

## FOOD WEB IMPLICATIONS OF $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ VARIABILITY OVER 370 KM OF THE REGULATED COLORADO RIVER USA

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Dual stable isotope analysis in the regulated Colorado River through Grand Canyon National Park, USA, revealed a food web that varied spatially through this arid biome. Down-river enrichment of  $\delta^{13}\text{C}$  data was detected across three trophic levels resulting in shifted food webs. Humpback chub  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from muscle plugs and fin clips did not differ significantly. Humpback chub and rainbow trout trophic position is positively correlated with standard length indicating an increase in piscivory by larger fishes. Recovery of the aquatic community from impoundment by Glen Canyon Dam and collecting refinements for stable isotope analysis within large rivers are discussed.

*Keywords:* *Cladophora*; Drift; Glen Canyon Dam; Macroinvertebrates; Native fish; Arid-biome river; Stable isotopes

### INTRODUCTION

Defining aquatic food webs using stable isotopes is becoming more routine as technology in mass spectrometry is further refined and more economically feasible. Typically, organic sources of an aquatic food web are estimated through determining the ratio between  $^{12}\text{C}$  and  $^{13}\text{C}$  ( $\delta^{13}\text{C}$ ) while trophic position is assigned with an estimate of the ratio between  $^{14}\text{N}$  and  $^{15}\text{N}$  ( $\delta^{15}\text{N}$ ) [1]. Studies have only recently examined the variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values over an extended aquatic community [2, 3]. In

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this study we investigated the variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data over a 370 km reach of the Colorado River drainage below Glen Canyon Dam (GCD) between 1997 and 1999.

Accordingly, this study had two objectives: 1) determine if there were spatial patterns in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements for algae, macroinvertebrates and fish in the aquatic community below GCD; 2) evaluate the relationship between standard length and  $\delta^{15}\text{N}$  measurements for a native and non-native fish.

### STUDY SITE

The aquatic community of the Colorado River in Grand Canyon National Park is structured by consistently cool ( $\sim 10^\circ\text{C}$ ) and clear releases from GCD, while tributaries create seasonally turbid conditions (Fig. 1) [4]. Including chironomids, the macroinvertebrate assemblage is comprised of < 60 species for the entire study area. This is likely in response to the combination of cool stenothermic conditions removing thermal cues needed for aquatic insects to complete their life history, and turbid conditions (due to tributary spates) reducing light availability and scouring the phyto-benthic community. Instability in flow from hydro-electric production also selects for algae and macroinvertebrates that can tolerate wide ranges of water velocity. Hydro-power is produced by GCD through fluctuating the discharge in response to electrical demand. Therefore, discharge varies on a seasonal, monthly, weekly, daily and hourly basis with a minimum flow of  $142\text{ m}^3/\text{s}$  and maximum flow of  $708\text{ m}^3/\text{s}$ . Water quality parameters including dissolved oxygen, pH and conductivity are usually consistent due to the hypolimnetic releases from GCD [4].

Tributaries within the study area consist of two types: 1) those that originate within Grand Canyon from springs and 2) watershed tributaries that originate from outside of the National Park [5]. Spring-source tributaries have higher biomass and richer benthic assemblages than the watershed tributaries. However, particulate organic drift at base flow is higher in watershed side streams than those originating from springs due in part to larger drainage areas.

Angradi [2] constructed a food web using  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  analysis in Glen Canyon, the tailwaters of GCD near Lees Ferry, and in selected tributaries downriver. Angradi [2] reported a food web dependent on *Clado-*

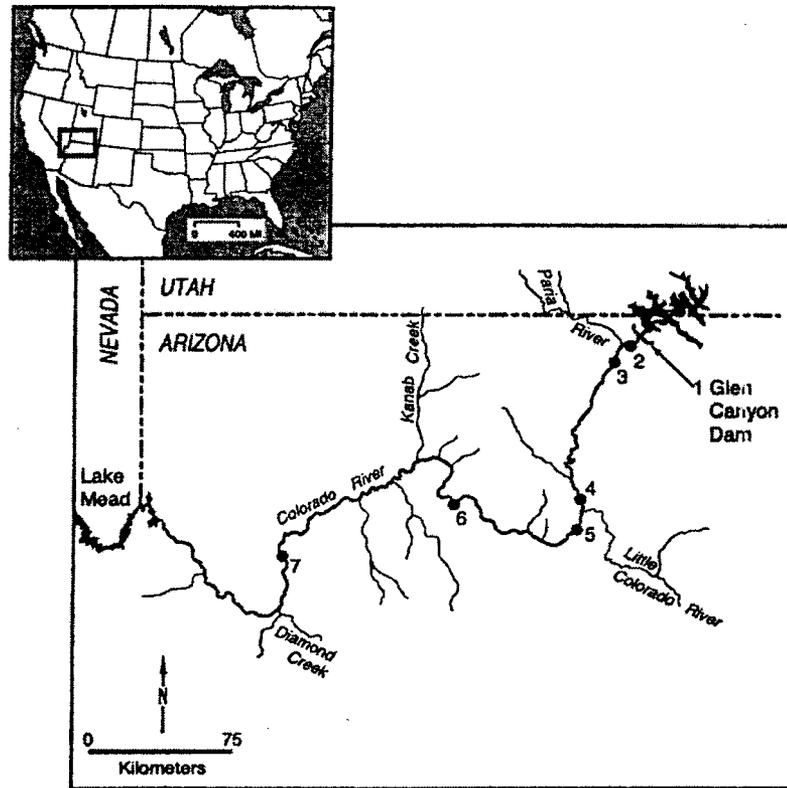


FIGURE 1 Collection sites below Glen Canyon Dam in the Colorado River through Grand Canyon National Park, Arizona, USA. Lees Ferry is designated as 0.0 River Kilometer (RKM).

Site	Name	RKM	Trophic Level		
			Algae	Macroinvertebrates	Fish
1	Glen Canyon Gauge	-23.2	18	6	54
2	Lees Ferry Gauge	0.0	31	54	27
3	2 Mile Walk	3.1	15	3	3
4	60 Mile Wash	95.7	15	12	36
5	Tanner Cobble	109.6	15	12	72
6	127 Mile Rapid	202.9	12	30	12
7	205 Mile Rapid	328.8	21	39	24

*phora glomerata*, a green filamentous alga, as the carbon source in Glen Canyon (the first 25 km below GCD) while fish near tributaries were dependent on carbon derived from that tributary. *Cladophora* is a common alga in many rivers and is a structural host for epiphytic diatoms that are grazed by macroinvertebrates in the Colorado River [6–8]. *Cladophora* biomass is not consistent throughout the river corridor due to storm related tributary input of suspended sediments and the amount of GCD discharge fluctuation [9–11].

Eight native fish were present in Grand Canyon at the turn of the century, with five remaining today including the humpback chub (*Gila cypha*) [12]. Introduction of some 20 alien fish species into this segment of the Colorado River began in the late 1800s with channel catfish (*Ictalurus punctatus*) and continues today with the annual release of thousands of rainbow trout (*Salvelinus gairdneri*) in the tailwaters of GCD by the Arizona Game and Fish Department [13, 14].

## METHODS

Benthic primary producer ( $n = 103$ ) and macroinvertebrate samples ( $n = 156$ ) were collected at seven locations below GCD in the spring, summer and fall from July 1997 through March 1999 (Fig. 1). These sites were selected to bracket the two largest perennial tributaries, the Paria River at river kilometer (rkm 1.0) and the Little Colorado River (rkm 98.6). Near-shore drift samples ( $n = 24$ ; 0–0.5 m deep) collections were taken in triplicate between 10:00 h and 15:00 h with a circular tow net (48 cm diameter opening with 500  $\mu\text{m}$  mesh) held in place behind a moored pontoon raft or secured to the river bank in March 1999. Samples were processed live within 48 h and sorted into *Cladophora* and detritus categories. Detritus was comprised primarily of allochthonous (tributary upland and riparian vegetation) flotsam.

Samples from eight fish taxa ( $n = 228$ ) were collected for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses from October 1997 through August 1998 at 17 sites from GCD to Diamond Creek (rkm 361.6; see Fig. 1 for site locations). These additional fish collection sites were grouped into the nearest benthic collection site. Samples from protected native fish, such as the humpback chub, were collected without harm using fin clips on small fish (<100 mm) while both fin clips and muscle plugs (removed with biopsy needles) were taken on large fish (>100 mm). Samples from alien fish also included muscle tissue and

fins. Fish standard length was recorded at the time of collection and grouped into the following size categories: 50–99, 100–149, 150–250 and >250 mm. Fishes were collected, air-dried in the field and kept on ice until they were oven-dried in the laboratory at 60 °C.

Water quality parameters were collected with a Hydro Lab Scout II<sup>®</sup> at the time of benthic collections. These parameters included temperature (°C), hydrogen-ion concentration (pH), specific conductance (mS/cm), dissolved oxygen (mg/l), and percent saturation of dissolved oxygen. Turbidity was estimated with a Secchi disk to determine water transparency and with a VWR Turbidimeter 200<sup>®</sup> (NTU).

Samples are ground to a fine powder with a Whir-L-Bug<sup>®</sup> and weighed in tin capsules (8 × 5 mm). Dual isotope data were measured with a Finnigan Delta Plus XL<sup>®</sup> mass spectrometer configured for continuous flow analysis of samples after Dumas combustion for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  determinations. All data were reported in ‰ relative to Pee Dee Belemnite (PDB), the standard for  $\delta^{13}\text{C}$  and air as a standard for  $^{15}\text{N}$ .

Collections below GCD through Grand Canyon are logistically constrained because of limited access. Collecting stations can only be accessed by white water rafting expeditions that take over 2 weeks to complete. Therefore, simultaneous collections of all sites over 370 km of difficult traveling is near impossible, so collection dates were combined into 35 day intervals with the month of the median date indicated as that sampling period.

#### Data Analysis

Multiple analysis of variance (MANOVA) was used to determine if spatial changes occurred in carbon source across trophic levels in the Colorado River below GCD. Response variables for each analysis were algae, macroinvertebrates and fish with collection site the predictor variable.

Multiple regression analysis was used to determine the relationship between *Cladophora*  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for cobble and drift samples over distance from GCD. Three independent and equal size ( $n=3$ ) samples of *Cladophora* from both habitats at sites 1, 2, 5, 6 and 7 were collected in March 1999.

Fin clip and muscle plug  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data from humpback chubs were examined with Student *t*-test in order to determine if each sampling technique was representative of the fishes isotopic composition. Fish size class  $\delta^{15}\text{N}$  data were analyzed using analysis of variance (ANOVA) with

Bonferroni adjustment for comparison of probabilities between size classes ( $\alpha = 0.03$ ).

All analysis of variance tests were done with SYSTAT version 5.2 [15] statistical software on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data without transformations.

## RESULTS

### Spatial Variability

*Cladophora* (cobble habitat), macroinvertebrates, and fish were all significantly enriched in  $\delta^{13}\text{C}$  with distance downriver for all collection dates (Wilks Lambda  $f = 12.1$ ;  $df = 12$ ;  $n = 702$ ;  $P < 0.001$ ; Fig. 2). These analyses showed a  $\delta^{13}\text{C}$  enrichment of 10‰ for algae, 7‰ for macroinvertebrates and 4‰ for fish over the 350 km study area. Standard deviations of the mean for each of the  $\delta^{13}\text{C}$  measurements depicted both temporal and within a collection site variation (Fig. 2), but were less than the spatial enrichment totals for each trophic level over the entire study area. Therefore, on average, spatial variability was greater than temporal variability for  $\delta^{13}\text{C}$  during the periods sampled.

We detected a significant enrichment in values of *Cladophora*  $\delta^{13}\text{C}$  with distance downriver from GCD within the same sampling period in March 1999 (Fig. 3). This *Cladophora*  $\delta^{13}\text{C}$  data illustrated that the multiple sampling data (Fig. 2) was not biased by temporal patterns.

*Cladophora* collected directly from cobbles and drifting *Cladophora*  $^{13}\text{C}$  were both more enriched at downriver sites but each habitat had different rates of enrichment. Drifting *Cladophora* was  $^{13}\text{C}$  enriched about 2.2‰ over a 350 km distance while *Cladophora* collected from cobbles was  $^{13}\text{C}$  enriched about 7.1‰ over the same distance. *Cladophora* showed no predictable relationship between collection sites and  $\delta^{15}\text{N}$  data for either drifting ( $P = 0.55$ ) or cobble ( $P = 0.06$ ) habitats.

Humpback chub  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data from muscle plugs and fin clips did not differ significantly and were combined for analysis ( $n = 27$ ;  $P = 0.4$ ). McCarthy and Waldron [16] also reported that adipose fin and white muscle  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements were statistically insignificant for the brown trout (*Salmo trutta*).

Trophic position, as indicated by  $\delta^{15}\text{N}$  data, was significantly ( $P < 0.01$ ) and positively related to size class indicating a change in feeding behavior

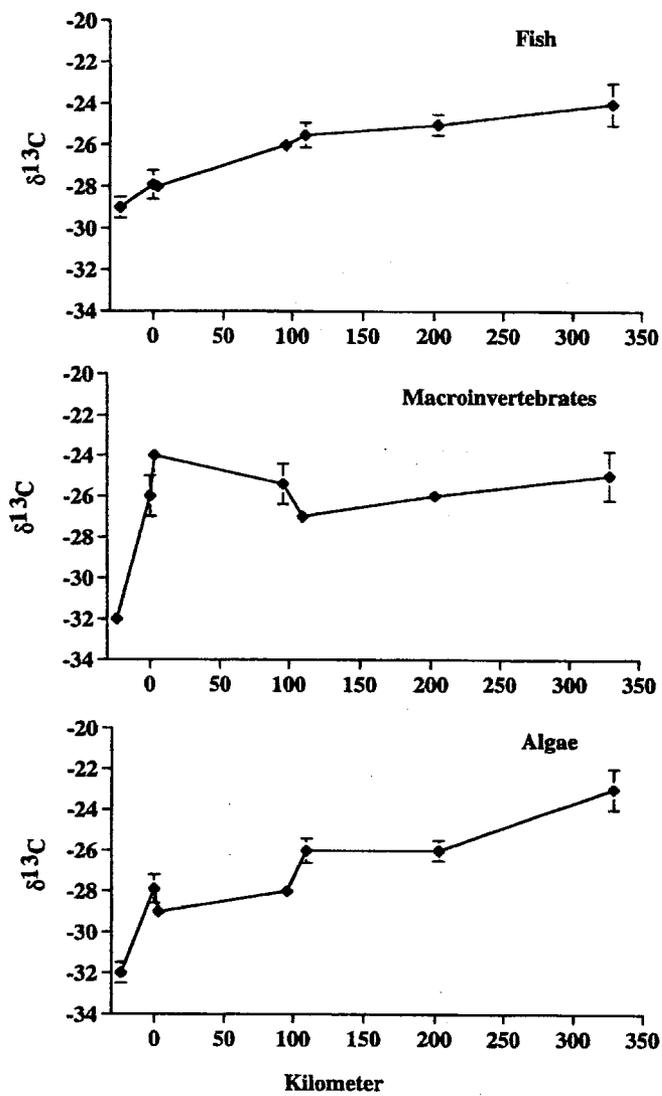


FIGURE 2 Average *Cladophora glomerata*, macroinvertebrate and fish  $\delta^{13}\text{C}$  data (in ‰,  $\pm$  s.d.) from the Colorado River below Glen Canyon Dam, AZ. Collections were from June 1996 through March 1999.

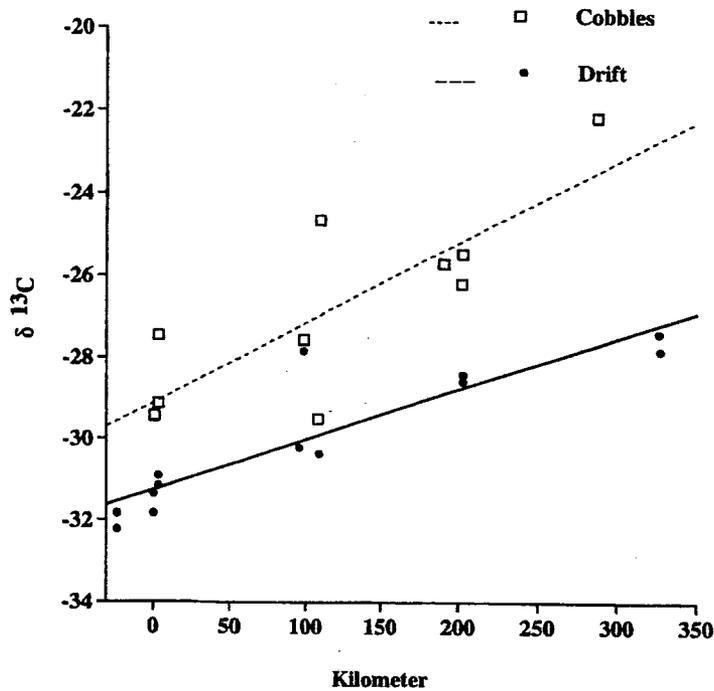


FIGURE 3 *Cladophora glomerata*  $\delta^{13}\text{C}$  data (in ‰) comparing cobble bar and drift habitats in the Colorado River below Glen Canyon Dam, AZ. Linear regression analysis indicated a significant  $\delta^{13}\text{C}$  enrichment for *C. glomerata* from cobbles ( $P = 0.001$ ;  $r^2 = 0.70$ ;  $n = 24$ ) and drift ( $P < 0.001$ ;  $r^2 = 0.82$ ;  $n = 24$ ) with distance from Glen Canyon Dam.

between size classes for both humpback chub and rainbow trout (Fig. 4). Values for  $\delta^{15}\text{N}$  suggested that smaller size classes fed on aquatic macroinvertebrates while larger fish had a more varied diet including fish as indicated by a 2‰ depletion across all four size classes.

### Water Quality

The temperature of Colorado River during the study period ranged from 8.6 °C at Lees Ferry in March 1988 to 14.9 °C at rkm 326 in June 1998. The average temperature was 10.5 °C ( $\pm 1.4$  s.d.) for all collection sites and dates. The pH of the Colorado River during the study period ranged from 7.7 at Lees Ferry in October 1997 to 8.3 at rkm 326 in October

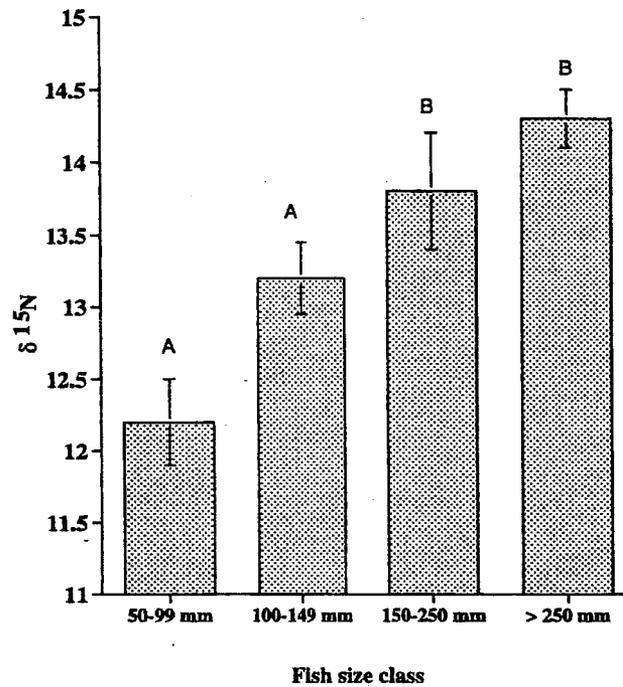


FIGURE 4 Fish size class and average  $\delta^{15}\text{N}$  values (in ‰,  $\pm$  s.d.) from humpback chub and rainbow trout collected from Colorado River below Glen Canyon Dam. Letters indicate significant differences between size classes ( $P < 0.03$ ).

1998. The average pH was 7.9 ( $\pm 0.2$  s.d.) for all collection sites and dates. Conductivity of the Colorado River during the study period ranged from 0.63 mS/cm at Lees Ferry in October 1998 to 0.89 mS/cm at rkm 326 in June 1998. The average conductivity was 0.77 mS/cm ( $\pm 0.07$  s.d.) for all collection sites and dates.

Dissolved oxygen concentrations (DO) of the Colorado River during the study period ranged from 8.6 mg/l at Lees Ferry in March 1999 to 14.0 mg/l at rkm 326 in March 1999. The average DO concentration was 12.3 mg/l ( $\pm 4.8$  s.d.) for all collection sites and dates. These data are typical for seasonal and site variability. Lake Powell in-flow, elevation, and resulting stratification account for the variability in DO near GCD while more than 165 rapids account for mechanical aeration of the river [6]. Percent DO saturation reflects this pattern with the water released from GCD at 70% saturation and increasing to 88% at Lees Ferry 25 km

downriver. By 100 km downriver water reached 100% saturation of DO and increased to 118% at rkm 326.

Turbidity varied both seasonally and between sites. The first 25 km below GCD had consistently clear water with Secchi depths > 7 m and NTU values always < 3. Below the first perennial tributary (Paria River, rkm 1.0) Secchi depths did not exceed 2 m and NTU values were always > 10.

## DISCUSSION

Dual stable isotope analysis in the Colorado River through Grand Canyon revealed a food web that varied spatially through 370 km of this arid biome. Fish trophic position was positively correlated with standard length suggesting piscivory by larger fishes.

Defining the carbon source, using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in constructing an aquatic food web is essential and sometimes problematic. Variability is common in benthic ecology, so it is not surprising that variability in  $\delta^{13}\text{C}$  research is found within complex benthic habitats. France [17] was critical of using stable isotope analysis in aquatic food webs because of the lack of consistency in algal  $\delta^{13}\text{C}$  values throughout the literature. Doucett [18] refuted the claims of France by justifying the variance as natural and novel to each stream under study. Finlay *et al.* [19] attributed some of this variation to water velocity altering the boundary layer around *Cladophora* filaments and changing the assimilation of dissolved organic carbon, which in turn would alter the  $\delta^{13}\text{C}$  value [20]. Finlay *et al.* [19] reported that *Cladophora*  $\delta^{13}\text{C}$  in high velocity habitats averaged 5‰ greater enrichment compared to low velocity habitats in a comparison of six streams.

Spatial variability in  $\delta^{13}\text{C}$  data for all trophic levels are an indication of the lack of stability in the regulated Colorado River below GCD. The aquatic community in the Colorado River through Grand Canyon continually adjusts between the effects of impoundment (clear, cool and fluctuating discharges) and landscape influence via flash flooding side streams (turbid, sediment and debris-rich discharges). Throughout the study site the trophic link between algae and fish is not linear as it passes through the macroinvertebrates. It is possible that we have neglected to include a carbon source such as tributaries. Shannon *et al.* [21] reported that the tributaries at base-flow contribute < 1% of the particulate organic drift in the mainstem at mean discharge, however, organic inputs from spates has not been quanti-

fied. On the other hand, fish do travel between tributaries. Two sonic tagged flannelmouth suckers were reported to have moved 98 km between the Paria and Little Colorado River in a 3-week period [22]. Watershed influence does not offset the impact of GCD on the structure of the Colorado River aquatic community after 370 km based on stable isotope analyses. Angradi [2] collected dissolved inorganic carbon (DIC)  $\delta^{13}\text{C}$  data in the Paria River at base flow and adjacent mainstem sites and found the Paria to be  $-2.9\text{‰}$  and the adjacent mainstem to be  $-7.0\text{‰}$  ( $\pm 0.1$  s.d.). This suggests that accumulating tributary input of DIC could be the source of downriver  $^{13}\text{C}$  enrichment across trophic levels (Fig. 2). Tributary input appears to play an important role in this pattern with abrupt  $^{13}\text{C}$  enrichment at the two largest perennial tributaries (Paria River; rkm 1.0 and the Little Colorado River; rkm 98.6; Fig. 3). Rosenfeld and Roff [23] reported between site variability for  $\delta^{13}\text{C}$  algal samples from several southern Ontario streams and attributed these deviations to groundwater DIC sources.

Traditional dual stable isotope analysis food web depiction, both average and variance box plots, is not possible for this entire study site because of the spatial variability. Therefore, inclusion or exclusion of sites for specific regions of the study area, such as the critical habitat reach for humpback chub near the Little Colorado River [14], need to be statistically evaluated before conclusions can be drawn about the food web of any region of interest within Grand Canyon.

Depletion of  $\delta^{15}\text{N}$  data with increasing fish size is possibly a result of fish predation. The food base with the study site is sparse in terms of biodiversity, therefore, if all size classes of fishes were eating the same food source one would expect a similar  $\delta^{15}\text{N}$  value. Speckled Dace (*Rhinichthys osculus*) do not grow longer than 100 mm and had an average  $\delta^{15}\text{N}$  value of  $11.9\text{‰}$  ( $n = 18$ ;  $\pm 0.23$  s.e.), indicating their food source is aquatic macroinvertebrates that had an average  $\delta^{15}\text{N}$  value of  $9.9\text{‰}$  ( $n = 81$ ;  $\pm 0.18$  s.e.). However, Brown trout (*Salmo trutta*) had an average  $\delta^{15}\text{N}$  value of  $15.9\text{‰}$  ( $n = 12$ ;  $\pm 0.13$  s.e.) and were all  $>250$  mm in standard length. Brown trout are well documented as strong ichthyo-predators [15, 16] and a  $6\text{‰}$   $^{15}\text{N}$  depletion over macroinvertebrates provides evidence of multiple trophic level increases.

Future stable isotope research on medium to large rivers with study reaches encompassing several hundred kilometers should include the following protocol for complete food web construction: 1) seasonal collections of above, within, and below tributaries to define the seasonal role of tribu-

taries in the food web, 2) adequate replication of carbon sources to better define carbon and trophic position, 3) dissolved organic and inorganic  $\delta^{13}\text{C}$  data from tributaries to define tributary influence to the mainstem, 4) collection of the same trophic levels, and taxa if possible, from various habitats such as pools, cobbles and drift (by size class) within a site, and, 5) collection of terrestrial components in the same sites as the aquatic samples so elevational differences can be defined in the terrestrial community.

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#### References

- [1] Petersen, B. J. (1999). Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review, *Acta Oecol.* **20**, 479–487.
- [2] Angradi, T. R. (1994). Trophic linkages in the lower Colorado River: multiple stable isotope evidence, *J. N. Am. Benthol. Soc.* **13**, 479–496.
- [3] Fry, B. (1999). Using stable isotopes to monitor watershed influences on aquatic trophodynamics, *Can. J. Fish. Aquat. Sci.* **56**, 2167–2171.
- [4] Stevens, L. E., Shannon, J. P. and Blinn, D. W. (1997). Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphic influences, *Reg. Rivers: Res. Man.* **13**, 129–149.
- [5] Oberlin, G. E., Shannon, J. P. and Blinn, D. W. (1999). Watershed influence on the macroinvertebrate fauna of ten major tributaries of the Colorado River through Grand Canyon, Arizona, *Southwest. Nat.* **44**, 17–30.
- [6] Blinn, D. W. and Cole, G. A. (1991). Algal and invertebrate biota in the Colorado River: comparison of pre- and post-dam conditions. In: Marzlof, G.R. (Ed.), *Colorado River Ecology and Dam Management* (Natl. Acad. Press: Washington, DC), pp. 102–123.
- [7] Dodds, W. and Gudder, D. A. (1992). The ecology of *Cladophora*, *J. Phycol.* **28**, 415–427.
- [8] Shannon, J. P., Blinn, D. W. and Stevens, L. E. (1994). The role of trophic interactions in structuring lotic benthic communities, *Freshwat. Biol.* **31**, 213–220.
- [9] Blinn, D. W., Shannon, J. P., Stevens, L. E. and Carter, J. P. (1995). Consequences of fluctuating discharge for lotic communities, *J. N. Am. Benthol. Soc.* **14**, 233–248.

- [10] Shaver, M. L., Shannon, J. P., Wilson, K. P., Benenati, E. P. L. and Blinn, D. W. (1997). Effects of suspended sediments and desiccation on the benthic tailwater community in the Colorado River, USA, *Hydrobiologia* 357, 63-72.
- [11] Benenati, E. P. L., Shannon, J. P. and Blinn, D. W. (1998). Desiccation and recolonization of phytobenthos in a regulated desert river: Colorado River at Lees Ferry, Arizona, USA, *Reg. Rivers: Res. Man.* 14, 519-532.
- [12] Minckley, W. L. (1991). Native fishes of the Grand Canyon region: an obituary? In: Marzloff, G.R. (Ed.), Colorado River Ecology and Dam Management (Natl. Acad. Press, Washington, DC), pp. 124-177.
- [13] Carothers, S. W. and Brown, B. T. (1991). The Colorado River through Grand Canyon; Natural History and Human Change (The University of Arizona Press: Tuscon, Arizona), pp. 235.
- [14] Hoffnagle, T. L., Valdez, R. A. and Speas, D. W. (1999). Fish abundance, distribution and habitat use, In: Webb, R.H., Schmidt, J.C., Marzloff, G.R. and Valdez, R.A. (Eds.), The Controlled Flood in Grand Canyon (Geophysical Monograph 110 American Geophysical Union: Washington DC, USA), pp. 273-287.
- [15] SYSTAT: Statistics, Version 5.2 Edition. Evanston, IL: SYSTAT, Inc., (1992) pp. 724.
- [16] McCarthy, I. D. and Waldron, S. (2000). "Identifying migratory *Salmo trutta* using carbon and nitrogen stable isotope ratios", *Rapid Communications in Mass Spectrometry* (in press).
- [17] France, R. L. (1996). Carbon-13 conundrums: limitations and cautions in the use of stable isotope analysis in stream ecotonal research, *Can. J. Aquat. Sci.* 53, 1916-1919.
- [18] Doucett, R. R., Barton, D. R., Karin, A., Guiguer, R. A., Power G. and Drimmie, R. J. (1996). Comment: critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems, *Can. J. Fish. Aquat. Sci.* 53, 1913-1915.
- [19] Finlay, J. C., Power, M. E. and Cabana, G. (1999). Effects of water velocity on algal carbon isotope ratios: implications for river web studies, *Limnol. Oceanogr.* 44, 1198-1203.
- [20] Keeley, J. E. and Sandquist, D. R. (1992). Carbon: freshwater plants, *Plant Cell Environ.* 15, 1021-1035.
- [21] Shannon, J. P., Blinn, D. W., Benenati, E. P. L. and Wilson, K. P. (1996). Organic drift in a regulated desert river, *Can. J. Fish. Aquat. Sci.* 53, 1360-1363.
- [22] McIvor, C. C. and Thieme, M. L. (1999). Flannelmouth suckers: movement in the Glen Canyon reach and spawning in the Paria River, In: Webb, R. H., Schmidt, J. C., Marzloff, G. R. and Valdez, R. A. (Eds.), The Controlled Flood in Grand Canyon (Geophysical Monograph 110 American Geophysical Union, Washington DC, USA), pp. 289-296.
- [23] Rosenfeld, J. S. and Roff, J. C. (1992). Examination of the carbon base in southern Ontario streams using stable isotopes, *J. N. Am. Benthol. Soc.* 11, 1-10.