomass by the resident piscivores that feed on migratory fishes.

[Fig. 3. Food web subsidy schematic]

Stable Isotopes and Trophic Ecology

Foodweb interactions have traditionally been inferred from direct feeding observations or analysis of stomach contents. Yet, these techniques provide relatively short-term assessments of consumption, and provide no information on assimilation and

limited information on rates of energy and nutrient acquisition at broader temporal and spatial scales (also see Schindler this volume). In some cases, ingested material may represent refractory material of low nutritive value to consumers. Conversely, labile material that is assimilated rapidly may be underestimated. Stomach contents data do not integrate the individual's diet over time, thus large amounts of dietary data are needed to gain insights about population response to long-term fluxes in food resources.

A useful approach to link flows of nutrients and energy with consumption is analysis of stable isotope ratios (Polis et al. and Schindler this volume). Carbon ($^{13}\text{C}/^{12}\text{C}$), nitrogen ($^{15}\text{N}/^{14}\text{N}$), and other isotopes exist in material pools, and their ratios can be measured with great precision using mass spectrometry (expressed as ^{13}C , ^{15}N , etc.; actually the isotope ratio of the sample divided by the ratio of a standard substance). Isotope ratios provide information on sources of organic matter important to consumers as well as insights about how materials are processed within trophic networks (Peterson and Fry 1987, Fry 1988, Harrigan et al. 1989, Hobson and Welch 1992, Yoshioka et al. 1994, Hansson et al. 1997, Anderson and Polis 1998, Polis et al. and Schindler this volume).

Carbon isotope ratios in primary producers reflect differential fractionation of the heavier isotope member relative to the lighter member during fixation of inorganic carbon (Rounick and Winterbourne 1986). For example, C_4 plants fix CO_2 via the Hatch-Slack photosynthetic pathway, resulting in $^{13}\text{C}/^{12}\text{C}$ ratios of -23 to -90/00, whereas terrestrial C_3 plants using the Calvin photosynthetic pathway fix carbon at ratios of -32 to -250/00. After fixation by autotrophs, there is little fractionation of carbon at successive trophic transfers (ca. 10/00), so that when producers have divergent isotope signatures, it is possible to determine the relative contribution of each source to consumers in the food

web (reviewed by Fry and Sherr 1984, Peterson and Fry 1987, Lajtha and Michener 1994).

In aquatic systems, primary producers have a range of carbon isotope ratios that reflect not only variability in sources of dissolved inorganic carbon (DIC), but also hydrological and geochemical conditions that occur during photosynthesis (Heckey and Hesslein 1995). Carbon isotope analysis has also been used to discriminate the trophic importance of different detrital sources in aquatic systems (McArthur and Moorhead 1996). Autochthonous organic matter (phytoplankton and macrophytes) can be distinguished from allochthonous (terrestrial) organic matter because terrestrial plants typically have a more negative carbon signature (-28‰) than phytoplankton (-20 to -25‰) and submersed aquatic plants (-12 to -30‰) (Boutton 1991). Detritus from aquatic macrophytes has long been assumed to support most estuarine and many freshwater food chains, but isotope studies have demonstrated that phytoplankton and periphytic algae are more important than their abundance suggests (Araujo-Lima et al. 1986, Hamilton et al. 1992, Forsberg et al. 1993).

The ability to distinguish various sources of organic matter can be increased by examining several isotopes (MacArthur and Moorehead 1996). The nitrogen ratio is fractionated by foodweb processes. ^{14}N is excreted by animals more efficiently than ^{15}N , therefore, as food webs become more complex (i.e., more trophic levels), ^{15}N accumulates at higher trophic levels. An approximate $3\text{--}4\text{‰}$ enrichment with each successive transfer has been used to assign trophic levels to species and enumerate trophic links within food webs (Minagawa and Wada 1984, Vander Zanden et al. 1997, Vander Zanden and Rasmussen in press). In many food webs, ^{15}N signatures increase $+10$ to $+15\text{‰}$ from autotrophs to top consumers, depending on the number of trophic transfers (Peterson & Fry 1987). In combination, ^{13}C and ^{15}N signatures can resolve

sources of organic matter and foodweb structure, and have been used successfully in a number of aquatic studies (Kline et al. 1990, Hesslein et al. 1991, Hamilton et al. 1992, Bunn and Boon 1993, Forsberg et al. 1993, Kidd et al. 1995, Bootsma et al. 1996, Schlacher and Wooldridge 1996, Schindler this volume).

Many fish species undergo diet shifts with age (Werner and Gilliam 1984), so that evaluation of ratios from different size classes within a species can indicate the life stage at which these shifts occur (Gu et al. 1997, Hentschel 1998). Most fishes live in habitats where the availability of different resource pools changes seasonally, and such changes are reflected in isotope signatures from tissues with short turnover times. Stable isotope analysis can estimate the relative importance of seasonal nutritional inputs (Goering et al. 1990), as well as ontogenetic diet shifts (Hesslein et al. 1993, Hobson 1993) and the nutritional origins of organisms that migrate between ecosystems (Hesslein et al. 1991). Many fishes living in tropical floodplain river systems accumulate fat stores during the flood period (Junk 1985, Goulding et al. 1988, Winemiller 1989, Jepsen and Winemiller unpublished data). However, it is not known whether or not this growth is simply a function of increased foraging opportunities in the aquatic habitat, or whether inundated terrestrial sources represent a significant input to the energy budget on a seasonal basis. Liver tissue turns over faster than muscle tissue, and our preliminary data show a mean difference (liver–muscle) of 2.50‰ for ^{13}C in Cinaruco *Semaprochilodus kneri* (n=9) and 3.20‰ for large *Cichla temensis* (n=5). In each case, the shifts are consistently in the predicted direction (see below) based on the size class and time of year the fishes were collected (e.g., liver more negative than muscle for immigrant *Semaprochilodus* following several months of residence in the blackwater river).

Estimation of Nutritional Subsidy using Stable Isotopes

Isotope signatures of dissolved inorganic carbon (DIC) and particulate organic carbon (POC) differ between whitewater and blackwater rivers. In a study of isotope geochemistry in the Orinoco Basin in Venezuela, Tan and Edmond (1993) reported DIC signatures ranging from -8 to -12‰ for whitewater rivers draining nutrient-rich soils of the Orinoco Basin, and values between -12 and -23‰ for blackwater rivers. They inferred that high negative values for black waters reflect a large fractionation from biogenic processes, whereas the less negative values of white waters reflect values close to atmospheric CO₂ or carbonate minerals. The main Orinoco channel shows a gradual transition in DIC ¹³C from its headwaters that receive black waters (-20.10‰) to its whitewater lower reaches (-11.3 to -16.00‰). POC ¹³C ranges from -34.80‰ for Venezuelan blackwater rivers to -24.10‰ for whitewater rivers. Provided that consumers of autochthonous production reflect these values, such differences provide a basis for comparing isotope signatures among various consumers from rivers with different chemical characteristics (Jepsen and Winemiller 2002).

Cichla temensis, *S. kneri*, and other common fishes and major food web components were collected monthly from the Río Cinaruco in the vicinity of Laguna Larga over the period October 1993 through June 1994 (Jepsen et al. 1997), and again during January-March 1997 and January 1998 for stable isotope analysis of muscle and liver tissues. Fishes were sacrificed, measured and weighed, then muscle and liver tissues (5 g) were removed and preserved in salt. In the lab, tissues were rinsed in de-ionized water, dried in an oven at 60°C for 48 hr, then ground into a powder (<250 μm) with a mortar and pestle. Powder samples were weighed with a precision balance and then sealed in tin capsules, labeled, and sent to the isotope lab at the University of Georgia (Institute of Ecology), where standard procedures were used for isotope analysis.

The isotopic signatures of comparable primary producers and detritus are different in blackwater and whitewater systems (Hamilton et al. 1992, Winemiller and Jepsen unpublished data). Muscle tissue samples taken from a wide variety of fishes from the blackwater Cinaruco and the whitewater Río Apure (a major Orinoco tributary ca. 150 km north of the Cinaruco) clearly indicate how fish assemblages of these two ecosystems have different mean ^{13}C values (Cinaruco $-300/00$ [n=117], Apure $-230/00$ [n=55])(Fig.4). Since fishes feeding on detritus and periphyton in whitewater ecosystems have more positive carbon isotope signatures than those feeding in blackwater systems, a shift in isotope signatures should be associated with the body size differentiating juveniles (first-year migrants) from adult *Semaprochilodus* returning to blackwater. A study of migratory *Semaprochilodus insignis* from the Río Negro clearly demonstrated very marked ontogenetic shifts in the carbon signature that coincide with early dietary shifts and migration from whitewater to blackwater (Fig. 5).

[Fig. 4. Frequency distributions of ^{13}C values for fishes of the R. Apure and Cinaruco]

To examine how isotopes record ontogenetic diet shifts, muscle tissue was examined from different size classes of *Semaprochilodus* and *Cichla*. Based on Fernandez's (1993) study in Brazil, shifts (on the order of $5-60/00$) in ^{13}C are predicted to coincide with the size class of YOY *Semaprochilodus* ascending the blackwater Cinaruco (ca. 10-13 cm SL). Preliminary data for Cinaruco *Semaprochilodus kneri* show the same isotopic pattern as *S. insignis*, although ^{13}C values are not as negative at each size interval (i.e., ca. $-270/00$ for 13–14 cm *S. kneri* vs. $-300/00$ for 11.5–12.5 cm *S. insignis*, and ca. -32 vs. $-360/00$ for adult *S. kneri* and *S. insignis*, respectively)(Fig. 6). The Río Negro has a more extreme blackwater geochemistry than the R. Cinaruco, which apparently causes a greater shift toward lighter ^{13}C ratios in its biota.

[Fig. 5. Ontogenetic shifts in ^{13}C values of *Semaprochilodus* from the Central Amazon- from Fernandez]

An end-member mixing model (eq. 1) was used to evaluate the percent contribution of whitewater and blackwater carbon sources (W, B) in the biomass assimilated by *Cichla* (Forsberg et al. 1993).

$$1) \quad \%W = (1 - ((^{13}\text{C}_{\text{consumer}} - ^{13}\text{C}_W) \div (^{13}\text{C}_B - ^{13}\text{C}_W))) \times 100$$

In the case of carbon, the model had end members that consisted of imported-whitewater carbon from YOY *Semaprochilodus* prey at -27.0‰ versus the weighted mean value for *in situ*-blackwater sources at -28.40‰. The weighted mean for *in situ* prey was based on findings from analyses of stomach contents and isotope ratios of prey taxa. There were two prey groups that caused mean ^{13}C for consumed *in situ* prey be lower than the overall average for the blackwater fish assemblage: the benthivorous cichlid *Geophagus surinamensis* (-27.3) which feeds primarily on burrowing midge larvae which themselves probably feed mostly on organic matter derived from terrestrial plants, and midwater characids, *Brycon* spp., (-25.2) that feed on fruits and seeds from terrestrial plants plus smaller fractions of terrestrial insects.

The ^{13}C values for Cinaruco *S. kneri* of different sizes indicate carbon assimilation histories consistent with their migration from whitewater to blackwater. Muscle tissue of larger *Semaprochilodus* have more negative ^{13}C signatures that reflect longer histories of consumption/assimilation of blackwater food resources and proportionally less assimilation of whitewater resources (Fig. 6). Again, this pattern is the same as that described by Fernandez (1993) for Río Negro-R. Amazonas *S. insignis* (Fig. 4), in which YOY individuals showed a rapid decline in ^{13}C at approximately 12.5 cm SL (the size of entry into black water).

[Fig. 6. ^{13}C by length for Cinaruco *Semaprochilodus kneri* and *Cichla temensis*]

Stomach contents analysis (expressed as volumetric proportions) estimated that 45% of the prey ingested by *Cichla temensis* >40 cm SL were YOY *Semaprochilodus* during the falling-water period. This major nutritional input is reflected in ^{13}C signatures (showing more positive, whitewater-like values) of muscle tissue from *Cichla* large enough (>40 cm) to exploit YOY *Semaprochilodus* (8.5–15.5 cm). Smaller *Cichla* (<40 cm) have more negative ^{13}C signatures reflecting feeding on a variety of smaller, nonmigratory fishes that reflect assimilation of *in situ* sources of organic matter (Fig. 6).

Tissue stable isotope signatures of carbon support the contention that *Semaprochilodus* is the major nutritional component for large *Cichla*, and the assimilation estimate (46%) closely matches the (falling-water period) consumption estimate from stomach contents analysis. The great importance of this nutritional input is reinforced by a more negative ^{13}C of liver tissue from adult *Cichla* captured during the mid and late falling-water period, which also corresponds to the period of peak condition and gonadal maturation in preparation for the major spawning period (April–May).

Ratios of stable isotopes of nitrogen (^{15}N) reflect inter- and intraspecific variation in trophic level (with a 3–4 ^{15}N shift with each successive consumption/assimilation step in a food chain) and have the potential to improve statistical resolution of different carbon sources (e.g., ^{15}N for equivalent primary producers can differ by as much as 30/00 between blackwater and clearwater, Jepsen and Winemiller 2002). *Semaprochilodus* revealed little size-based variation in ^{15}N (Fig. 7), indicating that juveniles and adults feed at similar trophic levels. Mean ^{15}N for large *Cichla* was about 30/00 greater than the mean for *Semaprochilodus* and 20/00 greater than the mean for all Cinaruco fishes. This nitrogen pattern indicates the high trophic position of large *Cichla*, the importance of *Semaprochilodus* in their diet, plus selective feeding on resident fishes lower than the mean trophic level. ^{15}N for small *Cichla* was only approximately 10/00 greater than the mean

for all Cinaruco fishes, an indication that these smaller predators feed mostly on small fishes from lower trophic strata (i.e., detritivorous and omnivorous characiforms, Jepsen et al. 1997, Winemiller et al. 1997).

[Fig. 7. ^{15}N by length for Cinaruco *Semaprochilodus* and *Cichla*]

Potential Indirect Effects of the Subsidy

The Río Cinaruco supports at least 250 fish species from 32 families, and most of these species are small (<10 cm SL) and feed at lower trophic strata (detritivores, algivores, omnivores, invertivores). *Cichla temensis* is an abundant, voracious predator that consumes a diverse array of characiform, siluriform, and perciform fishes (Jepsen et al. 1997, Winemiller et al. 1997), and thus may have the potential to influence population dynamics of prey. There are other piscivores in the Cinaruco, but none are as abundant within such a wide array of habitats as *C. temensis*. Nocturnal siluriforms are the dominant large piscivores of tropical whitewater rivers, but are uncommon in the blackwater Cinaruco. After *C. temensis*, the most abundant, large, diurnal piscivores of the Cinaruco are *Cichla orinocensis* (butterfly peacock) and *Serrasalmus manuela* (piranha). *Cichla orinocensis* is most common in lagoons and shallow shoreline habitats (Winemiller et al. 1997), and *S. manuela* is most common in deeper waters, especially in the river channel. Because *S. manuela* is not a gape-limited predator (pieces of flesh are removed from the prey), it has the potential to exploit migratory prochilodontids, but this has not yet been investigated. *Cichla orinocensis* is a gape-limited predator (ingests prey whole) and rarely grows to 40 cm SL in this system (Winemiller et al. 1997), so that feeding on migratory prochilodontids is probably uncommon.

Because *S. manueli* and *C. orinocensis* are abundant and consume a diversity of prey taxa, they could influence population dynamics of prey taxa within their respective habitats under appropriate conditions. Yet because *C. temensis* is larger, thus enabling consumption of a greater range of prey sizes, and occurs in a wider range of habitats, it should have greater potential to exert top-down effects on the food web. This potential for top-down effects would be increased by the predators' nutritional subsidy received from the abundant migratory fishes that import production from a distant landscape. It seems unlikely that migratory fishes import significant quantities of dissolved inorganic nutrients into the blackwater system via excretion of material assimilated from the whitewater system. This probably occurs during the initial period of migration, but , given that migrants continue to feed during their migrations, the net import of nutrients is probably insignificant.

Additionally, migratory fishes might have an indirect effect on resident prey populations if they reduce the availability of benthic algae and high-quality detritus in the oligotrophic system. This latter hypothesis could be tested with enclosure experiments. Visual observations of foraging fishes and stomach contents analysis indicate that *S. kneri* feeds mostly on diatoms and fine detritus taken from sand substrates. Standing biomass of diatoms and fine detritus is extremely low, but no quantitative estimates of benthic production in these systems have been made yet. During the low-water period, large shoals of *S. kneri* are observed grazing along shallow sandbank areas and potentially could reduce the availability of benthic algae and detritus for small, resident algivores and detritivores (25 species from 5 fish families). Manipulative research and quantitative models are needed to demonstrate the degree to which migratory fishes might enhance diversity via subsidization of piscivores and suppression of competitively-superior grazer populations, or reduce diversity via competition for limited benthic primary production.

Conclusions and Future Research

Migratory prochilodontids are major food web components of other hyperoligotrophic, blackwater ecosystems in South America, and thus may provide major foodweb subsidies derived from nutrient-rich, whitewater floodplains. Based on analysis of predator stomach contents, juvenile *Semaprochilodus* were estimated to provide approximately 45% of the annual biomass ingested by large *Cichla*. Preliminary data for tissue stable isotope signatures of carbon support the contention that *Semaprochilodus* is the major nutritional component for large *Cichla*, and the assimilation estimate (46%) closely matches the consumption estimate. Moreover, a major fraction (perhaps >50%) of *Cichla* egg production (potential fitness) should be derived from nutritional inputs from whitewater production. This prediction could be explored using information from a mixing model that estimates biomass assimilation using information from stomach contents analysis and stable isotope data from mature oocytes.

Our lab is now collecting larger diet and tissue samples to facilitate statistical inferences and to improve estimates of assimilation of whitewater sources of basal production. In addition to comparing fishes of different sizes during different periods, spatial variation in the connectivity of the river hydroscape will be exploited. We should observe a significant difference between large piscivores from lagoons that are isolated from the river channel compared with piscivores from connected lagoons that receive immigrating detritivores. Individuals from isolated lagoons should have more negative ^{13}C signatures (indicating assimilation of *in situ* food sources only) compared with conspecifics from lagoons connected to the river channel (indicating heavy feeding on immigrant YOY *Semaprochilodus*).

Quantitative estimation of food web subsidies from migratory fishes is important to conserve and manage neotropical river fisheries. The ongoing construction of dams in South America will have negative consequences not only for the migratory fish populations (Barthem et al. 1991, Barbarino et al. 1998), but also for predator populations of oligotrophic rivers that receive migratory fishes.

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List of Figures/Legends

Figure 1. Map showing the Río Orinoco and its blackwater tributary, the Río Cinaruco, in western Venezuela. Shaded regions are dominated by blackwater and clearwater rivers. The region north of the Río Orinoco drains the nutrient-rich terrain of the Andes Mountains, Coastal Range, and alluvial plains (llanos); the region south of the Orinoco drains the nutrient-poor terrain of the ancient Guyana Shield formation.

Figure 2. Volumetric proportions of YOY *Semaprochilodus* versus other fishes in the diet of large *Cichla temensis* (>40 cm) during the falling-water period and low-water periods during 1993-94 at the Río Cinaruco (sample N= 381).

Figure 3. Schematic of the food web subsidy to blackwater piscivores from migratory fish from whitewater floodplains. Compartment sizes represent the relative production of each web component (kg/ha/yr); arrows represent trophic pathways. DIC is dissolved inorganic nutrients. Detritus is presumed to be derived from both aquatic and terrestrial sources; the absolute contribution of terrestrial sources is not assumed to be different in the two systems.

Figure 4. Frequency distributions of ^{13}C values for fishes of the whitewater Río Apure (white bars) and blackwater R. Cinaruco (black bars) (Apure mode= -24.8, Cinaruco mode= -30.5).

Figure 5. Shifts in ^{13}C with increasing total length in migratory *Semaprochilodus insignis* of the blackwater Río Negro and whitewater Amazonas in Brazil (data from Fernandez (1993) and Forsberg et al. (1993)). The time from first-feeding larva to the first

ascending migration is approximately 4 mo. The trend in this system is similar to that shown by Río Cinaruco *S. kneri* in Figure 6.

Figure 6. Mean values (bars= 1 SE) of ^{13}C a wide variety of blackwater Cinaruco fishes, small YOY *Semaprochilodus kneri* with recent residence in the Cinaruco (SL<15 cm), large (age 1+) migratory *Semaprochilodus kneri* (SL>15 cm) in their second or third year of residence in the Cinaruco, small piscivorous *Cichla temensis* (SL<40 cm), and large *Cichla temensis* (SL>40 cm). Arrows show pathways for a mixing model of piscivore carbon isotope ratios (assuming ^{13}C shifts <10/00 during digestion and assimilation).

Figure 7. Mean values (bars= 1 SE) of ^{15}N a variety of blackwater Cinaruco fishes, small YOY *Semaprochilodus kneri* (SL<15 cm), large migratory *Semaprochilodus kneri* (SL>15 cm), small piscivorous *Cichla temensis* (SL<40 cm), and large *Cichla temensis* (SL>40 cm). Arrows show pathways for a mixing model of piscivore nitrogen isotope ratios, with nitrogen ratio assumed to increase 30/00 per trophic level. Consequently, both large and small *Cichla* are assumed to feed on a subset of the 117 resident prey fishes with ^{15}N lower than the group mean.