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Food base studies and stable isotope analysis of the diet of humpback chub
(Gila cypha) in the Little Colorado River, Coconino County, AZ.

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Abstract

One preliminary trip and 6 sampling trips were made from April 1998 through June 1999 to study the diet of the humpback chub (*Gila cypha*) and the standing mass and benthic community composition in the Little Colorado River, AZ (LCR). The LCR and one spring source (Salt Creek) were characterized by high specific conductivities ($\geq 3.3 \mu\text{S}$) and dissolved CO_2 concentrations (up to $30 \text{ mg}\cdot\text{L}^{-1}$). Preliminary analyses indicate that the algal community of the LCR is dominated by the yellow-green alga *Vaucheria* spp., whereas Salt Creek is dominated by the halophilic diatom, *Biddulphia* sp. The macroinvertebrate community in the LCR is dominated by a caseless caddisfly (Trichoptera), baetid mayflies (Ephemeroptera), and chironomids. Overall standing mass of the LCR community was an order of magnitude lower ($0.056 \text{ g}\cdot\text{m}^{-2} \text{ AFDM} \pm 0.011 \text{ SE}$ macroinvertebrates) than that at the confluence of the Colorado River in the LCR. Standing mass was negatively affected by high discharge with increased suspended sediment load. Long periods of base flow may allow for increased standing mass at sites above Chute Falls (km 14.5), while limiting the standing mass of downstream sites. Standing mass at downstream sites was negatively influenced by increased carbonate precipitation and turbidity during base flow conditions.

Tissue samples from benthic organisms, humpback chub and other native/nonnative fish were analyzed for stable isotope signals of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Preliminary results indicated that drift (coarse and fine particulate matter) is the primary carbon source for macroinvertebrates in the LCR. Relative $\delta^{15}\text{N}$ values indicated that algae is not the direct source for carbon to the LCR food web, except possibly for some herbivorous fish $>150 \text{ mm}$ (eg. bluehead suckers; *Pantosteus discobolus*). In turn, invertebrates are the main source of carbon for fish $<150 \text{ mm}$ within the LCR. Fish $>150 \text{ mm}$ collected in the LCR have a slightly enriched $\delta^{13}\text{C}$ value indicating that they may receive at least part of their carbon requirements from other sources than the Little Colorado. Fish $>150 \text{ mm}$ have enriched $\delta^{15}\text{N}$ values indicating piscivory in some cases (especially adult channel catfish; *Ictalurus punctatus*). Several native and nonnative species of fish $<150 \text{ mm}$ have overlapping $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signals indicating that there is likely interspecific competition for the limited food resources in the LCR.

Mineral carbonate contamination of samples may be affecting $\delta^{13}\text{C}$ signals and initial methods of cleansing with DI H_2O may not be totally effective at carbonate removal. Additional samples have been acidified in 0.01N HCl and sent for analysis to correct for carbonates.

Introduction

The diet of smaller size classes of humpback chub (*Gila cypha*) is important to our understanding the ecological limitations of these fish. No studies to date have described the diet requirements of young HBC either in the mainstem Colorado River or in the Little Colorado River (LCR). Food may be a factor limiting the survival of these fish. Kubly and Cole (1979) speculated that food may be limited in the LCR because of high travertine deposition. Valdez and Ryel (1995) showed that adult HBC from the mainstem Colorado River fed on the amphipod *Gammarus lacustris*, simuliids, and chironomids as well as terrestrial insects. However, they speculated that because sub-adult HBC use shore line talus, boulders, and vegetation rather than mid-channel habitats, food may be limiting to these size classes in the mainstem.

Stable isotopes of carbon, nitrogen and other elements have been cited as good tools for identifying the source of energy in food webs (Rosenfield and Roff 1992, Barrie and Prosser 1993, Parker et al. 1993, and Schell and Ziemann 1993). Dietary studies based on stomach content and volume are biased by variable rates of digestion for specific food items (Barrie and Prosser 1993, Parker et al. 1993). These studies may exaggerate the importance of food items that are large and easy to count in gut contents or have indigestible body parts. Small food items that are quickly digested may not appear in gut content analysis even though their overall contribution to the diet of the study organisms may be great. Stable isotope analysis eliminates these types of biases by measuring the isotopic signal of the tissue of the study organism, measuring only the signal of food items that have actually been assimilated into the organism. These signals can be tracked back to the available food items in the system to show the relative importance of specific energy sources (Angradi 1994).

This project had two main objectives. **The first was to estimate the standing crop and seasonal availability of the aquatic benthos in this system and the second was to describe the food resources of the HBC in the LCR using stable isotope techniques.** Information from this research will be used to develop understanding of the LCR ecosystem and the resources that it provides to the resident and transient HBC population. An understanding of these resources will help managers to better understand the ecology of native fishes that depend on the LCR for portions of their life history. In addition, the stable isotope analysis of food web construction in the LCR will be incorporated into a stable isotope project being conducted by the Northern Arizona University Colorado River Food Base monitoring lab. The objectives of this project are to describe a food web for the greater Grand Canyon Ecosystem. Methods developed and tested during this project for non-lethal sampling of stable isotopes in endangered fishes will be employed in future monitoring and research of these fishes.

Study Area

The Little Colorado River originates on Mt. Baldy in eastern Arizona. It flows 412 km and drains 69,832 km² before joining the Colorado River 122 km below Glen Canyon Dam (Loughlin 1983, Strength 1997). However, there is only perennial flow in the headwater reaches and the last 21 km before the confluence. Impoundment, diversion, and land-use practices have reduced flow to the point that there is no surface flow as the river crosses the Painted Desert, AZ, except during storm runoff events.

The lower 21 km of the LCR has perennial flow from a series of springs emanating from the Redwall Limestone and Muav Limestone formations. Blue Springs is the largest of the springs supplying approximately 56% of the 6.3 m³·s⁻¹ base flow in this reach (Loughlin 1983). Discharge from Blue Springs is characterized by high specific conductance (4075 μ S) and high dissolved CO₂ (Strength 1997). As CO₂ degasses with exposure to the atmosphere and photosynthetic activity increases, carbonate precipitates to form travertine deposits which are an important geomorphic feature of this reach of the river. The high mineral concentration of the water gives the LCR its characteristic light blue color during base flow.

Storm events and snow melt stochastically increase the discharge of the lower 21 km of the LCR (Fig. 1). Runoff from the upper portion of the basin increases the suspended sediment concentrations in this reach. Periods of flow exceeding base flow are normally bimodal with high flows resulting from winter storms and snow melt early in the year or convective storm activity in late summer. During this study, base flow was exceeded 66% of the days between January 1, 1998 and August, 30 1999. Maximum flows during this time period were approximately 54 m³·s⁻¹.

The Little Colorado River is critical habitat for the continued existence of the endangered cyprinid, humpback chub (*Gila cypha*) in the Grand Canyon (U.S. Fish and Wildlife Service 1994). The LCR and the mainstem Colorado River around the confluence is the site of the largest aggregation of HBC below Glen Canyon Dam. The importance of the LCR to the life history of these fishes in the Grand Canyon is two-fold. First, it is the location of a resident population of HBC (Douglas and Marsh 1996); secondly, it provides important warm water spawning habitat not found in the mainstem due to the metalimnetic releases from Glen Canyon Dam (Kaeding and Zimmerman 1983, Douglas and Marsh 1996, Gorman and Stone 1999). Adult HBC from the mainstem Colorado River migrate into the LCR to spawn and move out again after spawning (Douglas and

Marsh 1996, Valdez and Ryel 1995). Sub-adult chub numbers also increase in the mainstem Colorado River in response to LCR spawning runs (Valdez and Ryel 1995).

Methods

Site description- Seven sampling trips to the Little Colorado River gorge were conducted in 1998 and 1999 in cooperation with U. S. Fish and Wildlife Service native fish monitoring trips. The first trip in April 1998 was used as a preliminary scouting and planning trip. Collections were conducted in June 1998, August 1998, October 1998, December 1998, April 1999 and May 1999.

The water quality, benthos, and aquatic drift of the LCR were sampled at two different sites during the first year of the study (Fig. 1). The first site was above the Atomizer/Chute Falls complex 14.5 km above the confluence. The second site in the LCR was located 10.1 km above the confluence near Salt Canyon. One other site in Salt Creek, a tributary of the LCR, 10.0 km above the confluence was also sampled. This site was chosen to provide information on the influence that the numerous spring head systems have on the aquatic food base. Because these springs are not subject to high suspended sediments on a regular basis they may provide a source for recolonization of the LCR after high flows and may contribute food to fish within the LCR as drift.

For the two trips in the second year (April 1999 and June 1999), an additional site in the LCR was added at 0.9 km for comparison with the long-term data collected by the Northern Arizona Aquatic Food Base program. An additional spring site was added at Big Canyon (11.5 km) to compare with Salt Creek.

Water Quality- Selected water quality parameters were measured to characterize each sampling site. Discharge for the LCR was estimated from U.S. Geological Survey gages. Discharge in Salt Creek and Big Canyon Creek was estimated on two different sampling trips using a Marsh McBirney hand-held velocity meter and a tape measure. Dissolved oxygen (mg L^{-1}) and temperature ($^{\circ}\text{C}$) were determined using a YSI™ hand held DO meter. Continuous temperature records were collected near the mouth of the Little Colorado River (approximately 0.8 km upstream from confluence) with Grand Canyon Monitoring and Research Center data loggers. Dissolved CO_2 was measured using a HACH™ field titration kit or a hand-held CO_2 meter (O'Brien and Blinn 1999). Water samples were collected and stored on ice for determination of total alkalinity (mg CaCO_3 by titration), specific conductance (μS), turbidity (NTU), pH, and suspended particulate matter (mg L^{-1}) in the laboratory.

Benthic sampling- Hard benthic substrates were sampled using a Surber sampler. Six random samples were taken at each site (3 in Salt Creek).

Substrates were scraped for 30 s with a metal trowel to remove benthos. Depth and water velocity were recorded for each sample. Soft sediments in the LCR were sampled using a Petite Ponar. Six samples were collected along two transects running perpendicular to the shoreline. The three samples at each transect were taken with increasing distance from the shoreline to the thalweg. Depth and relative distance from shore were recorded for each sample. Additional samples of soft and hard sediments were taken for taxonomic purposes.

Drift- Both fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) drift were sampled. Both collections were made in triplicate at the water surface. CPOM was collected in a rectangular net (0.135 m², 0.5 mm mesh). FPOM was collected in a 0.3 m diameter net with a 153 μ m mesh. FPOM in the Salt Creek tributary was collected with a 0.14 m diameter net with a 153 μ m mesh because of the shallow depths in the tributary. Velocity for each sample was collected with a Marsh-McBirney electronic flow meter.

Sample processing- All CPOM and benthic samples were sorted live within 48 h of collection. Samples were sorted into 10 different categories including: annelid worms, tubificid worms (oligochaetes), simuliids, chironomids, gastropods, miscellaneous macroinvertebrates (aquatic insects and other invertebrates), Cladophora glomerata, cyanobacterial crust, detritus and miscellaneous algae, macrophytes and bryophytes. Samples were dried and weighed, combusted at 500°C for 1 h to determine ash-free-dry-mass (AFDM).

FPOM samples were stored in 70% ETOH and sorted in the laboratory using a dissecting scope. Samples were sorted into the following categories: Copepoda, Cladocera, Ostracoda, miscellaneous invertebrates, and detritus. Samples of invertebrates were dried and weighed. Detrital AFDM was determined by combustion for 1 h at 500°C.

Stable isotopes- Stable isotope samples were rinsed with distilled water then dried in the field and the laboratory. Each sample was ground to a fine powder with a Whirl-a-bug™ amalgam shaker, weighed and sent to Institute of Ecology, University of Georgia, Athens, GA for analysis.

Statistical analysis- Statistical analysis for benthic data were analyzed using $\ln(n+1)$ transformed data to improve homoscedascity. Specific patterns were detected using MANOVA techniques in Systat 5.2.1 for the Macintosh (Systat, Inc. 1992). We used substrate type, sample date and site as predictor variables for estimates of mass of biotic categories. Correlation tests (Pearsons) with Bonfferoni corrections to test correlations between biotic categories. The relation between stable isotope composition of fin clips and whole tissue of individual fish was tested using individual T tests.

Results

Discharge- Discharge estimates for the LCR below Blue Springs were estimated by adding the base flow discharge above the confluence of the LCR ($6.3 \text{ m}^3 \cdot \text{s}^{-1}$) to daily average flow at the Cameron, AZ gage, 86 km above the confluence. There was far less winter runoff in the second year of the study due to an abnormally dry winter (Fig. 2). High flows during the study period were approximately $54 \text{ m}^3 \cdot \text{s}^{-1}$. The maximum number of days of base flow between major spates was 138 d from late November 1998 to late March 1999 (Fig. 2). Between January 1, 1998 and September 30, 1999 base flow was exceeded on 66% of the days.

Discharge in the two tributaries measured was constant for each measurement. Big Canyon Creek had slightly more discharge ($0.03 \text{ m}^3 \cdot \text{s}^{-1}$) than Salt Creek ($0.02 \text{ m}^3 \cdot \text{s}^{-1}$). Although there is no continuous monitoring of the tributaries, we did not observe that they exceeded base flow during the study period except for a small, unmeasured spate from Big Canyon Creek in October 1998.

Water Quality- At base flow, the LCR showed a longitudinal pattern of increasing pH, turbidity, and conductivity and decreasing dissolved CO_2 . In May 1999, dissolved CO_2 decreased from $30.2 \text{ mg} \cdot \text{L}^{-1}$ to $17.4 \text{ mg} \cdot \text{L}^{-1}$ and $5.7 \text{ mg} \cdot \text{L}^{-1}$ at km 14.5, 10.1 and 0.9, respectively. Hydrogen-ion concentration increased from 7.39 to 7.61 and 7.91 at these sites, respectively. Turbidity was lowest at km 14.5 (2 NTU) increased to 19 NTU at km 10.1 and decreased to 7 NTU at km 0.9. Conductivity increased downstream from $3.3 \mu\text{S}$ at km 14.5 to $3.5 \mu\text{S}$ at km 10.1, and $4.1 \mu\text{S}$ at km 0.9.

When the LCR exceeded base flow conditions, increased suspended sediment and volume masked the longitudinal pattern of water quality. Suspended particulate concentrations in the top 0.3 m of the water column during a spate in August 1998 were approximately $2.8 \text{ g} \cdot \text{L}^{-1}$. As suspended sediment increased with flow, Secchi depth decreased. At km 14.5, Secchi depth decreased from $>2.5 \text{ m}$ to 0.01 m under high discharge. Turbidity measurements also reflected this increase in suspended sediments. Base flow conditions at km 14.5 were clear (2 NTU) while high discharge increased turbidity to $>5100 \text{ NTU}$ during spate events.

Big Canyon Creek and Salt Creek tributaries exhibited different water quality patterns than the LCR. Conductivity was higher in both tributaries than the LCR; 7.386 and $7.586 \mu\text{S}$, respectively. Both tributaries were clear (Salt Creek = 1 NTU and Big Canyon Creek = 3 NTU). The range of dissolved oxygen concentrations was lower in Salt Creek (5.02 to $5.09 \text{ mg} \cdot \text{L}^{-1}$) than either the LCR (7.08 to $8.66 \text{ mg} \cdot \text{L}^{-1}$) or Big Canyon Creek (7.96 to $7.99 \text{ mg} \cdot \text{L}^{-1}$). Salt

Creek also had a lower pH range than Big Canyon (6.59 to 6.87 mg·L⁻¹ compared to 7.74 to 7.81 mg·L⁻¹, respectively). Dissolved CO₂ concentrations were higher in Salt Creek (157 to 171 mg·L⁻¹) than either the LCR or Big Canyon Creek (6.2 to 8.8 mg·L⁻¹). Water temperatures in the tributaries were not continuously monitored; however, temperature in Salt Creek appeared relatively constant ranging from 21.8°C in December of 1998 to 23.3°C in August 1998. Water temperatures in Big Canyon Creek ranged from 19.6°C to 21.7°C for the two sampling periods in April and May 1999.

Benthic composition- The phytobenthic standing mass of the LCR was dominated by the filamentous yellow-green alga Vaucheria sp. (Chrysophyta: Tribophyceae). Certain species of Vaucheria are common in salt marshes (Sze 1993). The alga forms tufted mats attached to travertine dams with a thin film of water flowing over the surface. The mats also contain other filamentous algal forms such as Oscillatoria sp. and Spirogyra sp., as well as diatoms. The branched filamentous green alga (Cladophora sp.) was also present in very small amounts at km 10.1 and km 0.9.

The benthic invertebrate standing crop on hard substrates was composed mainly of mayflies (baetids) and caddisflies (Hydropsyche sp.), and some dipterans (mostly Chironomidae). We also found a hemipteran (Rhagovela sp.), Megaloptera (Corydalidae), and annelid worms.

Soft substrates contained mainly Chironomidae, oligochaetes, and occasionally a sediment burrowing odonate (Gomphus sp.). Snails were also present in samples that contained detritus.

Big Canyon Creek contained snails, Trichoptera (Hydropsychidae and Hydroptilidae), Ephemeroptera (Baetidae), Odonata (Argia sp.), Megaloptera (Corydalidae), as well as Diptera. The phytobenthos in Big Canyon Creek consisted of the cyanobacterian, Nostoc sp., and biofilm on hard substrates.

Salt Creek contained dipterans and odonates (Argia sp. and rarely Gomphus sp.). The phytobenthos in Salt Creek was dominated by the halophilic diatom Biddulphia sp. which formed colonial filaments several centimeters long.

Benthic Standing Mass- Benthic standing mass varied significantly by river kilometer (Wilks' Lambda = 0.27, df = 5,116, p < 0.001), sampling period (Wilks' Lambda = 0.14, df = 25,432, p < 0.001), and substrate type (Wilks' Lambda = 0.40, df = 5,116, p < 0.001). Spatial and temporal patterns for hard and soft substrates were analyzed separately.

Soft substrates- Benthic standing mass for soft sediments was concentrated in shallow near shore areas protected from higher velocities, as opposed to deeper areas towards midchannel. Macroinvertebrate standing mass in soft

substrates was highest at km 14.5 in response to a long period of base flow which allowed accumulations of algal and detrital biomass in protected pools. Macroinvertebrate mass at this site reached $1.17 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.62 \text{ SE}$) in April 1999 while combined algal/detrital mass reached $28.07 \text{ g}\cdot\text{m}^{-2}$ ($\pm 17.93 \text{ SE}$). In contrast, macroinvertebrate mass was $0.084 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.079 \text{ SE}$) at 10.1 km which is a less protected shoreline. Other than the April 1999 sampling period, there were no significant differences in any category of benthic standing mass in pool habitats at km 10.1 and 14.5. Detrital retention in pools was generally poor. Estimated mean detrital standing mass for all sites and trips other than April 1999 was $7.53 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.160 \text{ SE}$, $n = 60$). Invertebrate standing mass in pool habitats over the same period was $0.17 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.07 \text{ SE}$, $n = 60$).

Hard substrates- Standing mass of benthic macroinvertebrates on hard substrates in the LCR was significantly and positively correlated with algal standing mass (Pearson correlation = 0.59, $p < 0.001$). Algal standing mass (and corresponding macroinvertebrate mass) increased with longer periods of base flow at km 14.5 (Pearson $R = 0.96$, $p = 0.003$, $n = 6$) and decreased with distance downstream from km 14.5.

Highest standing mass of algae and macroinvertebrates were found at km 14.5 in June 1999 (Trip 6) after 201 consecutive days of near base flow (Fig. 3). Mean total invertebrate mass was $0.31 \text{ g}\cdot\text{m}^{-2} \text{ AFDM} \pm 0.07 \text{ SE}$ and algal biomass was $13.85 \text{ g}\cdot\text{m}^{-2} \text{ AFDM}$ ($\pm 3.91 \text{ SE}$). During June 1999, invertebrate and algal mass decreased at downstream sites to $0.16 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.10 \text{ SE}$) and $0.013 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.013 \text{ SE}$), respectively, at km 0.9 (Fig. 4). For sampling trips that were not preceded by at least 30 d of base flow (1 through 4, see Fig 2), invertebrate standing crop was lower and there was no pattern of diminishing standing crop with increasing distance downstream from km 14.5. Overall there was no significant difference in invertebrate standing crop for trips 1 through 4, and the overall mean standing mass of invertebrates during this time was $0.056 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.011 \text{ SE}$).

Standing crop of algae and macroinvertebrates at km 10.1 remained relatively stable except for a significant (Tukey test, $p < 0.5$) increase during October 1998 (Trip 3). Invertebrate mass at this site increased from an overall mean of $0.028 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.005 \text{ SE}$) to $0.098 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.027 \text{ SE}$) during October 1998 (Fig 3).

CPOM drift- Coarse particulate organic drift at km 10.1 and 14.5 consisted of aquatic and terrestrial macroinvertebrates, detritus, and algae. Invertebrate drift was low and constant with no significant increases among sampling periods or sites. Overall invertebrate drift in the LCR was $0.0004 \text{ g}\cdot\text{m}^{-3}$ ($\pm 0.0002 \text{ SE}$). Detrital drift was also low except for increases at both sites during high flows in August 1998 (Trip 2). Detrital drift increased from an overall mean of $0.0119 \text{ g}\cdot\text{m}^{-3}$ ($\pm 0.005 \text{ SE}$) to $2.170 \text{ g}\cdot\text{m}^{-2}$ ($\pm 0.390 \text{ SE}$) in August

1998. Algal drift increased at both sites during April 1999 (Trip 5) from an overall mean of $0.0001 \text{ g}\cdot\text{m}^{-3} \pm 0.0001 \text{ SE}$ to $0.010 \text{ g}\cdot\text{m}^{-2} \pm 0.002 \text{ SE}$.

Tributary drift was similar to LCR drift without the influence of increased flow. Drift was similar between the Salt Creek and Big Canyon Creek with an overall mean of $0.006 \text{ g}\cdot\text{m}^{-3} \pm 0.002 \text{ SE}$ for detritus, $0.003 \text{ g}\cdot\text{m}^{-3} \pm 0.001 \text{ SE}$ for algae, and $0.0002 \text{ g}\cdot\text{m}^{-3} \pm 0.0001 \text{ SE}$ for invertebrates.

FPOM drift- Composition of fine particulate organic matter drift varied between sites. FPOM drift consisted of detritus, zooplankton (cyclopoid and harpacticoid copepods, cladocerans, ostracods) and miscellaneous invertebrates (early instars of aquatic and terrestrial insects, Tardigrada, Collembola, Gastropoda, and the protozoa Astrameoba and Centropyxis). Detritus from Big Canyon Creek and Salt Creek contained the diatom, Biddulphia sp. Miscellaneous invertebrates made up approximately 75% of the total invertebrate weight of samples from km 14.5, km 10.1, and Salt Creek. Invertebrate FPOM drift from Big Canyon Creek was composed of 35% miscellaneous invertebrates by weight and was dominated by harpacticoid copepods and ostracods.

Fine particulate organic matter estimates drift did not differ for km 14.5 and km 10.1. Detritus and combined zooplankton and miscellaneous invertebrate drift increased in August 1998 (Trip 2) and April 1999 (Trip 5) at both sites. Highest invertebrate drift was at km 14.5 in April 1999 ($0.0021 \text{ g}\cdot\text{m}^{-3}$ dry mass $\pm 0.0008 \text{ SE}$). Detrital drift at this site was $0.0386 \text{ g}\cdot\text{m}^{-3}$ AFDM ($\pm 0.0122 \text{ SE}$). Highest FPOM drift detrital mass was at km 14.5 during August 1998 ($2.263 \text{ g}\cdot\text{m}^{-3}$ AFDM $\pm 1.378 \text{ SE}$). However, during this period invertebrate drift was only $0.0009 \text{ g}\cdot\text{m}^{-3}$ dry mass ($\pm 0.0003 \text{ SE}$). Trips associated with base flow and low turbidity (Trip 1, Trip 3, Trip 4, and Trip 6) had similar lower levels of invertebrate and detrital drift. Overall means for these periods in the LCR are $0.0003 \text{ g}\cdot\text{m}^{-3}$ dry mass ($\pm 0.0001 \text{ SE}$) for combined invertebrates and $0.0037 \text{ g}\cdot\text{m}^{-3}$ AFDM ($\pm 0.0006 \text{ SE}$) for detritus.

Overall invertebrate FPOM drift mass from Salt Creek ($0.0005 \text{ g}\cdot\text{m}^{-3} \pm 0.0001 \text{ SE}$ dry mass) was similar to FPOM drift from the LCR and we were unable to detect statistically significant temporal patterns. Composition of drift from Salt Creek was similar to drift in the LCR (77% miscellaneous invertebrates and 23% zooplankton).

Big Canyon Creek was only sampled during April and June 1999 (Trip 5 and 6). These samples indicated that mass of FPOM invertebrate drift was similar to Salt Creek and sites in the LCR ($0.0019 \text{ g}\cdot\text{m}^{-3} \pm 0.0011 \text{ SE}$ dry weight) even though composition of miscellaneous invertebrates was only 35% by weight. The zooplankton at this site consisted of harpacticoid copepods and ostracods.

Stable isotope analysis of trophic links- Approximately 260 samples of algae, detritus, invertebrates, and fish have been analyzed from the LCR for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Mineral carbonates may be diluting the $\delta^{13}\text{C}$ signal (showing depleted

or less negative $\delta^{13}\text{C}$ ‰). Samples are currently being processed that have been treated with 0.01 N HCl which will correct for carbonate contamination (Chanton and Lewis 1999) and allow for comparison of these results with other studies. Basic statistics for isotopic composition of samples collected are given in Appendix 1.

The aquatic food web of the Little Colorado River is based on drifting coarse and fine particulate organic matter. The primary carbon source for LCR fish <150 mm is aquatic invertebrates which consume particulate organic matter (Fig. 5). Organic particulate matter (CPOM, FPOM and detritus), aquatic invertebrates, and fish <150 mm (including humpback chub) had approximately equal isotopic signals for $\delta^{13}\text{C}$ and increasingly enriched $\delta^{15}\text{N}$. Algae and macrophytes had enriched $\delta^{13}\text{C}$ (-24.8 ‰ ± 4.8 SD) compared to organic particulate matter and $\delta^{15}\text{N}$ (7.6 ‰ ± 4.8 SD) was high compared to invertebrates from the LCR (6.5 ‰ ± 0.6 SD).

Fish <150 mm showed considerable overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition indicating little partitioning of food resources. Juvenile humpback chub, plains killifish (*Fundulus kansae*), fathead minnow (*Pimephales promelas*), juvenile channel catfish (*Ictalurus punctatus*), and speckled dace (*Rhinichthys osculus*) all had $\delta^{13}\text{C}$ composition between -22.9 and -24.2 ‰. Isotopic composition of $\delta^{15}\text{N}$ for these fish ranged from 9.4 to 11.58 ‰.

Fish >150 mm showed enriched isotopic signals for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (-24.5 ‰ ± 2.0 SD and 13.1 ‰ ± 1.8 SD, respectively; Fig. 5). Adult channel catfish showed enriched $\delta^{15}\text{N}$ (14.3 ‰ ± 1.5 SD) and a $\delta^{13}\text{C}$ composition similar to LCR fish <150 mm (-23.7 ‰ ± 2.4 SD) indicating piscivory on the smaller fish of the LCR. Other fish in this category (humpback chub, bluehead sucker (*Pantosteus discobolus*), and flannelmouth sucker (*Catostomus latipinnis*) had enriched $\delta^{13}\text{C}$ (-24.8 to -25.5 ‰) compared to carbon sources in the LCR except algae.

Fin clip samples of fish showed good concordance with whole tissue samples of the same fish. T-tests on fin clip samples vs whole tissue samples of the same fish were not significantly different ($p < 0.05$) for 6 out of 7 individual HBC tested. The one HBC that showed significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition was an adult captured in the LCR near the confluence during April 1998. Fin clips from this individual were higher ($+ 4.12$ ‰) for $\delta^{13}\text{C}$ and ($+ 0.4$ ‰) for $\delta^{15}\text{N}$.

Discussion

As measured by the standing mass of invertebrates, energy available for higher trophic levels from the LCR was low compared to the Colorado River

near the confluence with the LCR. Mean standing mass of aquatic invertebrates from the cobble bar in the Colorado River at the confluence of the LCR ($0.25 \text{ g} \cdot \text{m}^{-2} \pm 0.11 \text{ SE}$) was an order of magnitude higher than the km 10.1 site in the LCR during this study period. These findings are similar to Oberlin et al. (1999). Standing mass is higher at the km 14.5 site after long periods of base flow. However, this standing mass may not be directly available to humpback (HBC) since this site is upstream of the range of HBC in the LCR (Robinson et al. 1996) and we found drift of invertebrates to be minimal. Long-term monitoring data from near the mouth of the LCR at km 0.9 may underestimate standing mass for sites upstream of km 14.5 in the LCR during periods of baseflow.

Water quality at base flow conditions becomes increasingly harsh for benthic life with increasing distance from Blue Springs. Increasing pH, due to degassing of CO_2 and photosynthesis, increases the precipitation of travertine (Stumm and Morgan 1970). Carbonate precipitation in this system has been estimated to be $1.05 \cdot 10^{-5} \text{ moles} \cdot \text{L}^{-1} \cdot \text{s}^{-1}$ (Strength 1997). Carbonate precipitation increases turbidity, which reduces light available for photosynthesis and also physically interferes with organisms. We found algae and detritus totally encrusted with solid travertine, restricting both growth and grazing. In addition, we found that caddisfly webs became totally solidified forming a tube instead of a capture net.

Standing mass of invertebrates and algae are limited by floods with high suspended sediments. Increased flow and suspended sediment reduces algal standing mass by scour and light limitation (Grimm and Fisher 1989, Newcombe and MacDonald 1991) and increases invertebrate drift (Rosenburg and Weins 1978). Duration of base flow between spates was short for the first half of the study period, limiting the amount of time for recolonization and establishment of the LCR benthic community. However, even extended periods of base flow did not increase productivity for the areas below km 14.5 that contained most of the HBC population for the LCR.

Springs may be a more stable food supply and source for colonization after scouring floods; however, there is a limited surface area of springs compared to the main body of the LCR and standing mass is no greater than in the LCR. Drift rates from the springs studied are no greater than the LCR and the total volume of flow from springs is orders of magnitude less than the total volume of the flow from Blue Springs.

There are several factors to consider when using stable isotope composition to interpret trophic linkages. First, as an organism metabolizes a food resource there is very little fractionation (metabolic change in atomic mass) of carbon so the isotopic signal of $\delta^{13}\text{C}$ remains constant for a specific food source during trophic transfer (DeNiro and Epstein 1978, Fry and Sherr 1989). This means

that organisms utilizing the same food source should have similar $\delta^{13}\text{C}$ composition. However, it should be noted that it is possible for two different food sources to have very similar $\delta^{13}\text{C}$ composition which can confound interpretation (Bootsma et al. 1996). Second, an organism's $\delta^{13}\text{C}$ composition may reflect a mixture of several food sources which are integrated over time (Hobson and Clark 1992). An organism's carbon isotope composition reflects the signal of food resources that are actually assimilated into the tissues of the organism in contrast to gut analysis which may measure food resources that are ingested but of little nutritional value (Kling et al. 1992). Third, nitrogen isotopic composition is helpful in interpreting an organism's trophic position because it does change in a systematic way during trophic transfer. As a nitrogen source is metabolized by an organism, $\delta^{15}\text{N}$ enriches by 3-5 ‰ per trophic level (Hesslein et al. 1991).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of particulate organic matter and aquatic macroinvertebrates in the LCR indicated that the first and second trophic levels of a trophic system with HBC <150 mm being the tertiary level. The likely source of particulate matter is from allochthonous sources given the low standing mass of algae and macrophytes in the LCR.

Our study indicates that algae are not a direct source of nutrition to small fish in the LCR. Isotopic composition of $\delta^{13}\text{C}$ is enriched compared to fish <150 mm, indicating that algae do not contribute directly to the diet of macroinvertebrates since $\delta^{15}\text{N}$ composition is not enriched compared to algae. Heavy encrustation of carbonates in the filaments retards attachment of epiphytic diatoms and grazing. However, algae may provide a good substrate for invertebrates in a system that is heavily armored with little interstitial space. However, algae and macrophytes may contribute to particulate matter as it decomposes.

Given the low standing mass of invertebrates in the LCR, it seems likely that there is interspecific competition for food resources by fish within the <150 mm size class. Several other species of fish <150 mm have similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition to HBC <150 mm indicating use of similar food resources. Our data indicate species that are most likely competitors with sub-adult HBC in the LCR are fathead minnow, speckled dace, channel catfish, and plains killifish. Studies that describe habitat partitioning, feeding behavior, and population dynamics of these fish in the LCR will be helpful in defining the intensity of competition with HBC.

Our study supports previous studies indicating that channel catfish are significant predators on fish in the LCR (Marsh and Douglas 1997). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition for adults of this species indicate piscivory on fish from within the LCR. Evidence of piscivory for HBC in the LCR is suggested by our

data and has been shown by other studies (Kaeding and Zimmerman 1983, Stone 1999). However, alternative hypotheses may explain the isotope patterns. Nitrogen isotopic composition for adult HBC is enriched relative to small fish in the LCR; however, $\delta^{13}\text{C}$ is also enriched indicating that HBC within the LCR may have a carbon source other than particulate organic matter in the LCR. Kaeding and Zimmerman (1983) found that HBC within the LCR had less items in their stomachs than HBC captured from the mainstem Colorado River. Adult HBC that have been shown to move from the LCR into the mainstem may be doing so because of low food availability in the LCR. Possibly, a major portion of their total energy requirement is gathered from the mainstem Colorado River. Isotopic signals of food resources in the Colorado River are enriched for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compared to the LCR, which could explain the enriched signals for adult HBC in the LCR. These signals may also help to explain the diet of adult flannel mouth suckers and bluehead suckers in the LCR which also have enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Comparisons of isotopic signals from the LCR and Colorado River cannot be undertaken until the role of carbonates in isotopic composition of organisms from the LCR has been quantified. Sulfur ($\delta^{34}\text{S}$) composition may also help to pinpoint the source of food for fish that move between tributaries and the mainstem (Angradi 1994). In addition, records of fish movement through PIT™ tag data and fish densities will help to define fish movement in relation to food base changes in the LCR and how food resources limit the population of HBC in the LCR.

This study indicates that the food resources of sub-adult HBC in the LCR are dependant on allochthonous inputs from the drainage basin of the LCR, pointing out the importance of wise management in this drainage for the well being of this fish.

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Appendix 1. Basic statistics for stable isotope composition ($\delta^{13}\text{C}/\text{‰}$ and $\delta^{15}\text{N}/\text{‰}$) of fish taxa and benthic categories for organisms sampled from the Little Colorado River near Grand Canyon, Arizona from April through October 1998.

All fish < 150 mm

	CARBON	NITROGEN
N OF CASES	77	76
MINIMUM	-29.58000	8.35000
MAXIMUM	-20.86000	14.77000
MEAN	-23.29922	10.82908
VARIANCE	3.06734	1.90047
STANDARD DEV	1.75138	1.37857
STD. ERROR	0.19959	0.1813

All fish > 150 mm

	CARBON	NITROGEN
N OF CASES	77	76
MINIMUM	-28.44000	8.46000
MAXIMUM	-18.82000	16.28000
MEAN	-24.54156	13.09237
VARIANCE	4.08468	3.26135
STANDARD DEV	2.02106	1.80592
STD. ERROR	0.23032	0.20715

Fathead minnow

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-25.07000	9.07000
MAXIMUM	-22.58000	9.66000
MEAN	-23.93889	9.39444
VARIANCE	0.99076	0.06013
STANDARD DEV	0.99537	0.24521
STD. ERROR	0.33179	0.08174

Red shiner

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-22.49000	9.78000
MAXIMUM	-21.17000	10.66000
MEAN	-21.89333	10.32111
VARIANCE	0.23828	0.09754
STANDARD DEV	0.48813	0.31231
STD. ERROR	0.16271	0.10410

Plains killifish

	CARBON	NITROGEN
N OF CASES	6	6
MINIMUM	-28.41000	9.78000
MAXIMUM	-21.17000	12.93000
MEAN	-23.16833	10.84333
VARIANCE	7.67874	1.59059
STANDARD DEV	2.77105	1.26118
STD. ERROR	1.13128	0.51488

Carp

	CARBON	NITROGEN
N OF CASES	3	3
MINIMUM	-19.82000	8.63000
MAXIMUM	-19.51000	8.90000
MEAN	-19.69000	8.79667
VARIANCE	0.02590	0.02123
STANDARD DEV	0.16093	0.14572
STD. ERROR	0.09292	0.08413

Channel cat > 150 mm

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-27.01000	12.88000
MAXIMUM	-21.43000	16.28000
MEAN	-23.73333	14.24889
VARIANCE	5.76380	2.15376
STANDARD DEV	2.40079	1.46757
STD. ERROR	0.80026	0.48919

Channel cat < 150 mm

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-23.38000	11.41000
MAXIMUM	-22.25000	11.65000
MEAN	-22.95000	11.54667
VARIANCE	0.26965	0.00697
STANDARD DEV	0.51928	0.08352
STD. ERROR	0.17309	0.02784

Speckled dace

	CARBON	NITROGEN
N OF CASES	6	6
MINIMUM	-24.77000	10.24000
MAXIMUM	-23.53000	12.96000
MEAN	-24.18167	11.58000
VARIANCE	0.30762	2.04108
STANDARD DEV	0.55463	1.42866
STD. ERROR	0.22643	0.58325

Bluehead sucker > 150 mm

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-25.06000	13.12000
MAXIMUM	-24.55000	13.91000
MEAN	-24.85556	13.50667
VARIANCE	0.04218	0.08845
STANDARD DEV	0.20537	0.29741
STD. ERROR	0.06846	0.09914

Flannelmouth sucker > 150 mm

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-28.42000	13.41000
MAXIMUM	-24.66000	14.50000
MEAN	-25.56889	13.92222
VARIANCE	1.25431	0.14097
STANDARD DEV	1.11996	0.37546
STD. ERROR	0.37332	0.12515

Humpback chub < 150 mm

	CARBON	NITROGEN
N OF CASES	38	37
MINIMUM	-29.58000	8.35000
MAXIMUM	-20.86000	14.77000
MEAN	-23.38658	11.03270
VARIANCE	4.34875	2.50875
STANDARD DEV	2.08537	1.58390
STD. ERROR	0.33829	0.26039

Humpback chub > 150 mm

	CARBON	NITROGEN
N OF CASES	46	46
MINIMUM	-28.44000	8.46000
MAXIMUM	-18.82000	14.86000
MEAN	-24.72543	12.90283
VARIANCE	3.63960	3.30447
STANDARD DEV	1.90777	1.81782
STD. ERROR	0.28129	0.26802

Algae and macrophytes

	CARBON	NITROGEN
N OF CASES	12	11
MINIMUM	-30.77000	1.31000
MAXIMUM	-19.04000	13.17000
MEAN	-24.84750	7.56273
VARIANCE	12.91646	23.48350
STANDARD DEV	3.59395	4.84598
STD. ERROR	1.03748	1.46112

aquatic invertebrates

	CARBON	NITROGEN
N OF CASES	27	27
MINIMUM	-27.94000	5.53000
MAXIMUM	-15.48000	7.54000
MEAN	-23.29185	6.55074
VARIANCE	9.13888	0.41029
STANDARD DEV	3.02306	0.64054
STD. ERROR	0.58179	0.12327

CPOM

	CARBON	NITROGEN
N OF CASES	18	18
MINIMUM	-26.74000	-0.76000
MAXIMUM	-22.86000	3.95000
MEAN	-23.50111	1.63889
VARIANCE	0.73363	1.74155
STANDARD DEV	0.85652	1.31968
STD. ERROR	0.20188	0.31105

FPOM

	CARBON	NITROGEN
N OF CASES	9	9
MINIMUM	-24.96000	0.69000
MAXIMUM	-18.42000	5.12000
MEAN	-21.96667	2.20333
VARIANCE	7.62923	1.92300
STANDARD DEV	2.76211	1.38672
STD. ERROR	0.92070	0.46224

Detritus

	CARBON	NITROGEN
N OF CASES	2	1
MINIMUM	-21.44000	0.45000
MAXIMUM	-20.81000	0.45000
MEAN	-21.12500	0.45000
VARIANCE	0.19845	.
STANDARD DEV	0.44548	.
STD. ERROR	0.31500	.

Fig. 1. Map of the study area showing collection sites in the Little Colorado River and tributaries.

Fig. 2. Temperature and discharge for the Little Colorado River during the study period. Temperature (mean daily °C) was collected near the mouth of the Little Colorado River by Grand Canyon Monitoring and Research Center data loggers. Discharge (mean daily $\text{m}^3 \cdot \text{s}^{-1}$) was measured at the U.S. Geological Survey gage near Cameron, AZ, and added to discharge from Blue Springs to estimate discharge at the study site. Trip dates are shown as: Trip 1 = June 1998, Trip 2 = August 1998, Trip 3 = October 1998, Trip 4 = December 1998, Trip 5 = April 1999, and Trip 6 = June 1999.

Fig. 3. Invertebrate standing mass (AFDM $\text{g} \cdot \text{m}^{-2}$) from km 14.5 and km 10.1 in the Little Colorado River for six trips from June 1998 through June 1999. Increased period of base flow have opposite effects on the standing mass of macroinvertebrates (AFDM $\text{g} \cdot \text{m}^{-2}$) on hard substrates at km 14.5 and km 10.1 in the Little Colorado River. Baseflow conditions allow for increasing standing mass at km 14.5 and reduce standing mass at km 10.1. Numbers at the top of each column represent the number of consecutive days near base flow preceding the collection period.

Fig. 4. Invertebrate standing mass (AFDM $\text{g} \cdot \text{m}^{-2}$) from km 14.5, km 10.1 and km 0.9 in the Little Colorado River from June 1999 (Trip 6) after 201 consecutive days near base flow. Trend of diminishing aquatic invertebrate standing mass (AFDM $\text{g} \cdot \text{m}^{-2}$) downstream of km 14.5 during base flow in the Little Colorado River.

Fig. 5. Total coarse particulate organic drift (AFDM $\text{g} \cdot \text{m}^{-3}$) increases with increasing flow in the Little Colorado River. Data shown are from km 14.5.

Fig. 6. Dual stable isotope plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ‰ values for fish and potential food resources in the Little Colorado River from June - August 1998. Middle of each boxes is formed from the mean and while height and width represent standard deviation of available samples for each group. Thick arrows show trophic links indicated by stable isotope analysis while dashed arrows indicate potential or weak links.

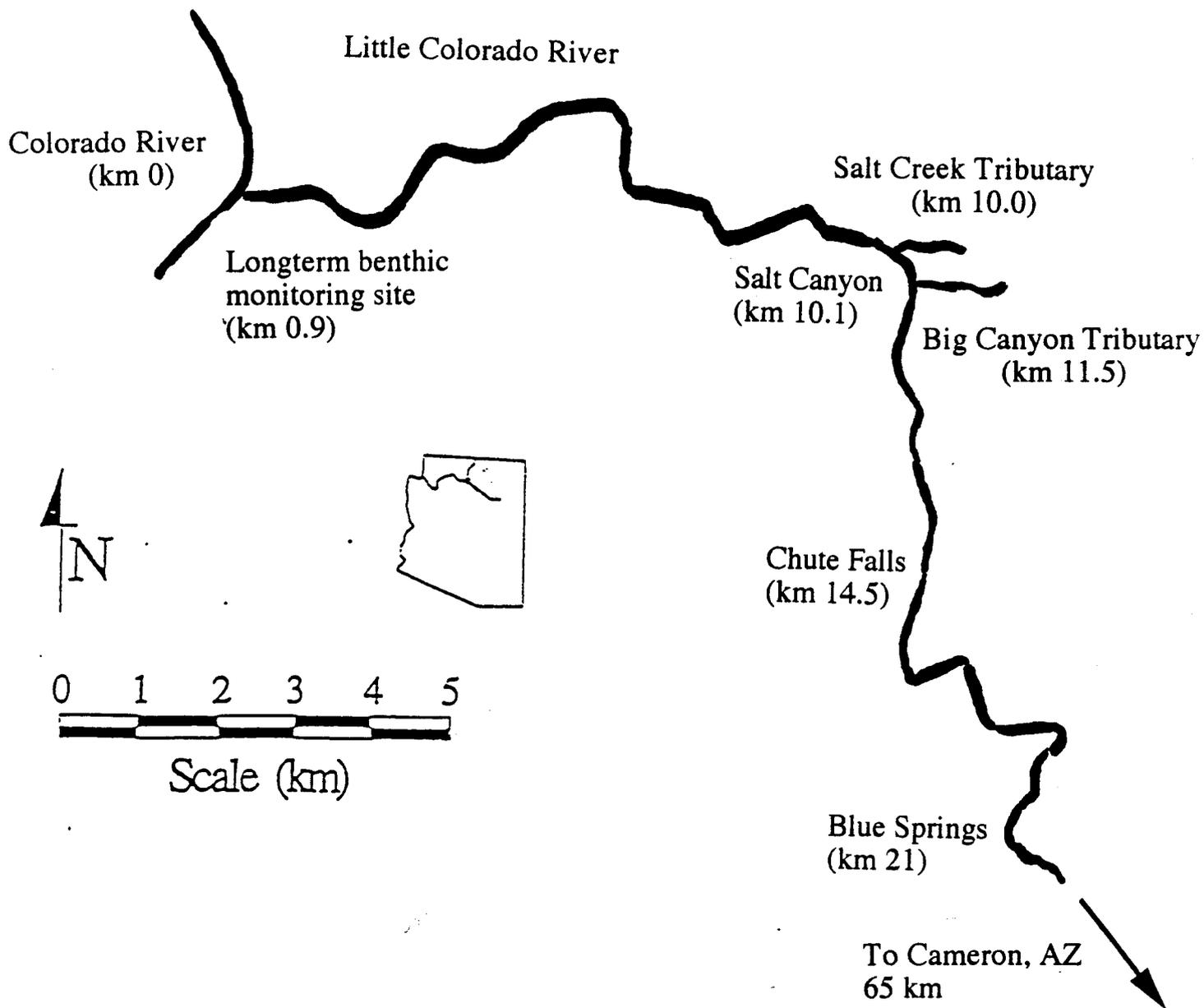
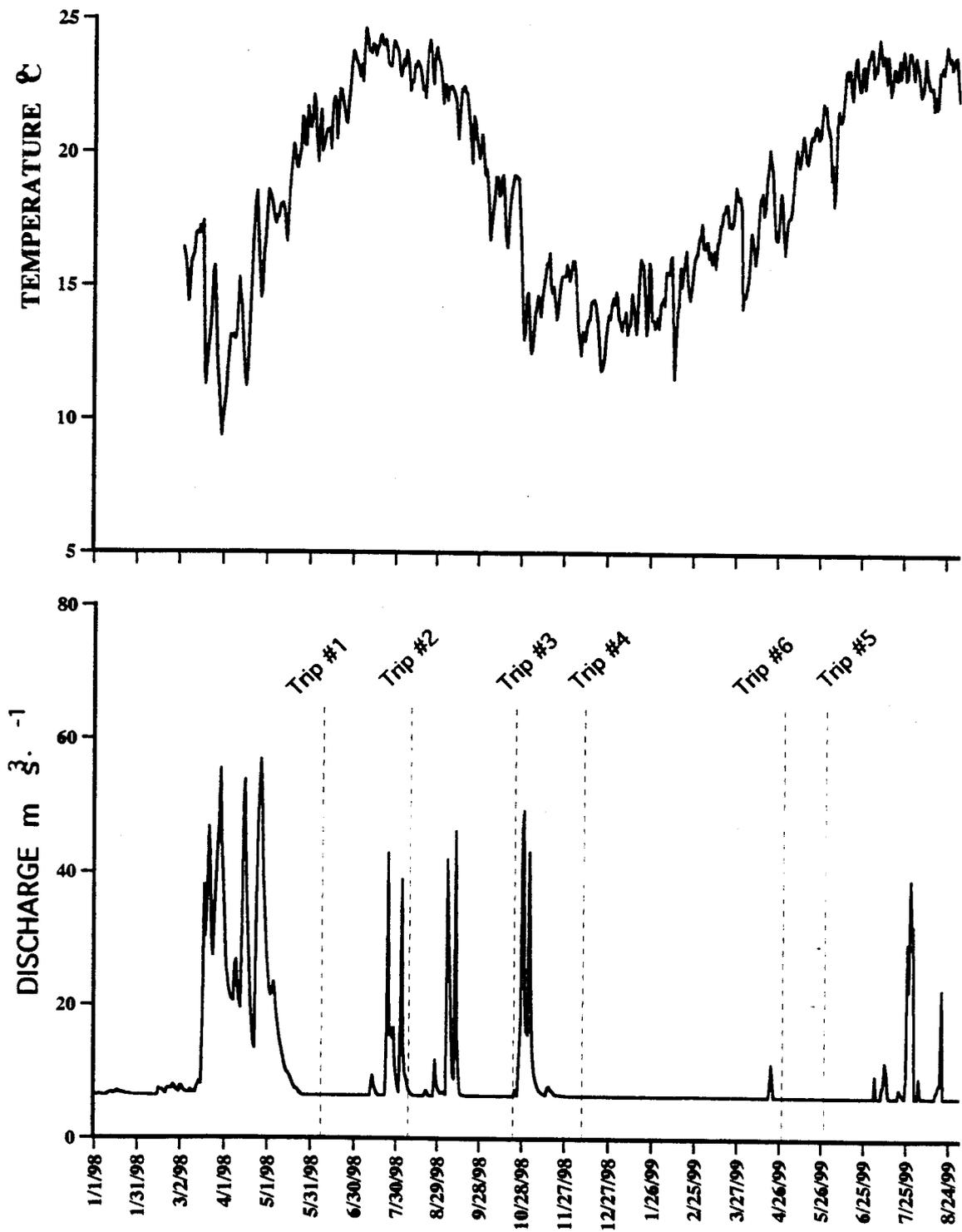


Fig. 1



DATE

Fig. 2

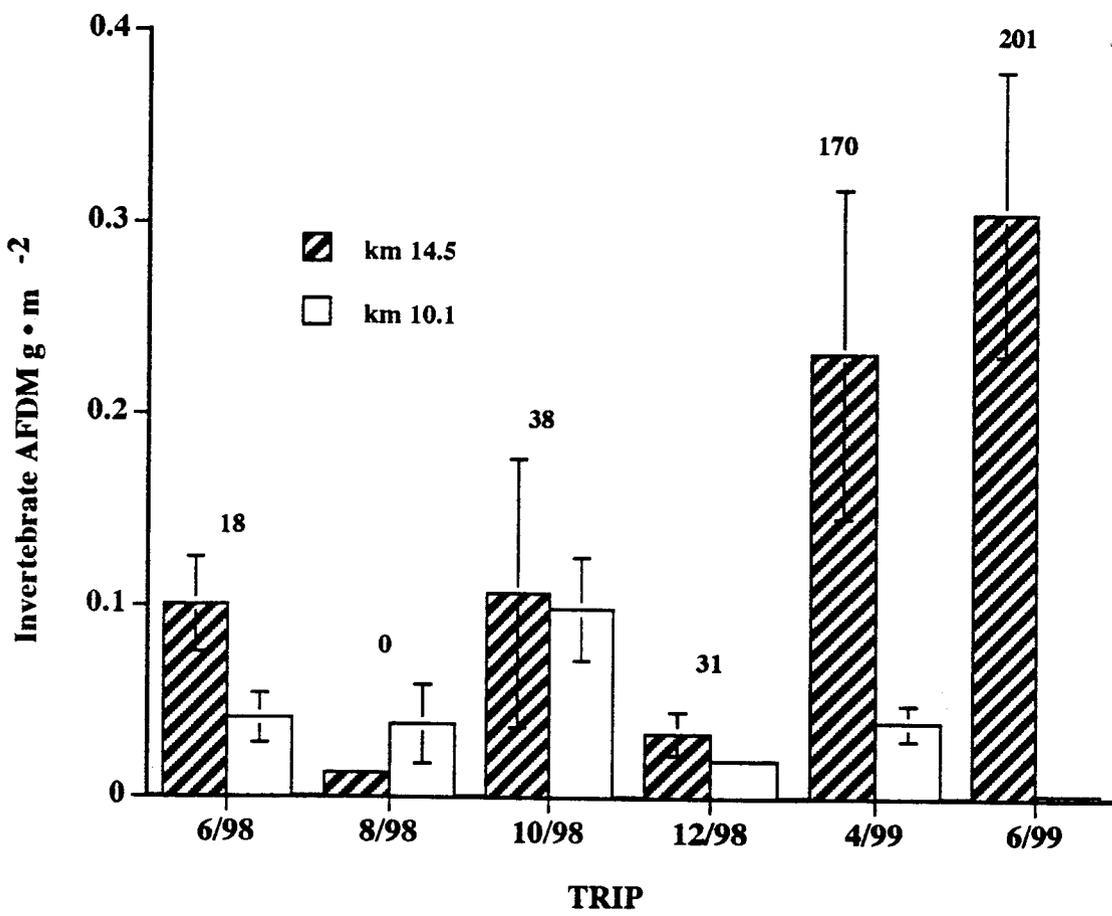


Fig. 3

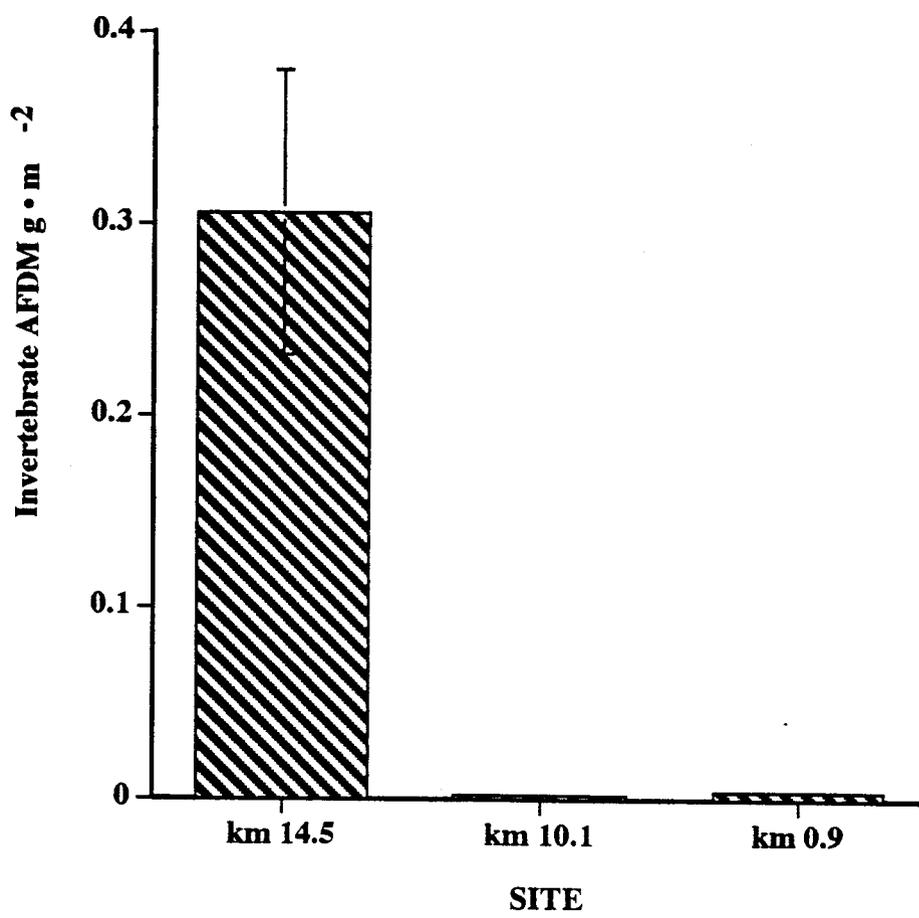


Fig. 4

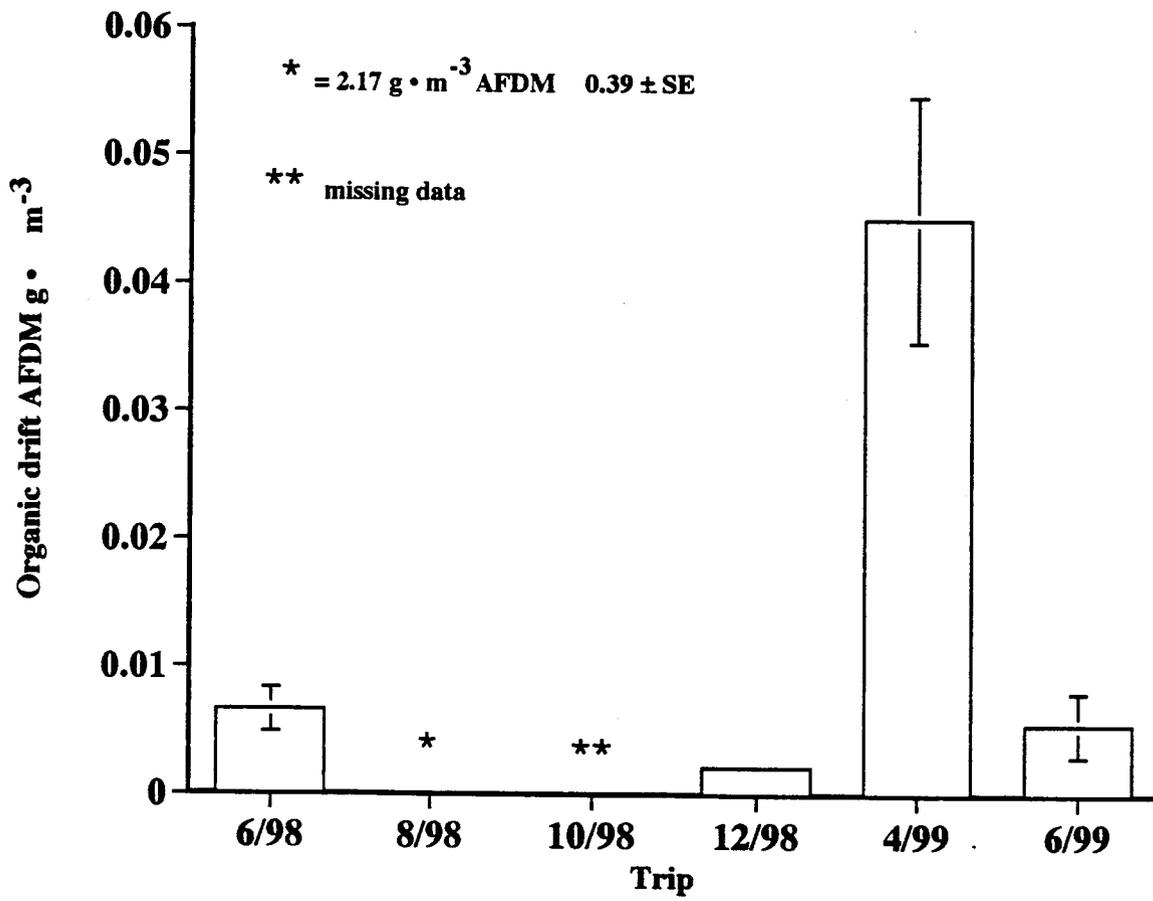


Fig. 5

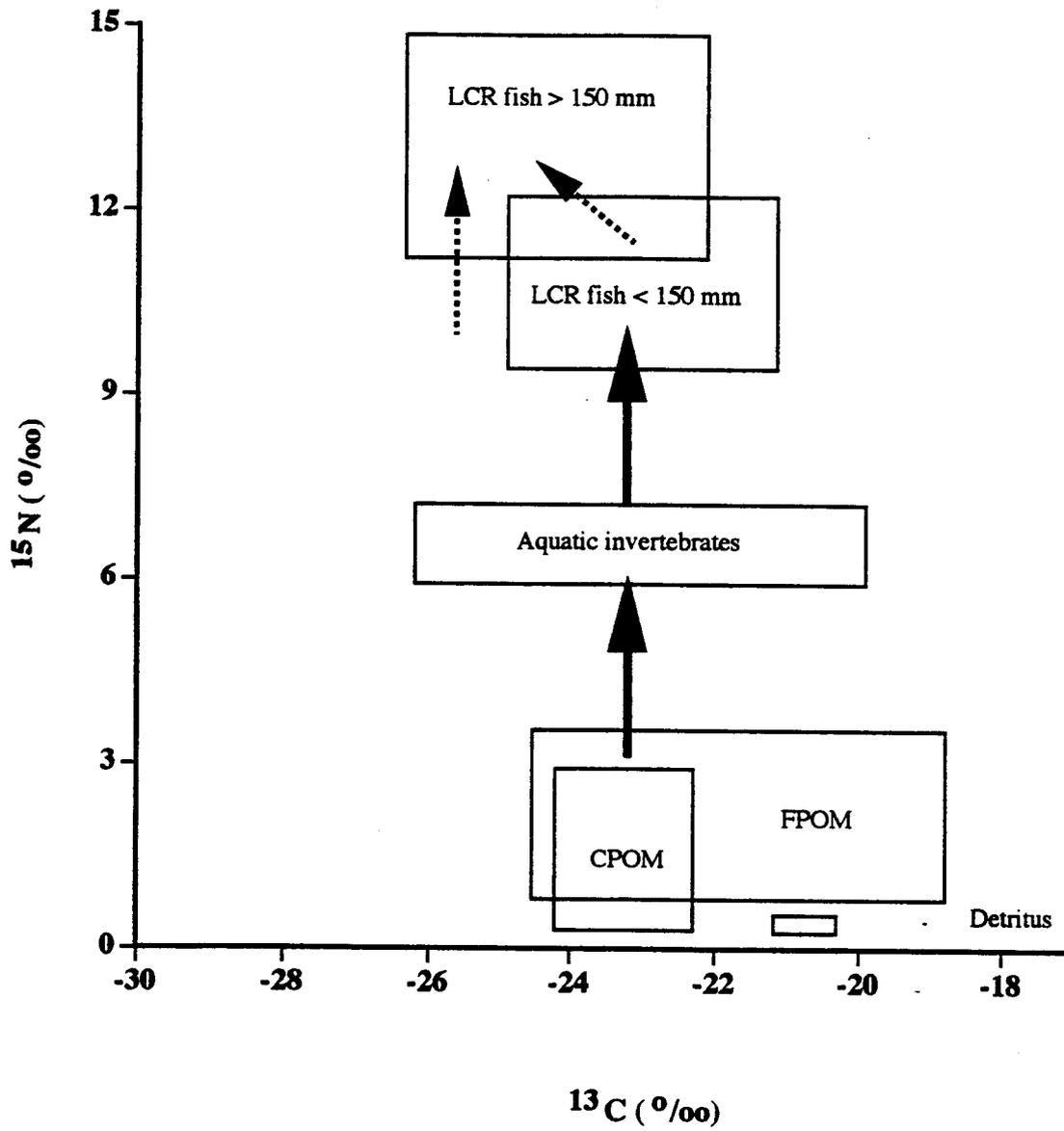


Fig. 6