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Food webs in two neotropical stream systems as revealed by stable isotope ratios

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Introduction

Trophic relationships in the tropics are thought to be obscured to some extent by a high degree of omnivory. The role of omnivory in food webs has recently been addressed both theoretically (DIEHL 1995) and experimentally (PRINGLE et al. 1993a, PRINGLE & BLAKE 1994, LODGE et al. 1994, MCCORMICK 1994, PRINGLE 1996). In exclosure studies in a stream in Costa Rica, PRINGLE & HAMAZAKI (1998) showed that both shrimps and fishes can significantly affect insect biomass, algal biovolume and community structure. The effects of fishes were generally greater than those of shrimps because of the higher densities and foraging pressures of fishes. Their data supported the predictions of DIEHL (1995) that when the body size differences between top omnivorous consumers and intermediate consumers (insects) are large, there should be strong direct feeding effects on intermediate consumers and resources that override indirect effects.

Stable isotopes can be useful tools for determining the degree of such omnivory (HECKY & HESSLEIN 1995). For example, the diverse fishes of Lake Malawi were thought to be eating the same few food types, but a recent stable isotope study showed that they were highly partitioning their food bases (BOOTSMA et al. 1996). Stable isotopes are widely used to elucidate the fate and transfer of organic matter and the food-web relationships in aquatic systems (FRY & SHERR 1989, FRY 1991, PETERSEN et al. 1993, FRANCE 1995), including tropical systems (HAMILTON & LEWIS 1992, HECKY & HESSLEIN 1995, BOOTSMA et al. 1996). The $\delta^{13}C$ values in general indicate the source of the fixed carbon because there is little isotopic fractionation of carbon during trophic transfer (DENIRO & EPSTEIN 1978, FRY & SHERR 1989, FRANCE 1995). Terrestrial C_3 plants typically have $\delta^{13}C$ values of −28‰ with very little variation (FRANCE 1995). The signal for algae is much more variable. Lentic phytoplankton are generally similar to or isotopically lighter than (more negative $\delta^{13}C$ values, down to −37‰) terrestrial plants, and benthic algae are typically heavier (ca. −10 to −20‰; HECKY & HESSLEIN 1995). Phytoplankton can be close to equilibrium with dissolved carbon dioxide, especially in well-aerated streams, because they have a high surface to volume ratio and are widely dispersed in a turbulent environment. Benthic algae, on the other hand, are subject to boundary layer effects causing highly variable $\delta^{13}C$ values because growth can be carbon-limited and diffusion-limited. Top consumers usually have a narrow range of $\delta^{13}C$ reflecting increasing omnivory up the food web (HECKY & HESSLEIN 1995). The $\delta^{15}N$ value is an indicator of trophic transfer, because there is an increase of about 3–4‰ with each trophic level increase (WADA et al. 1993, HECKY & HESSLEIN 1995). Pollution of the hydrosphere owing to microbial processes can drastically affect the $\delta^{15}N$ values at the base of food webs (HEATON 1986, CABANA & RASMUSSEN 1996). These stable isotope ratios give a picture of the feeding history of the animal in question in the order of weeks to years (PETERSEN et al. 1993).

The purpose of this study is to provide some baseline stable isotope data for food webs in two neotropical stream systems, one in Costa Rica (Rio Salto), and the other in Puerto Rico (Quebrada Toronja and Quebrada Bisely). Both systems have large top omnivores, but the community structures differ primarily in the relative importance of fishes and shrimps.

Methods

Samples were obtained from one stream in Costa Rica and two streams in Puerto Rico. The Rio Salto is located in La Selva Biological Station in northern Costa Rica (10° 26' N, 84° 01' W) at the transition between Caribbean lowland plains and the steep foothills of the central mountain range. More than 95% of the Rio Salto watershed is in primary forest which is protected within both La Selva and the Braulio Carrillo National Park. La Selva receives ca. 4 m of rainfall annually and the vegetation is tropical wet forest. The Rio Salto is a third-order stream that

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drops from 300 m to ca. 36 m above sea level (a.s.l.) where it empties into the Rio Puerto Viejo. The stream is very low gradient, with the stream bottom comprised of clay and fine sediments at the sampling site. Its watershed drains an early Pleistocene andesitic/basaltic lava flow (PRINGLE et al. 1990). The Rio Salto has high solute levels (e.g. Na, Cl, SO_4, Si, Mg, PO_4-P) relative to the streams in Puerto Rico as a result of groundwater inputs that are derived from geothermal weathering of subsurface minerals (PRINGLE et al. 1993b, TRISKA et al. 1993). Samples were collected for isotope analysis from the lower reaches of the Rio Salto at 50 m a.s.l. at approximately 0.5 km from its confluence from the Rio Puerto Viejo.

The Quebrada Toronja (Espiritu Santo watershed) and Quebrada Bisley (Mameyes watershed) are located in the Luquillo Experimental Forest (Caribbean National Forest) in northeastern Puerto Rico (18° 18' N, 65° 47' W; LUGO 1986). They are first-order perennial streams in separate adjacent watersheds with mean discharges of ca. 1.7 m^3 s^{-1} (U.S. GEOLOGICAL SURVEY 1990). Precipitation ranges from 250 to 450 cm $year^{-1}$. The vegetation is primarily tabonuco (*Dacryodes excelsa*) and palms are common on steep slopes and in poorly drained sites in each watershed. The streams are in volcanoclastic geological formations, with steep gradients and stream bottoms comprised of bedrock, boulders and cobbles, and fine silt and sediments between boulders and in depositional pools. Samples for stable isotope analysis were collected from both streams at 300 m a.s.l.

Samples of different trophic components were collected in Puerto Rico and Costa Rica in 1992 in early February and mid-March, respectively. Additional samples of water and freshly fallen leaves were collected in both streams in Puerto Rico in December 1994. Water samples (2 L) were preserved with HgCl for transport back to the USA. Fine detritus and coarse detritus were collected from the stream bed. Attached algal periphyton was scraped from rocks with a toothbrush and filtered onto pre-fired (550 °C for 4 h) glass fiber filters. Insects were collected using Surber samplers. The extremely low biomass of insects present in the Costa Rica stream resulted in insufficient insect mass collected for isotope analysis (30–50 mg dry mass are necessary for analyses); however, a sufficient insect mass was collected in the Puerto Rico streams. Shrimps were collected from all three rivers by placing unbaited minnow traps in stream pools. Fishes were collected from the Rio Salto in Costa Rica using a seine net. Samples of biota were placed in ziplock bags for transport back to the laboratory for drying. Samples for isotopic analyses were collected from abdominal muscle tissue (gut removed) of both shrimps and fishes. All tissue samples and leaves were rinsed in deionized water and dried in a drying oven at 60 °C. Additionally, fine particulate organic matter was collected for analyses from 2-L stream water samples that were filtered onto pre-fired glass fiber filters and then dried at 60 °C.

Isotope ratios were measured at Boston University Stable Isotope Laboratory by R. Michener using the Finnigan-MAT D-S isotope mass spectrometer. Front-ended to the mass spectrometer was a Heraeus carbon-nitrogen analyzer and a Finnigan CT-box for cryogenic separation of gases. This allowed automated stable isotope analysis for most samples. Samples were weighed to the nearest 0.01 mg on a Mettler AE240 electronic balance. All samples were compared to international standards obtained from the National Bureau of Standards in Gaithersburg, MD, USA. A daily check on the instrument was made using a second gas that was isotopically different from the standard gas, and analysis was stopped if there was any deviation from the long-term record. Internal precision for the instrument was 0.014‰. A laboratory standard (peptone; Sigma Chemical) was run every 15 samples and had to be within 0.15‰ of its documented value.

Results

Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ for the food webs in the three streams are shown in Table 1. The $\delta^{13}C$ values were uninformative for distinguishing among autotrophs because they were in a very narrow range from –26 to –31‰. Leaves, algae and detritus all had similar values and the animal consumers reflected this food base. The shrimp all had somewhat more positive $\delta^{13}C$ values than the autotrophs or detritus. One insect sample in the Quebrada Toronja had a very low $\delta^{13}C$ value of –37.0‰.

In all streams, the $\delta^{15}N$ values increased with increasing trophic position of the species, as expected (Table 1). There was a marked difference in the $\delta^{15}N$ in the two streams in Puerto Rico from the one in Costa Rica. The Rio Salto in Costa Rica had high $\delta^{15}N$ values for the dissolved inorganic nitrogen (DIN) in the water (about 4‰; Table 1) and in the food base (3.2–6.8‰) compared to the two streams in Puerto Rico (0.4–2.2 for DIN; –0.1 to 3.6‰ for food). Because the food base had a higher $\delta^{15}N$ signal in the Rio Salto in Costa Rica (aver-

Table 1. Stable isotope values (‰) for carbon and nitrogen for the three neotropical streams, the Rio Salto in Costa Rica and the Quebrada Bisley and Quebrada Toronja in Puerto Rico. (*Samples collected December 1994). Length (cm) of macrobiotic organism(s) sampled is indicated under sample name.

Sample	R. Salto		Q. Bisley		Q. Toronja	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Water	–27.5	4.4				
Filtered water	–25.9	3.9	–27.1	2.2	–28.2	0.4
Fine detritus			–29.4	1.0	–29.7	0.4
Coarse detritus	–30.9	3.2				
Leaves*			–30.3	0.7	–29.4	–0.1
Algae/sand	–28.6	4.9	–28.7	1.8		
Filamentous algae	–28.7	6.8				
Diatoms					–30.7	3.5
					–30.3	3.6
Insects			–26.8	3.3	–37.0	2.1
Atya lanipes (7–8 cm)			–26.3	5.9	–24.5	7.0
Xiphocaris elongata (3.0–4.5 cm)			–25.7	6.3	–23.6	5.6
					–23.6	5.5
Macrobrachium carcinus	–26.0	8.6	–24.6	7.1	–23.9	7.3
(4.4–10.0 cm)	–25.9	8.7				
Brycon quatemalensis (10 cm)	–25.5	7.5				
Neoheterandria umbratilis (2.8–3.6 cm)	–29.6	8.9				

age 5.0‰ compared to 1.7‰ for Puerto Rico), the herbivores and carnivores had higher $\delta^{15}N$ values than in Puerto Rico. For example, *Macrobrachium* had similar $\delta^{13}C$ values in the two regions (7% difference between regions), but the $\delta^{15}N$ values were 20% higher in Costa Rica than in Puerto Rico (Table 1).

Discussion

The streams in Costa Rica and Puerto Rico have quite different consumer communities (Fig. 1). The Rio Salto (Fig. 1A) has a much more complex community than the island streams in Puerto Rico (Fig. 1B). This river is densely shaded with a low algal standing crop and a relatively high diversity of fishes. The Quebrada Toronja is dominated by shrimps, particularly *Atya* spp. and *Xiphocaris elongata*, with lesser numbers of *Macrobrachium*, and very low numbers of algivorous fishes and insects (PRINGLE et al. 1993a, PRINGLE & BLAKE 1994, PRINGLE 1996). The shrimps can reach densities of 5–25 m^{-2} and algal biovolume is extremely low, ca. 30–180 mm^3 m^{-2}, except in the very fringe area <3 cm depth when there is sufficient light penetration to the stream channel (PRINGLE 1996). In contrast, the Quebrada Bisley is dominated by *Macrobrachium* spp., with few *Atya* and *Xiphocaris* and the predaceous fish, *Agonostomus monticola*, is present (PRINGLE 1996). This stream has a far greater algal biovolume (ca. 10,000–20,000 mm^3 m^{-2}; PRINGLE 1996) than the Quebrada Toronja. The importance of atyid shrimp in altering the sediment characteristics and algal biovolume in Quebrada Toronja was demonstrated by PRINGLE and coworkers (PRINGLE & BLAKE 1994, PRINGLE et al. 1993a, PRINGLE 1996). Total sediment, fine and coarse particulate organic mate-

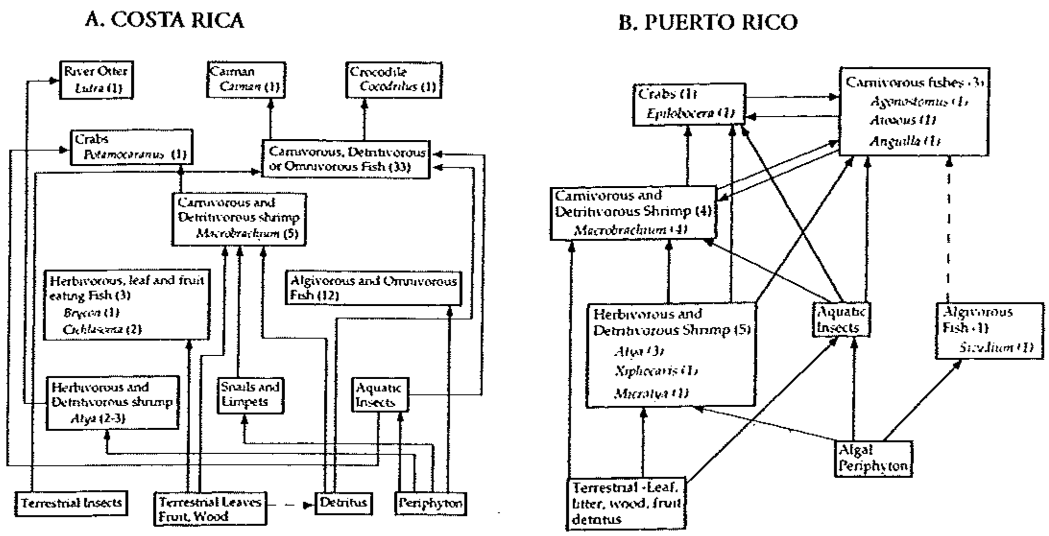

Fig. 1. The trophic relationships in (A) the food webs of the Rio Salto in Costa Rica, and (B) the Quebrada Bisley in Puerto Rico. The Quebrada Toronja has the same trophic relationships as in (B), but does not have any carnivorous fishes. Numbers in parentheses indicate the numbers of species present.

rial, and algal biovolume were all significantly greater in shrimp exclosures.

PRINGLE & RAMIREZ (1998) investigated stream invertebrate communities in Costa Rica along an altitudinal gradient that included areas with (low elevation streams) and without (highland streams) fishes. They showed that the importance of some components of these communities, especially shrimps, could be underestimated when using certain standard sampling techniques. In Puerto Rico, PRINGLE et al. (1999) showed that a stream, similar to the Quebrada Toronja (without predaceous fishes) and in the same drainage system, supported a large shrimp population. Shrimps also maintained low levels of benthic particulate organic matter and associated nitrogen in this stream. The benthic depositional environment was greatly affected by the nature of the macrobiotic assemblages and there was a strong linkage between species and ecosystem processes.

The differences in trophic complexity in these two well-studied stream systems made them appropriate sites for investigating stable isotope relationships in neotropical lotic food webs. The carbon sources in these food webs (detritus, leaves, algae) were very difficult to distinguish because they all had similar $\delta^{13}C$ values, averaging –29.7‰ (Table 1). The consumers had $\delta^{13}C$ values over a broader range, from –23.5 to –37‰. This indicates that there may have been sources of organic material for these consumers that were not measured in this study. FRANCE (1995) showed that consumers in lotic food webs frequently have quite a broad range in carbon isotopes which means they are not just consuming leaf litter because terrestrial C_3 plants have a narrow range of $\delta^{13}C$ around –28‰. He concluded that autochthonous autotrophs in forested headwaters are much more important to lotic food webs than suggested by particulate inputs alone, and that carbon stable isotope analysis for identifying trophic patterns in stream ecosystems is not very useful. HECKY & HESSLEIN (1995) reviewed stable isotope data for lentic food webs from the tropics to the arctic, and found that the carbon sources of primary consumers could often be distinguished if benthic and planktonic algae had different $\delta^{13}C$ values. The range of these $\delta^{13}C$ values decreased as omnivory became more important at higher consumer levels.

The $\delta^{15}N$ values in the food base (detritus, leaves, algae) were much higher in the Rio Salto in Costa Rica (mean of 5.0‰) than in the two streams in Puerto Rico (mean of 1.7‰). What could cause this increase? Because the Rio Salto is in a protected watershed, there is unlikely to be pollution from anthropogenic sources that could raise this value (HEATON 1986, CABANA & RASSMUSSEN 1996). However, bacterial action, such as in soil mineralization, can increase $\delta^{15}N$ values above the typically zero values for autotrophic production from atmospheric sources (HEATON 1986). The higher $\delta^{15}N$ values are likely to be the result of the high contribution of runoff to the nitrogen budget of the Rio Salto. The geothermal groundwaters are low in nitrate and the high nitrate levels (200 µg L^{-1}) in the Rio Salto are due to mineralization in the catchment and surface runoff into the stream rather than groundwater inputs (PRINGLE 1993, TRISKA et al. 1993). DUFF et al. (1996) measured nitrate reduction and denitrification in the stream sediments of the Rio Salto and found that inorganic nitrogen increased along a stretch of the stream, primarily as a result of mineralization. In a study of a low gradient stream in a small Amazonian catchment, BRANDES et al. (1996) found dissolved inorganic nitrogen (DIN) in the stream to be 4.5‰. This is very similar to the value for the DIN in Rio Salto water samples (mean 4.2‰), and much higher than the Puerto Rico streams (mean 1.3‰). After considering a number of possible explanations, BRANDES et al. (1996) concluded that remineralization of organic matter within the stream itself was the major source of DIN, and that the stream DIN may be substantially decoupled from adjacent groundwater DIN. Forest soils of La Selva have extremely high infiltration capacities (PARKER 1985, 1994). ROBERTSON (1984) documented high rates of nitrification and nitrogen mineralization in these forest soils that were at the high end of nitrifying activity for tropical soils. On the basis of a comparison of ecosystem parameters from seven tropical forests (including Puerto Rico) JORDAN (1985) concluded that La Selva in Costa Rica was among the most eutrophic of rainforests.

The Rio Salto is a much lower gradient system than the streams sampled in Puerto Rico, so there is a greater contribution of nitrogen from the forest soils through surface runoff. The higher gradient streams in Puerto Rico are more aerated and likely have a higher contribution of nitrogen from rainfall in equilibrium with the atmosphere to their nitrogen budget. In contrast to the streams draining La Selva, streams draining the Luquillo Experimental Forest are very low in nitrate (MCDOWELL & ASBURY 1994) and this is typical of streams draining other islands in the Caribbean (MCDOWELL et al. 1995). One would expect more microbial activity and thus more opportunity for N transformation and recycling in the hot, humid, 'eutrophic' environments in lowland Costa Rica (50 m a.s.l.) than in the cooler, lower montane, nutrient-poor rain forests of the Luquillo Experimental Forest in Puerto Rico (300 m a.s.l.). We conclude that the high $\delta^{15}N$ values we observed in the food base in the Rio Salto were a result of a higher proportion of bacterially reworked nitrogen entering the food web than in the Puerto Rico streams. Tropical streams in general may prove to have higher $\delta^{15}N$ values for the food base because of rapid mineralization and nitrification rates in the surrounding soils. In a review by HECKY & HESSLEIN (1995), the only $\delta^{15}N$ values for the first level in benthic food webs in lakes that were as high as those found in the Rio Salto were from Arctic food webs.

A few values of stable nitrogen isotopes from the Luquillo Experimental Forest in Puerto Rico were reported by FRY (1991). Data in Fig. 2 of that paper indicated that the $\delta^{15}N$ values for terrestrial plants and algae were about 0.5–1.5‰ and for "omnivores" were 5–6.5‰. These data are fully in line with those reported here.

The $\delta^{15}N$ values reflect consumer feeding relationships and increase about 3‰ for each step in the food web. The insects in the Quebrada Bisely and Quebrada Toronja are about 2‰ higher than the fine detritus, one likely source of food, making them primary consumers. The insect sample from the Quebrada Toronja (a grazing mayfly, *Cloeodes maculipes*) had a $\delta^{13}C$ value that was very negative (–37‰) and did not reflect the carbon signal of the fine detritus. This value was either aberrant or reflected an unknown food source. The shrimps in the genera *Atya* and *Xiphocaris* have $\delta^{15}N$ values about 5‰ higher than the food base and 3‰ higher than insects in Quebrada Bisely, making them largely secondary consumers. *Atya* species feed with appendages that can be used either as brushes or filters and are known to eat algae, detritus and insects (COVICH 1988). In contrast, *Xiphocaris* species use pincers to collect leaves and other particles. The presence of the mountain mullet (*Agonostomus monticola*) in Quebrada Bisley keeps the *Atya* and *Xiphocaris* biomass lower, with consequently greater algal biomass (especially diatoms) than in the Quebrada Toronja (PRINGLE 1996). The sample labeled algae/sand (Table 1) is representative of this diatom mat which likely contributes to the food base of the shrimps. The *Macrobrachium* shrimps have a slightly higher $\delta^{15}N$ value (about 5.5–6‰ higher than the average food base) than the other shrimps reflecting their somewhat more carnivorous habit. The shrimps in the Quebrada Toronja, an essentially fishless stream dominated by shrimps, have a few subtle differences from the Quebrada Bisley. The *Atya* are much more like the *Macrobrachium* than the *Xiphocaris* in their $\delta^{15}N$ values. Because the food base in Quebrada Bisley includes much higher standing crops of diatoms (PRINGLE 1996) and insects (BUZBY 1998) which have a much higher $\delta^{15}N$ signal than leaves or detritus, there may be a difference in the relative importance of the different food items in the diets of the different taxa of shrimps. In the Quebrada Toronja, *Xiphocaris* appear to be more omnivorous than the other two shrimp taxa. Greater similarity of *Atya* and *Xiphocaris* in the Quebrada Bisley (versus the Quebrada Toronja) may be because their access to food resources is restricted by predaceous fishes; *Atya* and *Xiphocaris* tend to occur in shallower areas of pools, possibly as a predation avoidance strategy.

The *Macrobrachium* shrimps seem to be somewhat lower in the food web (more omnivorous) in the Rio Salto in Costa Rica than in the Puerto Rico streams. Their $\delta^{15}N$ values are only 3.6‰ higher than the average food base in the Rio Salto, while they are 5.5‰ higher than the average food base in the Puerto Rico streams. This may be because the *Macrobrachium* that we sampled in the two Puerto Rico streams were larger (7–10 cm long) than those sampled in the Costa Rican stream (4.4–4.7 cm) and this size difference may be reflected by trophic preference, with smaller individuals feeding lower in the food web. Also, *Macrobrachium* are kept in check to a much greater extent in the more complex, fish-dominated food webs in La Selva (PRINGLE & HAMAZAKI 1998) than in the streams in Puerto Rico, where it is either the major predator biomass as in Quebrada Toronja, or shares predator status with fishes as in Quebrada Bisely (PRINGLE 1996).

Freshwater shrimps exhibit migratory amphidromous life-history strategies in both Costa Rica (PRINGLE AND RAMIREZ 1998) and Puerto Rico (COVICH & MCDOWELL 1996, MARCH et al. 1998). Adult female shrimps release planktonic larvae (length <2 mm) that drift downstream from a freshwater habitat to the estuary. Larvae spend 50–110 days in the estuary before migrating back upstream as metamorphosed postlarvae (CHACE & HOBBS 1969). Their isotopic signal is to some degree integrative of their biological activity in both freshwater and estuarine ecosystems, but the values reported here are for muscle mass of adult shrimps which are likely to be most indicative of their freshwater feeding activities.

The two fish species sampled in the Rio Salto in Costa Rica are very different in their feeding habits, as reflected in their $\delta^{15}N$ values. *Brycon quatemalensis* is insectivorous when small, and herbivorous when it is greater than 80 mm in length (BURCHAM 1987). The *B. guatemalensis* used for analysis was 100 mm in length, and its $\delta^{15}N$ value reflects this herbivorous habit of large fish. *Neoheterandria umbratilis* appears to be more of an omnivore, with almost the same $\delta^{15}N$ signal as the shrimp *Macrobrachium*.

Conclusions

Trophic relationships in tropical streams are obscured to some extent by a high degree of omnivory and stable isotopes can be useful in determining the degree of omnivory in such systems. We measured isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in major trophic levels in three streams of varying trophic complexity that were located at two major neotropical research sites: La Selva Biological Station in Costa Rica and the Luquillo Experimental Forest in Puerto Rico. In all streams, the $\delta^{15}N$ values increased with increasing trophic position of the species, as expected. One shrimp species, *Macrobrachium*, may be more of an omnivore in Costa Rica than in Puerto Rico where it feeds higher in the food web. The two fish species in the Rio Salto, Costa Rica, were also clearly distinguished in their trophic positions by their $\delta^{15}N$ values.

There was a marked difference in the $\delta^{15}N$ at the base of the food web in two streams in Puerto Rico compared to the one in Costa Rica, which was significantly higher. The Rio Salto in Costa Rica had high $\delta^{15}N$ values for the food base (mean 5.0‰) compared to the two streams in Puerto Rico (mean 1.7‰). We concluded that this was because of the larger contribution of remineralized nitrogen to and within the stream in Costa Rica.

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