

Spatial variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes in the San Juan River, New Mexico and Utah: implications for the conservation of native fishes

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Received 1 February 2005

Accepted 6 January 2006

Key words: stable isotopes, food web, spatial variation, introduced species, trophic interactions, longitudinal gradients

Synopsis

Spatial patterns of resource use by small-bodied fishes in the San Juan River were examined using stable isotopes. Using $\delta^{15}\text{N}$ of fishes as an index of trophic position, our data suggest both native and non-native fishes primarily consumed macro-invertebrates. The $\delta^{13}\text{C}$ of these fishes further suggested a detritus-based food web, from which most species fed on chironomids in low-velocity habitats. A two-way ANOVA revealed a significant interaction between trophic level of fish species and longitudinal position in the river. This interaction was primarily attributed to a decline in trophic level of non-native red shiner *Cyprinella lutrensis*, relative to other species, in upstream reaches of the river. In addition, ANCOVA results suggest trophic position of fishes was dependent on channel type (primary vs. secondary), as there was less variability in resource use in secondary channels. These data provided a spatial framework of trophic interactions that can be used to predict the outcome of management actions. Overall, we confirmed high overlap in resource used between native and non-native fishes. However, spatial variation in trophic interactions both longitudinally and laterally in the river present a challenge to resource managers attempting to managing entire river systems.

Introduction

Native fishes in drainages west of the Continental Divide, U.S.A. are a highly endangered fauna because of their life-history attributes, human-induced modifications to habitats and establishment of non-indigenous species (Minckley & Deacon 1991). Efforts to conserve this fauna include manipulation of reservoir releases (Valdez et al. 2001, Propst & Gido 2004), introduced species removals (Thompson & Rahel 1996, Tyus & Saunders 2000), and repatriation (Minckley et al. 2004, Mueller & Wydoski 2004). However,

conservation of western native fish communities is complex and must be guided by a thorough understanding of the ecology of these highly modified systems. In particular, the establishment of alien species can alter the extent and modes of species interactions (e.g., Li & Moyle 1981), and modified flow regimes can disrupt both natural patterns of reproduction (Brouder 2001, Marchetti & Moyle 2001, Propst & Gido 2004) and habitat heterogeneity (Nilsson & Berggren 2000).

In the San Juan River of New Mexico, Colorado, and Utah, U.S.A., impoundment by Navajo Dam and encroachment of non-native woody

riparian vegetation (salt cedar *Tamarix chinensis* and Russian olive *Elaeagnus angustifolia*) have drastically altered the hydrology and geomorphology of the river. This hydrologic and geomorphic change is coupled with either extinction or severe reduction in abundance of several native species, including razorback sucker *Xyrauchen texanus*, Colorado pikeminnow *Ptychocheilus lucius*, bonytail chub *Gila elegans*, and roundtail chub *Gila robusta* (Platania et al. 1991). In addition, several introduced species, such as red shiner *Cyprinella lutrensis*, fathead minnow *Pimephales promelas* and channel catfish *Ictalurus punctatus* are common, and in many low-velocity habitats, account for the majority of individuals captured (Gido & Propst 1999).

Empirical evidence from laboratory and field studies of Colorado River basin fishes (Karp & Tyus 1990, Douglas et al. 1994) suggests that non-natives can potentially displace native fishes. In previous studies on the San Juan River fishes, we reported high levels of overlap in mesohabitat (1 – 10 m²) use among native and non-native fishes in secondary channels, and the numerical dominance of non-natives in these habitats (Gido et al. 1997, Gido & Propst 1999). Assuming overlap in diet among these fishes and resource limitations, we hypothesized that competition for resources among non-natives and natives was detrimental to native fishes. The main goal of this research was to

conduct a qualitative analysis of trophic interactions in the San Juan River to further understand potentially negative interactions among native and non-native fishes and to identify basal sources of energy in the food web. Specifically, our objectives were to (1) quantify longitudinal variation in trophic relationships among small-bodied fishes and their resources, (2) compare food web structure between primary and secondary channels, and (3) evaluate resource overlap among native and non-native fishes.

Stable isotopes (¹⁵N and ¹³C) were used to characterize spatial variation in food web structure and resource use. The relative amount of ¹⁵N in fish tissue provided an estimate of trophic position (Cabana & Rasmussen 1996), and was assumed to be greatest in fishes that consumed primarily high trophic level prey items (e.g., macro-invertebrates vs. algae). Relative amounts of ¹³C varies less across trophic levels, and therefore was used to differentiate among organic matter sources that differ in their ¹³C signatures (e.g., algae vs. detritus from riparian trees). If algae were the primary basal carbon source, the ¹³C signature also should reflect habitat use among fishes (Martinez et al. 2001), as algae in habitats with elevated current velocity are more depleted in ¹³C than low-velocity habitats (Finlay et al. 1990).

The trophic relationships among fishes in the San Juan River were predicted to vary longitudinally

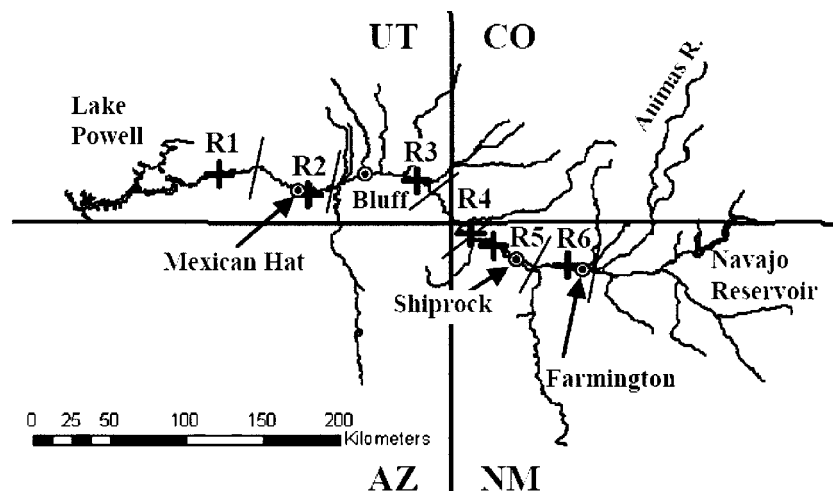


Figure 1. Location of sample sites in six geomorphic reaches of the San Juan River sampled between July 7 and 13, 2003. The primary channel was sampled in reaches 1 through 6 and secondary channels were sampled in reaches 3, 4, and 5.

because of changes in form and energy inputs along the river continuum. Upstream, hypolimnetic releases from Navajo Dam alter stream temperature, turbidity, and discharge from preimpoundment conditions. As the influence of the dam diminishes downstream, there are geomorphologic changes as the river shifts from flowing through a moderately open floodplain and having cobble and sand substrates, to confined canyon reaches with sand substrates. Population centers and agricultural inputs are greatest in the reaches upstream of Shiprock, NM (Figure 1) and may influence food web interactions because of increased nutrient loading. Finally, the relative importance of allochthonous and autochthonous production is likely to vary along the river continuum, favoring different functional groups of organisms (Vannote et al. 1980, Thorp and Delong 2002).

Trophic interactions may also vary laterally within braided reaches of the San Juan River. Specifically, middle reaches of the river (river km [RK] 67 to 160; historical confluence of San Juan and Colorado rivers = RK 0) are characterized by extensive braiding with numerous secondary channels that provide considerable low-velocity habitat for both native and non-native fishes (Gido et al. 1997). Compared to the main channel, secondary channels are presumed to be more productive because of shallower depths, increased light penetration, and higher temperatures. Thus, we predict differences in productivity and food web interactions between secondary and primary channels.

Study area

The San Juan River arises in the San Juan Mountains of southwest Colorado and flows about 484 km to Lake Powell on the Colorado River in Utah (Figure 1). There are few permanent tributaries and all, except the Animas River, normally contribute little to its total discharge. During much of the year, discharge is largely controlled by releases from Navajo Reservoir (operated primarily as a water storage and irrigation delivery facility). During summer, however, storm-induced inflows, including that of intermittent tributaries, can substantially increase discharge of the river.

The river, downstream of Navajo Dam, was divided into eight geomorphic reaches (Bliesner & Lamarra 2000): Reaches 1 (RK 0 to RK 27) and 2 (RK 27 to RK 67) had mainly sand and boulder substrata. Sand and silt, locally mixed with gravel and cobble, were the most common substrata in Reach 3 (RK 68 to RK 106). Reach 4 (RK 107 to RK 130) was geomorphically transitional between Reaches 5 and 3; sand was common, but cobble and gravel were present throughout Reach 4. Cobble and gravel were predominant substrata in most of Reaches 5 (RK 131 to RK 154) and 6 (RK 155 to RK 180). The two upper-most reaches (Farmington to Navajo Dam) were outside our study area. The river was restricted to a single channel in canyon-bound Reaches 1 and 2. Channels (primary and secondary) in Reach 3 tended to be broader and less shaded than those in upper reaches. Riparian vegetation (mainly non-native Russian olive and tamarisk) was denser along Reaches 5 and 6 than Reaches 4 and 3. Secondary channels were uncommon in Reach 6, but Reaches 3, 4 and 5 had abundant secondary channels. Secondary channels had a higher proportion (per area) of low-velocity habitats than the primary channel.

Methods

Data on ^{13}C and ^{15}N isotope signatures of the San Juan River fish assemblages and their potential food were collected from Reaches 1 through 6 between 7 and 13 July, 2003. Fishes were collected from wadeable habitats (<1.5 m deep) with seines. Of the large-bodied fishes collected (e.g., flannel-mouth sucker *Catostomus latipinnis*, bluehead sucker *Catostomus discobolus*, channel catfish and common carp *Cyprinus carpio*), only juveniles were used in our analyses. Macro-invertebrates were collected from habitats with coarse substrata (>64 mm in diameter) and visibly flowing water with a kick net. A core sampler and a 250 μm sieve were used to sample macro-invertebrates from habitats with fine substrata and low current velocity. Macro-invertebrates were separated from algae and detritus and allowed to evacuate their guts in a container with freshwater overnight. Fine particulate organic matter (FPOM) was scraped from the substrate into a sealable plastic bag.

Suspended organic matter was collected by filtering 4 l of water through a glass fiber filter (Gelman A/E, 1 μ m pore size). All materials were immediately frozen on dry ice and returned to the laboratory for processing.

Tissue samples from fishes and other organisms were thawed, dried at 50°C for 48 h, and ground to a powder with mortar and pestle. Algae were separated from FPOM by centrifuging in colloidal silica as described by Hamilton & Lewis (1992). The light fraction of the FPOM was confirmed to be primarily diatoms through microscopic examination, thus herein referred to as algae. We analyzed both the composite FPOM sample and the algae separately. Ground samples were analyzed using a ThermoFinnigan Delta Plus mass spectrometer. Stable isotope ratios were calculated in standard notation:

$$\delta^{15}\text{N} = \left[\frac{^{15}\text{N}}{^{14}\text{N}}_{\text{sample}} / \frac{^{15}\text{N}}{^{14}\text{N}}_{\text{standard}} \right] - 1 \times 1000$$

$$\delta^{13}\text{C} = \left[\frac{^{13}\text{C}}{^{12}\text{C}}_{\text{sample}} / \frac{^{13}\text{C}}{^{12}\text{C}}_{\text{standard}} \right] - 1 \times 1000$$

Values were expressed on a per mil (‰) basis. Because carbonates are known to bias carbon isotope ratios, a separate aliquot was taken from organic matter (non-fish) samples, acidified to remove carbonates, and then analyzed as described above.

When available, tissues from three separate individuals were collected to represent fish species at each site. We felt the use of three, or in some instances fewer, individuals was adequately representative because there was little variability in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ among individual fishes from the same site; mean coefficient of variation (CV; mean/SD * 100) = $2.28 \pm 1.24\%$ SD for $\delta^{13}\text{C}$ and mean CV = $4.70 \pm 4.36\%$ SD for $\delta^{15}\text{N}$. For invertebrates, FPOM and algae, a single composite sample (many individuals) was used to represent those groups at each site, thus should represent a robust estimate for the site.

Data analysis

Resource use in primary and secondary channels

In Reaches 3, 4 and 5, we obtained samples from both primary and secondary channels. We excluded Reaches 1, 2 and 6 because secondary channels were rare in Reach 6 and absent in Reaches 1 and 2. Fishes not sampled in both

primary and secondary channels in each reach also were excluded, leaving five species for these analyses. To test for differences in $\delta^{13}\text{C}$ signatures between secondary and primary channels we used a factorial ANOVA with sample reach as a covariate to control for variation attributed to longitudinal position. In addition, we used ANOVA to test for differences in trophic position of fish species between primary and secondary channels. Trophic position was calculated relative to average $\delta^{15}\text{N}$ of a dominant primary consumer at each study site following the formula of Cabana and Rasmussen (1996), which assumes a 3.4‰ enrichment in $\delta^{15}\text{N}$ of animals relative to their diet:

Trophic position

$$= [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{primary consumer}}) / 3.4] + 2$$

We chose mayfly larvae (Ephemeroptera) over chironomids as the primary consumer because they were larger and, as reported in Cabana and Rasmussen (1996), were expected to have lower variability in $\delta^{15}\text{N}$ across sites. Separate ANOVAs were used to test for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of macro-invertebrates (2 taxa) and benthic organic matter between primary and secondary channels. Prior to analysis, all data were evaluated for normality and appropriate transformations were applied to reduce heteroscedasticity.

Longitudinal variation in resource use

Biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all items were generated for each river reach to qualitatively evaluate differences in food web structure among reaches. In addition, we used separate two-way ANOVAs for each trophic group (fishes, macro-invertebrates and FPOM) to simultaneously test for differences in $\delta^{13}\text{C}$ isotope signatures and trophic position (or $\delta^{15}\text{N}$) among taxa (fishes and macro-invertebrates) and across reaches. In reaches with secondary channels, we pooled data for taxa that were collected in both primary and secondary channels.

Resource overlap among native and non-native fishes

Mean $\delta^{13}\text{C}$ and trophic position for native (n = 3) and non-native fish species (n = 7) were compared using ANCOVA. For these analyses, we only used isotopic signatures and trophic position for fishes

collected in Reaches 3, 4, 5 and 6. Reaches 1 and 2 were excluded because too few specimens (< 3) of native species were collected. To control for potential interactions with longitudinal and lateral position, we used reach and channel type as covariates.

Correlates with $\delta^{13}C$ and trophic position

The $\delta^{15}N$ signature of fishes relative to basal resources (i.e., trophic position) should be greatest in fishes that consume primarily high trophic level food (e.g., macro-invertebrates vs. algae; Cabana & Rasmussen 1996). Thus, we evaluated our ability to predict trophic position of fish based on the proportion of macro-invertebrates in the diet using linear regression analysis. Food habits of all fishes that were used in the stable isotope analysis were quantified based on the contents of the upper portion of the gut to the first bend in the digestive tract (Bowen 1996). Contents were spread on a 0.8 mm grid in a petri dish, macro-invertebrates were identified to order or family, and percent area for each food item was recorded. We assumed the area each diet item occupied on the grid was proportional to its volume (Hellawell & Abel 1971) to get relative proportions of macro-invertebrates and algae.

Because algae in habitats with higher current velocity should be more depleted in $\delta^{13}C$ (Finlay et al. 1990), and because these basal levels of $\delta^{13}C$ should be relatively conserved in consumers ($\Delta\delta^{13}C < 1\text{‰}$; Peterson & Fry 1987, Vander Zanden & Rasmussen 2001), we tested our ability to predict $\delta^{13}C$ of fishes based on habitat use using regression analysis. Although we did not characterize habitat use in this study, mean current velocity in habitats used by each of the species collected for this study was reported in a previous study (range 0.3–48.9 cm s^{-1} ; Appendix II in Gido & Propst 1999).

Results

Of the 11 fish species collected, only two native (*C. latipinnis* and *R. osculus*) and one non-native (*C. lutrensis*) species were captured in Reaches 2 through 6, and in both primary and secondary channels. *Pimphales promelas* and *I. punctatus* were only missing from one reach each (Reach 2 and 6, respectively), and therefore were included in the analysis contrasting channel types. Only *C. lutrensis* was captured in Reach 1, thereby eliminating Reach 1 from our statistical analyses.

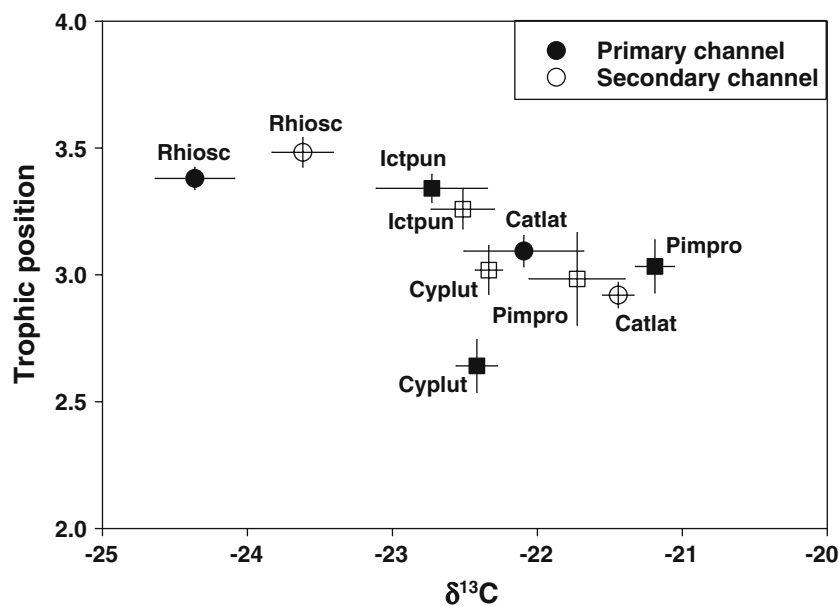


Figure 2. Mean (\pm SE) $\delta^{13}C$ and trophic position of fishes in sample reaches 3, 4, and 5. Values for each species are plotted separately for primary and secondary channels. Circles represent native species and squares non-native species. Species codes are given in Table 1.

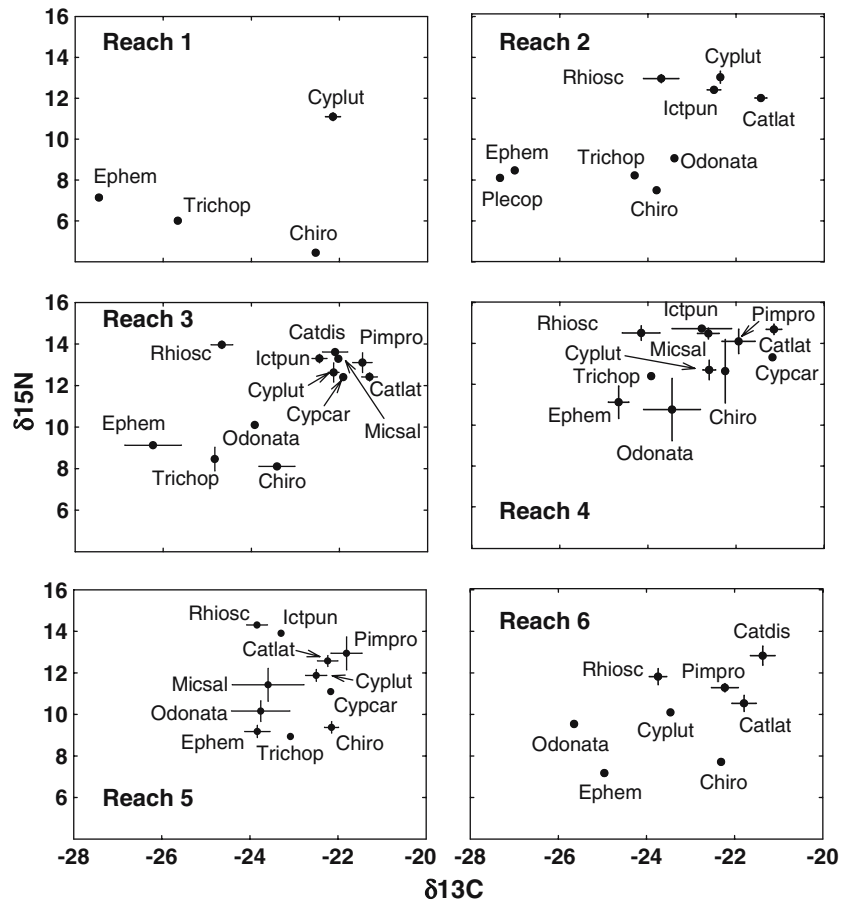


Figure 3. Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fishes and macro-invertebrates for each reach sampled. Items with similar values indicate similar positions in the food web. Species codes are given in Table 1.

In addition, the only macro-invertebrate taxa collected across all reaches and channel types were ephemeropterans and chironomids. Thus, our analyses of lower trophic groups were restricted to comparisons of these taxa, as well as FPOM and algae. All species analyzed in addition to Reach 1 data, however, were included in Figure 3 to illustrate general patterns.

Resource use in primary and secondary channels

Although the main effect of channel type was not significant for either $\delta^{13}\text{C}$ or trophic position, there was a significant interaction between species and channel type for trophic position ($F_{4,82} = 2.741$, $p = 0.049$) and marginally significant interaction for $\delta^{13}\text{C}$ and channel type

($F_{4,84} = 2.147$, $p = 0.082$). In general, there was less variation in isotopic signatures and trophic position among species in secondary channels ($CV_{\delta^{13}\text{C}} = 3.5\%$; $CV_{\text{TP}} = 7.4\%$) than in the primary channel ($CV_{\delta^{13}\text{C}} = 5.3\%$; $CV_{\text{TP}} = 12.0\%$; Figure 2). There was no difference in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between primary and secondary channels for macro-invertebrates, FPOM, or algae (all p -values > 0.500).

Longitudinal variation in resource use

Fishes, macro-invertebrates, and organic matter differed in their carbon and nitrogen isotopic signatures across reaches (Figure 3). The most notable difference was that all taxa had comparatively high $\delta^{15}\text{N}$ values in Reach 4. Trophic position of

Table 1. Scientific names, taxa codes, sample sizes and grand mean isotopic signatures of fishes averaged across all reaches and channel types. Number of samples represents the number of individuals for fishes and the number of composite samples from sites for macro-invertebrates, algae and FPOM.

Scientific name	Taxa code	Number samples	Grand mean $\delta^{13}\text{C}$	Grand mean $\delta^{15}\text{N}$
<i>Amierus melas</i>	AMENAT	2	-20.12	8.04
<i>Catostomus discobolus</i>	CATDIS	8	-21.96	12.95
<i>C. latipinnis</i>	CATLAT	33	-21.71	13.04
<i>Cyprinus carpio</i>	CYPCAR	7	-22.11	11.65
<i>Cyprinella lutrensis</i>	CYPLUT	29	-22.39	12.42
<i>Fundulus zebrius</i>	FUNZEB	1	-17.51	9.49
<i>Ictalurus punctatus</i>	ICTPUN	12	-22.60	13.55
<i>Micropterus salmoides</i>	MICSAL	10	-22.85	13.44
<i>Pimephales promelas</i>	PIMPRO	21	-21.62	12.82
<i>Ptycocheilus lucius</i>	PTYLUC	3	-22.34	13.63
<i>Rhinichthys osculus</i>	RHIOSC	25	-23.88	13.72
Chironomidae	Chiro	9	-22.73	8.88
Ephemoptera	Ephem	9	-25.43	9.07
Odonata	Odonate	7	-23.91	10.08
Trichoptera	Trichop	7	-24.40	8.86
Algae	Algae	8	-25.23	6.64
Fine particulate organic matter	FPOM	7	-23.73	6.75

fishes showed a significant species \times reach interaction ($F_{14,94} = 2.042$, $p = 0.022$), suggesting a different trophic relationships among species across reaches. This shift was related mainly to a decline in trophic position of *C. lutrensis* in reaches 4, 5 and 6, whereas other species trophic position remained constant across reaches (Figure 4).

Resource overlap among native and non-native fishes

Using reach and channel type as covariates, there was a significant difference in $\delta^{13}\text{C}$ ($F_{1,113} = 4.96$,

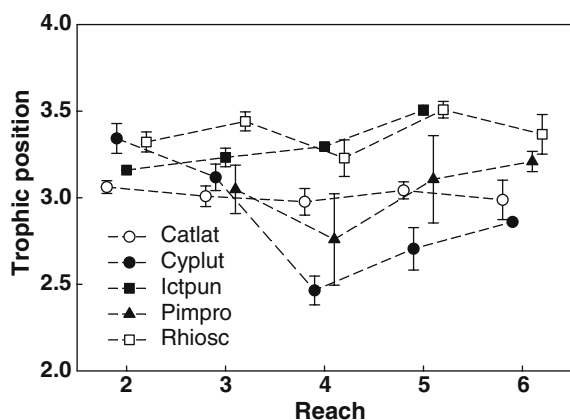


Figure 4. Mean (\pm SE) trophic position for common species across Reaches 2–6. Native fishes are represented by open symbols and non-natives by closed symbols. Species codes are given in Table 1.

$p = 0.028$) and trophic position ($F_{1,113} = 5.85$, $p = 0.017$) between native and non-native fishes. On average, $\delta^{13}\text{C}$ of native fishes (estimated marginal mean = -22.64‰) was more depleted than non-native fishes (-22.18‰), and native fishes fed at a higher trophic position (3.18) than non-natives (3.03).

Correlates with $\delta^{13}\text{C}$ and trophic position

When data from all reaches and channel types were combined, and less abundant taxa included, three distinct trophic levels were apparent; secondary consumers (fishes), primary consumers (macro-invertebrates) and FPOM/algae (Figure 5). Fishes were about one trophic position (enriched 3.8‰) above macro-invertebrates, which were enriched approximately 2.5‰ above FPOM and algae. Although we did not find a correlation between trophic position of fishes and their diet ($r^2 = 0.180$, $p = 0.343$), the narrow range of values among species suggested all fishes acquired energy from approximately the same trophic level.

There was considerable variation in $\delta^{13}\text{C}$ among taxa at all trophic levels. For fishes, much of this variation could be explained by current velocity (Figure 6), as $\delta^{13}\text{C}$ values could be accurately predicted by mean current velocity (square-root transformed) in habitats occupied by these fishes ($r^2 = 0.554$, $p = 0.02$; velocity data from Gido

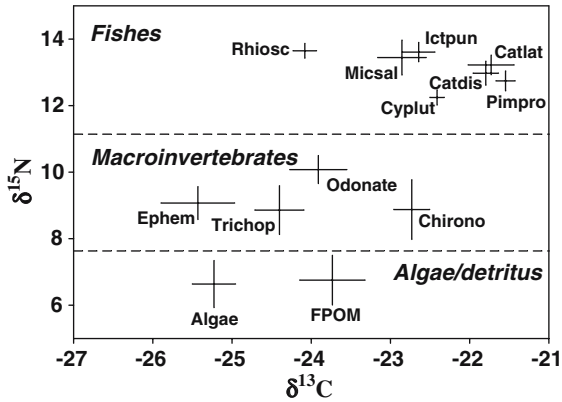


Figure 5. The mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for common species across all reaches and channel types. Species codes are given in Table 1.

& Propst 1999). However, most fishes typically occupied low-velocity habitats; and the observed pattern was largely driven by *R. osculus* and *I. punctatus*, which tended to occur in habitats (e.g., riffles and runs) with higher current velocity (and lower $\delta^{13}\text{C}$).

Discussion

Results of this study provide a framework that can be used to characterize trophic interactions across habitats in the San Juan River. Specifically, we found one species (*C. lutrensis*) to vary longitudinally

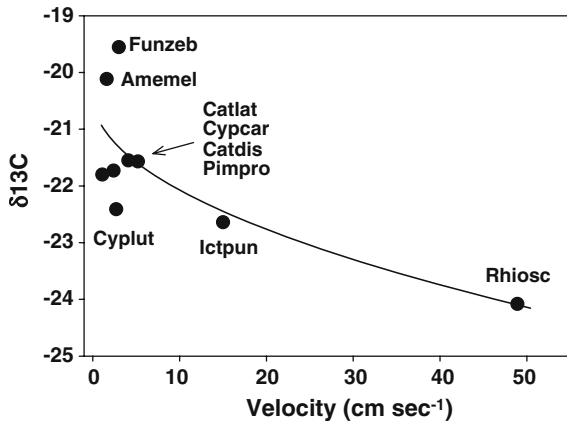


Figure 6. $\delta^{13}\text{C}$ values plotted against water velocity of habitat occupied by fishes. Regression line was fit to the equation: $\delta^{13}\text{C} = -0.528 * \text{squareroot}(\text{velocity}) - 20.40$. Species codes are given in Table 1.

in trophic position, as well as differences in trophic interactions between secondary and primary channels. There was a strong tendency for the $\delta^{15}\text{N}$ signature of examined taxa to peak in Reach 4, likely a consequence of runoff from agricultural lands and sewage effluent (e.g., Steffy & Kilham 2004) in reaches between Shiprock and Farmington (mainly Reaches 5 and 6). After controlling for these baseline levels of $\delta^{15}\text{N}$, trophic position of *C. lutrensis* was lower in samples taken from these upstream reaches. There are a number of biotic and abiotic factors that vary longitudinally in the San Juan River that could cause a trophic shift by *C. lutrensis*, including the influence of reservoir releases, nutrient loading, geomorphology, and fish community composition and structure. Although our most-upstream sample site was 44 km downstream of Navajo Dam, water temperature there was cooler, turbidity lower, and nutrient loading higher than in downstream reaches. River substrata also shifted from predominantly cobble, gravel, and sand in the upper reaches to mostly silt and sand in the lower reaches. In addition, abundance of native fishes was greatest in upstream reaches, and, in particular, the abundance of *C. lutrensis* was substantially less (Propst & Gido 2004). Regardless of these distinct longitudinal patterns, there was no clear indication why *C. lutrensis* would feed at a lower trophic level in upstream reaches. Based on lower abundance of *C. lutrensis* in upper reaches, we only can speculate these reaches provided sub-optimal habitats for *C. lutrensis*, and as a generalist water-column omnivore (Hale 1962), they were forced to shift their diet to a lower trophic level. Whether such a presumed diet shift was the result of interactions with other species or a result of resource availability is unknown.

Differences in $\delta^{13}\text{C}$ and trophic position between the primary and secondary channel indicated that fishes living in secondary channels converge on a similar resource, as indicated by a significant interaction between species and channel type for trophic position, and marginally significant difference for $\delta^{13}\text{C}$ (Figure 2). Because secondary channels have a narrower range of habitat conditions (mainly manifested by greater proportion of low-velocity habitats) than the primary channel, food variety may be restricted to comparatively few invertebrate taxa. In addition, increased light penetration to benthic surfaces in

secondary channels (KBG, personal observation) might increase productivity of those taxa, further increasing overlap in resource use among species. Although convergence of $\delta^{13}\text{C}$ among fishes in secondary channels was not significant ($p=0.082$), this trend was consistent with the narrower range of velocities (i.e., predominately low-velocity) in these channels.

The use of stable isotopes provided an index of trophic position and habitat use, both of which suggested a high degree of overlap among native and non-native fishes. When pooled across reaches and channels, it appeared that all fishes fed as secondary consumers and occupied low-velocity habitats, with the exception of *R. osculus* and possibly *I. punctatus*. These patterns of habitat use, as inferred by $\delta^{13}\text{C}$, were consistent with a previous study that quantified habitat use of these species (Gido & Propst 1999). However, both isotopic signatures and coarse habitat measurement may not reflect resource partitioning at extremely fine spatial scales (e.g., 1–100 cm). Nevertheless, based on the conservation of $\delta^{13}\text{C}$ across trophic levels, it also appeared that the primary invertebrate prey for small-bodied fishes in the San Juan River were chironomids. This was supported by the diet, in that 28.9% (by volume) of the food items consumed were chironomids.

Isotopic signatures also suggest the basal source of energy in these food webs was detritus, as the $\delta^{13}\text{C}$ of chironomids and most fishes was much more enriched than algae separated from our FPOM samples. Although we did not have a pure detritus sample (FPOM was a composite of algae and detritus), we assumed the $\delta^{13}\text{C}$ of the non-algal fraction of the FPOM to be enriched relative to algae, thus indicating a terrestrial carbon sources (i.e., riparian vegetation; Finlay 2001) as the basal energy source for fishes.

Although our diet data were limited (i.e., in most cases <10 individuals were examined for diet), the general order that species were ranked according to prevalence of macro-invertebrates in their diet (i.e., *P. promelas* and *C. discobolus* as herbivore/detritivores and *R. osculus* and *M. salmoides* as invertivores) is consistent with diet reported in the literature (e.g., Angradi et al. 1991, Childs et al. 1998). The lack of concordance between diet and trophic position might have been because of inadequate representation of the diet

because of small sample sizes and the short temporal scale of sampling. However, low variation in trophic position among fishes indicated that energy acquisition from algae and detritus was low, and most species acquired a substantial proportion of their energy from macro-invertebrates.

Abiotic and biotic characteristics changed longitudinally in the San Juan River. In particular, native species were less abundant than non-natives in low-velocity habitats in downstream reaches (Propst & Gido 2004). Our isotope data concurred with previous studies that reported concentration of small-bodied fishes in low-velocity habitats and additionally indicated their primary food was chironomids (Childs et al. 1998, Fisher et al. 2001). With the exception of *C. lutrensis*, this pattern was consistent along the longitudinal gradient of the river. Laterally, convergence in resource use was greatest in secondary channels, suggesting the greatest potential for negative interactions among native and non-native fishes occurs in these habitats. Our findings thus raise several questions relevant to conservation of the native fish fauna of the San Juan River. First, is high resource-use overlap in secondary channels because resources are limiting or because specific resources (i.e. low-velocity habitat and prey taxa) are highly abundant? Field studies that evaluate the relationship between resource abundance and growth or survival of fishes might provide insight into this question.

A second question that arises from this study concerns the role of primary channel habitats in alleviating resource overlap among native and non-native fishes. Primary channels clearly provide important habitats for many large-bodied native and non-native fishes. These channels also provide larger, more heterogeneous habitats and food resources, thus potentially reducing competitive interactions among small-bodied species. Alternatively, essential resources may be scarce and predator densities may be high in primary channel habitats, thus driving small-bodied fishes into low-velocity habitats of secondary channels. Because habitats in the San Juan River have been highly modified by abatement of natural flows and encroachment of non-native riparian vegetation, studies to investigate interactions of habitat heterogeneity and food web dynamics would help evaluate the relative importance of habitat

modifications for the conservation of native fishes. In particular, conservation of native fish populations will require the maintenance or enhancement of habitats necessary to sustain all life stages of native fishes.

Implications for management of native fishes

Through the use of stable isotopes, we qualitatively estimated energy pathways for fishes in the San Juan River. This information can be used by managers to predict how various management activities (e.g., hydrologic modification, non-native species removals) will alter energy availability for native fishes. Absent from our analyses were samples from endangered *P. lucius* and *X. texanus*. Considerable effort, including stocking, are currently underway to restore both species to the San Juan River. It remains uncertain if success (loosely defined herein as maintenance of self-sustaining populations) can be achieved in a system where a large proportion of resources are consumed by non-native fishes. In addition, it is unknown which habitats are critically needed by each life stage in this highly modified system to assure their persistence. If resource use (habitat and food) tendencies of young *P. lucius* and *X. texanus* are similar to those of species reported herein, it will be challenging to enhance their resource availability without benefiting non-native fishes. Quantitative evaluation of resource use among *P. lucius* and *X. texanus*, other native fishes, and non-native fishes would aid in refining and improving restoration efforts in this system.

Acknowledgements

Assistance in the field was provided by G. Layne Knight. Funding to K. Gido and D. Propst was provided by The San Juan River Basin Recovery Implementation Program via U.S. Bureau of Reclamation. Analysis of stable isotopes was conducted at the Stable Isotope Mass Spectrometry Laboratory (SIMSL) in the Division of Biology at Kansas State University with the assistance of Roxane Fagan. Collecting permits were graciously provided by Navajo Nation, US Fish and Wildlife Service, and New Mexico Department of Game and Fish. Use of animals in this research was

approved by Kansas State University Institutional Animal Care and Use Committee (Protocol number 2177).

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