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Author(s): Ted R. Angradi

Source: *Journal of the North American Benthological Society*, Vol. 13, No. 4 (Dec., 1994), pp. 479-495

Published by: The North American Benthological Society

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Trophic linkages in the lower Colorado River: multiple stable isotope evidence

TED R. ANGRADI¹

Arizona Department of Game and Fish,
Phoenix, Arizona 85023 USA

Abstract. Trophic linkages in Glen and Grand Canyons of the lower Colorado River downstream from Glen Canyon Dam were examined using multiple stable isotope analysis. The $\delta^{13}\text{C}$ values of dissolved inorganic carbon (DIC), and the $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values of seston, aquatic and terrestrial plants, and aquatic animals were determined. The $\delta^{13}\text{C}$ value of DIC varied among sites. DIC from the epilimnion of the reservoir (Lake Powell) and from a tributary was more ^{13}C -enriched than DIC in the Colorado River, probably as a result of variation in aquatic primary production and dissolution of carbonate among sites. Four potential bases of aquatic secondary production: upland vegetation, riparian vegetation, reservoir plankton, and benthic algae were isotopically ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) distinct from each other. Analysis of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ showed that seston from the dam tailwater (Glen Canyon) consisted of lotic algae and zooplankton from Lake Powell, except for the ultra fine fraction (<0.053 mm) which was derived from Lake Powell particulate organic matter. Longitudinal variation in the composition of Glen Canyon seston was generally small. Seston from a tributary (the Paria River) was derived from a mixture of upland and riparian vegetation and was isotopically distinct from Colorado River seston. Isotope analysis revealed three trophic levels in Glen Canyon: algae (*Cladophora glomerata* and diatoms), macroinvertebrates (e.g., *Gammarus lacustris* and chironomids), and fish (primarily rainbow trout, *Oncorhynchus mykiss*). Trout also consumed zooplankton exported from Lake Powell. Direct assimilation of algal N by trout was not indicated despite the high incidence of algae in trout stomachs. Isotope values of fishes (trout and speckled dace, *Rhinichthys osculus*) from Grand Canyon tributaries reflected variation in the trophic basis of fish production; one tributary fish population appeared to be supported by tributary autochthonous production or mainstem organic matter sources, and others were linked to riparian or upland organic matter inputs.

Key words: Colorado River, dam, stable isotopes, ^{13}C , ^{15}N , ^{34}S , seston, food webs, trophic level, *Gammarus*, *Cladophora*, fish.

Predicting how the operation of a large hydroelectric facility on the lower Colorado River, Glen Canyon Dam, influences downriver aquatic communities required an understanding of the linkages among Colorado River communities (e.g., reservoir-tailwater, upstream-downstream, riparian-lotic, upland-lotic, and tributary-mainstem linkages). Particulate organic matter (POM) is a key link. The origin of organic matter moving through lotic ecosystems determines the connections between stream detritivores, their predators, and upstream or upslope ecosystems.

Analysis of stable isotopes of carbon, nitrogen, and sulfur (i.e., $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, and $^{34}\text{S}/^{32}\text{S}$) in biogenic materials can be used to establish a chemical outline of the trophic structure

of aquatic communities (Fry 1991). These isotopes undergo a change in the ratio of heavy to light isotopes (fractionation) in chemical and biochemical reactions. As a result, biogenic materials often have unique isotope ratios which can be used to trace C, N, and S through ecosystems (Fry and Sherr 1984, Rounick and Winterbourn 1986, Peterson and Fry 1987, Fry 1991, Gearing 1991). Stable isotopes are useful in trophic studies because isotopes move with little or predictable alteration through food chains (Rounick and Winterbourn 1986). The $\delta^{13}\text{C}$ values of animals reflect that of the assimilated part of the diet averaged over weeks or months, but with about a 1 part per thousand (‰) enrichment per trophic level (Fry and Sherr 1984). The $\delta^{15}\text{N}$ values of animals are usually +2 to +5‰ enriched relative to the diet (mean = 3.4‰, Minagawa and Wada 1984). Generally, no change is associated with trophic transfer for ^{34}S (Peterson and Fry 1987). Two advantages of stable isotope analysis over other methods of

¹ Present address: United States Forest Service, Northeastern Forest Experiment Station, Timber and Watershed Laboratory, Parsons, West Virginia 26287 USA.

examining trophic linkages are (1) the origin of visually unidentifiable POM can often be determined isotopically, and (2) stable isotope values reflect the C, N, and S that is *assimilated* by organisms, rather than what is merely consumed (Rosenfeld and Roff 1992).

Stable isotope analysis may be particularly effective for studying organic matter dynamics and food webs in regulated rivers because dam effects (e.g., retention of lotic POM and export of lentic POM, tributary origin of coarse POM, and physical and chemical alterations in water quality and river habitat) can cause discontinuities in organic matter sources along the river profile (Ward and Stanford 1983), and may result in relatively distinct isotopic separation among organic matter sources and food web components (Angradi 1993, Junger and Planas 1994).

The objectives of my study were to examine the trophic structure of the dam tailwater (referred to herein as Glen Canyon) and to survey trophic linkages in the Grand Canyon and its tributaries, with emphasis on fishes, using analysis of stable isotopes of carbon, nitrogen, and sulfur occurring naturally in POM and organisms. Several questions were addressed in the study: (1) what is the trophic basis of aquatic secondary production in Glen Canyon? (2) Does the origin of organic seston (suspended POM) vary downstream within the tailwater reach? (3) How many lotic trophic levels are there in Glen Canyon? (4) How much trophic interaction is there between tributaries and the Colorado River in Grand Canyon? and (5) Does the basis of production differ among Glen Canyon, Grand Canyon, and Grand Canyon tributaries?

Methods

Study site

Glen Canyon Dam, near the Utah-Arizona (USA) border (Fig. 1), forms Lake Powell, a 653-km² warm-monomictic reservoir (Stanford and Ward 1991). Glen Canyon extends 26 km downstream from the dam to the confluence with the first tributary, the Paria River (Fig. 1); Grand Canyon (including Marble Canyon) extends 450 km thence. Daily range in discharge from the reservoir was about 150-400 m³/s during this study (U.S. Bureau of Reclamation, unpublished data). Flows in the Paria River range from

0 to >450 m³/s. Mean discharge is only about 1 m³/s despite a drainage area of 3651 km² (Hofknecht 1981).

The physical environment of the Colorado River in Glen and Grand canyons has been greatly altered by the construction and operation of Glen Canyon Dam. Unlike the pre-dam Colorado River, flows from hypolimnetic reservoir releases are perennially cold (7-11°C) and contain little particulate organic matter (POM) or suspended sediment (Stanford and Ward 1991). Mean seston concentration in Glen Canyon is rather low, <1.0 mg AFDM/L (Angradi and Kubly, in press), compared with other large rivers (Webster et al. 1979).

The flora and fauna of the river downstream from the dam are depauperate (Blinn and Cole 1991). The filamentous green algae *Cladophora glomerata* (L.) Kutz. is the dominant attached alga and is an important substrate for diatoms (Blinn et al. 1986). Epilithic *Cladophora* often attains a biomass in excess of 500 mg chlorophyll *a*/m² in Glen Canyon (Angradi and Kubly 1993). High turbidity caused by suspended sediment exported from tributaries limits the growth of *Cladophora* in Grand Canyon (Usher and Blinn 1990). The blue-green alga *Oscillatoria* is abundant in some Grand Canyon reaches (D. W. Blinn, Northern Arizona University, personal communication).

Chironomids, oligochaetes, and the amphipod *Gammarus lacustris* dominate the Glen Canyon macroinvertebrate assemblage (Blinn and Cole 1991; D. W. Blinn, personal communication). The altered thermal regime and shortage of suitable food for shredders (coarse POM) and filter feeders (fine seston) caused by impoundment and hypolimnetic release account for the invertebrate assemblage dominated by gatherers (Ward 1975, Webster et al. 1979, Blinn and Cole 1991). The invertebrate communities of most tributary streams within Grand Canyon are much more diverse than the mainstem fauna (Hofknecht 1981).

The fish assemblage consists of five native species and about 15 non-native species (Minckley 1991). The speckled dace (*Rhinichthys osculus* [Girard]) is the most widespread and abundant native species in Grand Canyon and its tributaries. In Glen Canyon the non-native rainbow trout (*Oncorhynchus mykiss* [Walbaum]) is abundant. The native flannelmouth sucker (*Catostomus latipinnis* [Baird and Girard]) and non-na-

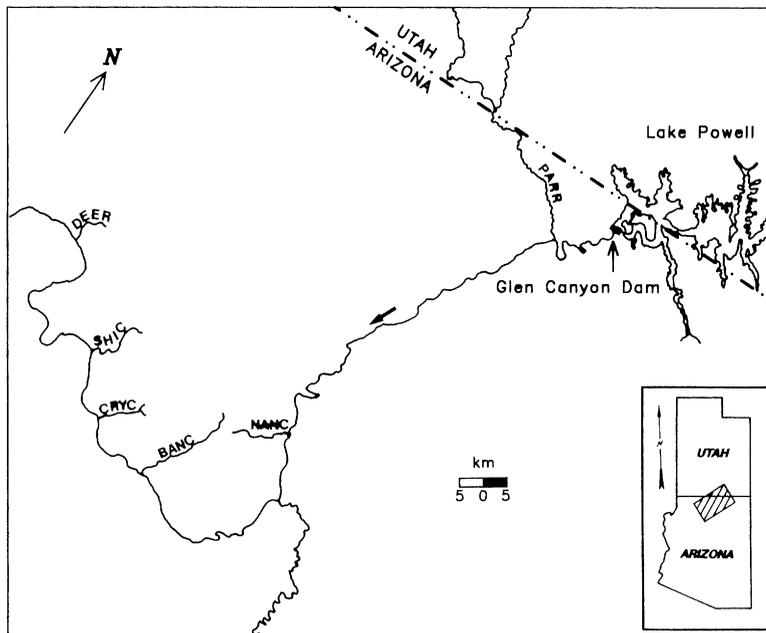


FIG. 1. The study reach of the lower Colorado River. Reach of river between the dam and the Paria River (PARR) is referred to as Glen Canyon. Other tributaries are Nankoweap Creek (NANC), Bright Angel Creek (BANC), Crystal Creek (CRYC), Shinumo Creek (SHIC), and Deer Creek (DEER). Approximately 260 km of the Colorado River is shown, not including Lake Powell. Only the lower third of Lake Powell is shown. Inset map shows location of the study reach.

tive carp (*Cyprinus carpio* [Linn.]) are common; other species are rare. Rainbow trout are also present in the Grand Canyon and are known to spawn in Grand Canyon tributaries (Maddux et al. 1987).

Woody vegetation of the Glen Canyon riparian zone is dominated by tamarisk (*Tamarix ramosissima*), willows (*Salix* spp.), and seepwillow (*Baccharis* spp.) (Johnson 1991). Upland vegetation of the inner gorge of Grand Canyon is Great Basin desertscrub and Mojave desertscrub; headwaters of larger North Rim tributaries drain pinyon-juniper woodlands (Brown and Lowe 1980).

Sample collection and analysis

Samples for stable isotope analysis were collected between March and May of 1992 (Appendix 1). Water samples for dissolved inorganic carbon (DIC) were collected from the epilimnion (6 m depth) and hypolimnion (46 m depth) of Lake Powell at a site 100 m uplake of the dam. Water samples were also collected from dam penstocks, from sites in the Colorado

River (CR) 2 km, 11 km, and 25 km downriver from the dam (sites CR02, CR11, CR25, respectively—all Colorado River distances given here are relative to the dam), and from the Paria River near its confluence with the Colorado River. Water samples for DIC analysis were filtered (Millipore, 0.47- μm pore size) and preserved with HgCl_2 . POM was collected at the same sites using the following methods. POM <80 μm from Lake Powell was collected by pumping lake water through an 80- μm mesh plankton net and then filtering (Whatman GF/F; effective pore size: 0.7 μm). POM >80 μm was collected by pumping about 1500 L of lake water through an 80- μm mesh plankton net. Although zooplankton is exported from the reservoir as evidenced by zooplankters in seston samples (Haury 1988; T. R. Angradi, personal observation), insufficient material >80 μm was collected in the hypolimnetic sample for analysis. Samples from dam penstocks were filtered (Whatman GF/F) without pre-straining. Seston was collected at sites CR02, CR11, and CR25 by towing a pair of plankton nets (1.5 m long, 0.25 m diameter, 0.053-mm mesh) upriver behind a

boat. At the Paria River site, a net was tethered to a bridge support in midchannel. Each sample of seston was acidified (1 N HCl) to prevent carbonate contamination (Boutton 1991), washed, and wet sieved into three size fractions: coarse particulate organic matter (CPOM, >1 mm); fine particulate organic matter (FPOM, <1 mm and >0.25 mm); and very fine particulate organic matter (VFPOM, <0.25 mm and >0.053 mm). Whether acidification, a common procedure in stable isotope studies (e.g., Boutton 1991, Bunn et al. 1989, Estep and Vigg 1985, Hesslein et al. 1991, Rosenfeld and Roff 1992, Rounick et al. 1982), altered the $\delta^{15}\text{N}$ values of samples is not known (see Goering et al. 1990). Ultra fine particulate organic matter (UFPOM, <0.053 mm) was collected by filtering (Whatman GF/F) samples of pre-strained (0.053 mm) river water. During the collecting trip to the Paria River, discharge was above baseflow, and a high inorganic load prevented collection of an UFPOM sample. An additional sample of Paria River CPOM was collected using a minnow seine with a mesh size of 3 mm. Replicate seston samples were analyzed separately.

Riparian vegetation and litter were grab sampled in Glen Canyon and along the Paria River. At the Paria River, two flood-deposited litter accumulations were sampled; these deposits consisted of a mixture of conifer needles, cones, berries, nuts, bark, and wood. A sample of immersed cottonwood (*Populus fremonti*) leaves was also collected from the Paria River. Seston, plant and litter samples were dried (60°C) and ground before analysis.

Cladophora glomerata was collected at sites CR02 and CR22. At each site, samples of *Cladophora* with few epiphytes and samples with a high epiphyte load were collected. In Glen Canyon, the relative epiphyte load of littoral *Cladophora* is zoned by depth and results from variation in the amount of exposure to the atmosphere resulting from dam operations (T. R. Angradi, personal observation). A subsample of the high-epiphyte-load *Cladophora* from CR02 was partially stripped of epiphytes by placing the filaments in a plastic bag with distilled water and shaking vigorously. Detached epiphytes were collected on pre-ashed filters (Whatman GF/F).

To determine if in situ processing (e.g., leaching of labile compounds, microbial colonization) caused shifts in the stable isotope ratios of detached *Cladophora* filaments, samples of each

type of *Cladophora* from the CR02 site were harvested from cobbles and placed in litter bags (2-mm mesh), four each, and anchored in the permanently inundated channel at CR02. Bags were collected after 25 and 53 d.

A sample of the green alga *Ulothrix tenuis-sima* Kutz. was collected from the dam spillway. An epilithic algal-crust presumed to contain the blue-green alga *Oscillatoria* was collected from a cobble bar on the Colorado River 330 km below the dam. Algal samples were acidified, rinsed, dried, and ground in a mill before analysis.

Gammarus lacustris was collected with a dipnet at CR02, CR11, and CR22. About 20 animals from each site were held live in mesh-bottom cages for 48 h to clear their guts, then were dried, ground with a mortar and pestle, acidified, rinsed, and redried. Replicates are subsamples from a single pooled sample from each site. Oligochaetes were collected at CR11 and processed similarly.

Adult rainbow trout (39–46 cm total length) were collected in Glen Canyon at CR01 and CR19. Rainbow-trout fry (<5 cm) were collected at CR02 and CR25. Two flannelmouth suckers (>40 cm) were collected at CR19. Two adult rainbow trout (>20 cm) were collected in Nankoweap Creek 10 m upstream from the confluence with the Colorado River at CR109. Rainbow trout fry (<3.5 cm) were collected 1370 m upstream from the confluence of Bright Angel Creek and the Colorado River at CR166, and 75 m upstream from the confluence of Deer Creek and the Colorado River at CR244. Speckled dace (4–10 cm) were collected at six sites: >2 km up the Paria River; 45 and 1500 m up Nankoweap Creek; 500 m up Crystal Creek (CR183); and 10 and 700 m up Shinumo Creek (CR200).

Boneless, skinless fillets were removed from the dorsal musculature of adult trout and suckers. Trout fry and speckled dace were eviscerated, skinned, and the head and fins were removed. The vertebrae of small fish were assumed to produce no bias in isotope ratios relative to a pure muscle sample (Gearing 1991). Fish tissue was dried and ground with a mortar and pestle. Several (2–4) trout fry were pooled for each site; fish were otherwise analyzed individually. Selected gut contents of adult trout were dried and ground for analyses.

Isotope ratios were determined by mass spectrometry at the Stable Isotope Laboratory at Bos-

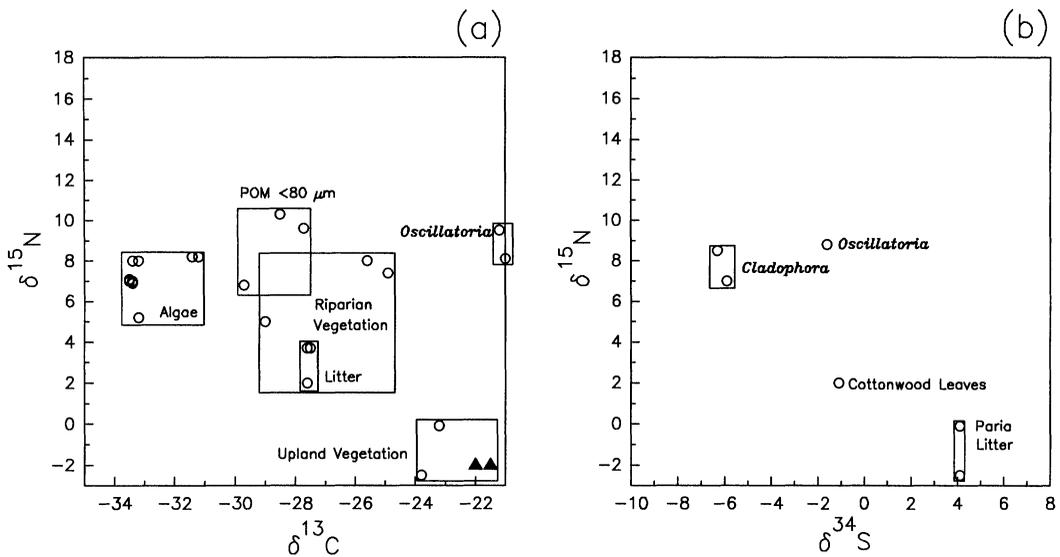


FIG. 2. Dual isotope plots for primary producers in Glen Canyon. In (a), $\delta^{15}\text{N}$ is plotted against $\delta^{13}\text{C}$. In (b), $\delta^{15}\text{N}$ is plotted against $\delta^{34}\text{S}$. Values are expressed as parts per thousand (‰). Each open circle represents a single sample. Means are given in Appendix 1. Filled triangles are for pinyon and juniper leaves and twigs. Conifer $\delta^{13}\text{C}$ values are from Leavitt and Long (1986, fig. 1; pinyon, -22‰) and (1982, table 1; juniper, -21.5‰). $\delta^{15}\text{N}$ values for pinyon and juniper are estimated from values for conifers in Angradi (1993, table I). "Algae" refers to *Cladophora* and its epiphytes.

ton University ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and at the Marine Biological Laboratory, Woods Hole, Massachusetts ($\delta^{34}\text{S}$). Isotope ratios are reported in delta (δ) notation as parts per thousand (per mil, ‰) deviation from isotope standards: atmospheric nitrogen for $\delta^{15}\text{N}$, PeeDee belemnite carbonate for $\delta^{13}\text{C}$, and Canyon Diablo troilite for $\delta^{34}\text{S}$:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} \text{ or } \delta^{34}\text{S}\text{‰} \\ = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where R denotes $^{15}\text{N}/^{14}\text{N}$, $^{13}\text{C}/^{12}\text{C}$, or $^{34}\text{S}/^{32}\text{S}$ (Peterson and Fry 1987). Well homogenized replicates are usually within a 0.2‰ range (R. Michener, Boston University, personal communication). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined for all samples; $\delta^{34}\text{S}$ was determined for a subset of samples.

Results

Dissolved inorganic carbon

Dissolved inorganic carbon (DIC) was more ^{13}C -depleted in the Colorado River in Glen Canyon and the hypolimnion of Lake Powell ($< -6.9\text{‰}$) than in the epilimnion of Lake Pow-

ell (-5.1‰) or in the Paria River (-2.9‰ , Appendix 1). $\delta^{13}\text{C}$ values of DIC did not vary among Glen Canyon sites.

Primary producers

The $\delta^{13}\text{C}$ values of terrestrial and aquatic plant materials ranged from -33.5 to -21‰ (Fig. 2a). The $\delta^{13}\text{C}$ values of all lotic plant material except *Oscillatoria* (-21‰) was $< -31\text{‰}$, and that of all terrestrial plants and plant litter was $> -29\text{‰}$. *Cladophora* with and without epiphytes, and an extract of epiphytes (diatoms), had similar $\delta^{13}\text{C}$ values ($\sim -33\text{‰}$). *Cladophora* from CR22 and *Ulothrix* from the dam spillway were slightly enriched ($+2\text{‰}$) compared with other algae samples. Lake Powell POM $< 80 \mu\text{m}$, which presumably contains a high proportion of phytoplankton and is therefore included with other primary producers, was more $\delta^{13}\text{C}$ -enriched than lotic algae (-27.7 to -29.7‰) (Fig. 2).

Riparian vegetation had a broad $\delta^{13}\text{C}$ range, from ~ -25 to -29‰ , and partially overlapped the $\delta^{13}\text{C}$ range of Lake Powell POM $< 80 \mu\text{m}$ (Fig. 2). Willow leaves were the most ^{13}C -depleted (-29‰); *Equisetum* was the most ^{13}C -en-

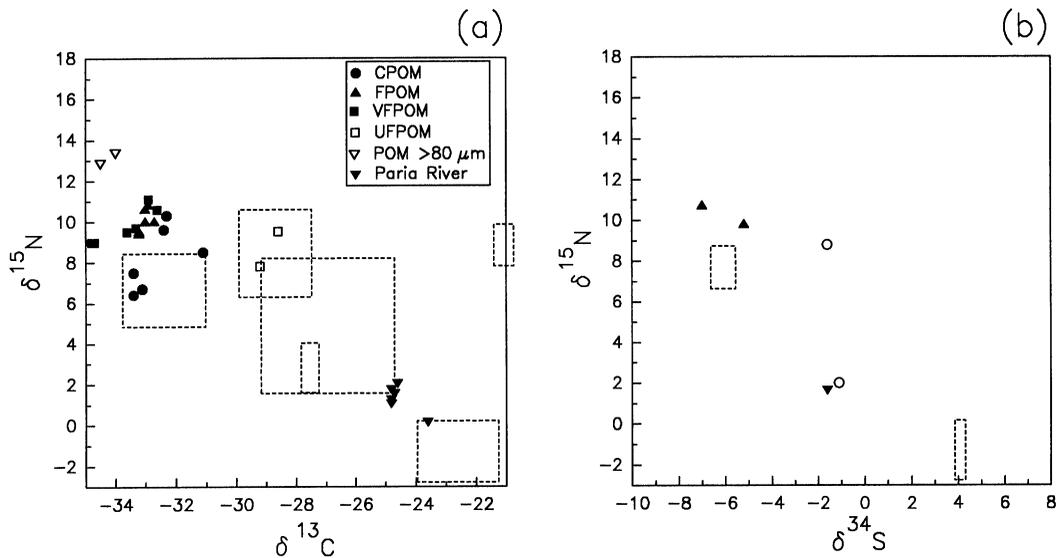


FIG. 3. Dual isotope plots for Glen Canyon and Paria River seston and Lake Powell POM. In (a), $\delta^{15}\text{N}$ is plotted against $\delta^{13}\text{C}$. In (b), $\delta^{15}\text{N}$ is plotted against $\delta^{34}\text{S}$. Values are expressed as parts per thousand (‰). Boxes and open circles (in plot b) correspond to primary producers plotted in Fig. 2. Each point represents a single sample. Means are given in Appendix 1.

riched (-24.9‰ , Appendix 1). Riparian litter (cottonwood and tamarisk leaves) had a mean $\delta^{13}\text{C}$ value of -27.6‰ . Litter from the Paria River floodplain was ^{13}C enriched ($> -24\text{‰}$) compared with other terrestrial materials (Appendix 1, Fig. 2).

The $\delta^{15}\text{N}$ values of plant material ranged from -2.5 to 10.3‰ . Lake Powell POM $<80\ \mu\text{m}$ was the most ^{15}N -enriched (Fig. 2b, Appendix 1). Litter from the Paria River floodplain was the most ^{15}N depleted ($<0\text{‰}$). Riparian litter (2 to 3.7‰) was more ^{15}N depleted than live vegetation, based on a small number of samples.

Isotopic separation of primary producers based on $\delta^{34}\text{S}$ values was similar to that obtained with ^{13}C (Fig. 2b), with the exception that *Oscillatoria* (-1.6‰) had a value similar to cottonwood (-1.1‰).

There was little effect of in situ incubation of *Cladophora* samples on $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for high- and low-epiphyte-load samples after 0, 25, and 52 d were within a 1.1‰ range (Appendix 1). I obtained similar results in a previous study (Angradi 1993), as did Junger and Planas (1994) for ^{13}C .

In general, the $\delta^{13}\text{C}$ range of primary producers (-21 to -34‰) was similar to that of other published studies of freshwater ecosys-

tems (e.g., Boutton 1991, Fry 1991, Angradi 1993). The $\delta^{15}\text{N}$ range of aquatic primary producers (5 to 11‰) was somewhat higher than reported elsewhere for an unregulated stream (Fry 1991, Angradi 1993).

Seston

The $\delta^{13}\text{C}$ values of seston ranged from ~ -35 to -24‰ (Fig. 3a). Values fell into three groups: $> -25\text{‰}$ for Paria River seston, -27 to -30‰ for UFPOM, and $< -31\text{‰}$ for CPOM, FPOM, and VFPOM from Colorado River sites and for POM $>80\ \mu\text{m}$ from the epilimnion of Lake Powell (Appendix 1, Figs. 3, 4). Glen Canyon UFPOM was about $+4\text{‰}$ ^{13}C -enriched compared with other size fractions (Figs. 3, 4), and was similar isotopically to POM $<80\ \mu\text{m}$ from Lake Powell.

The $\delta^{15}\text{N}$ of seston ranged from ~ 0 to 13‰ (Fig. 3). Epilimnetic POM $>80\ \mu\text{m}$ ($\sim 13\text{‰}$) and Paria River seston ($<2\text{‰}$) were isotopically distinct from other samples. $\delta^{15}\text{N}$ values for Glen Canyon FPOM and VFPOM were within a narrow range (9 to 12‰).

The $\delta^{13}\text{C}$ values of VFPOM decreased about 2‰ between CR02 and CR25 (Fig. 4); decreases with distance downriver for other size fractions were $<1\text{‰}$. Small ($<1.7\text{‰}$) decreases with dis-

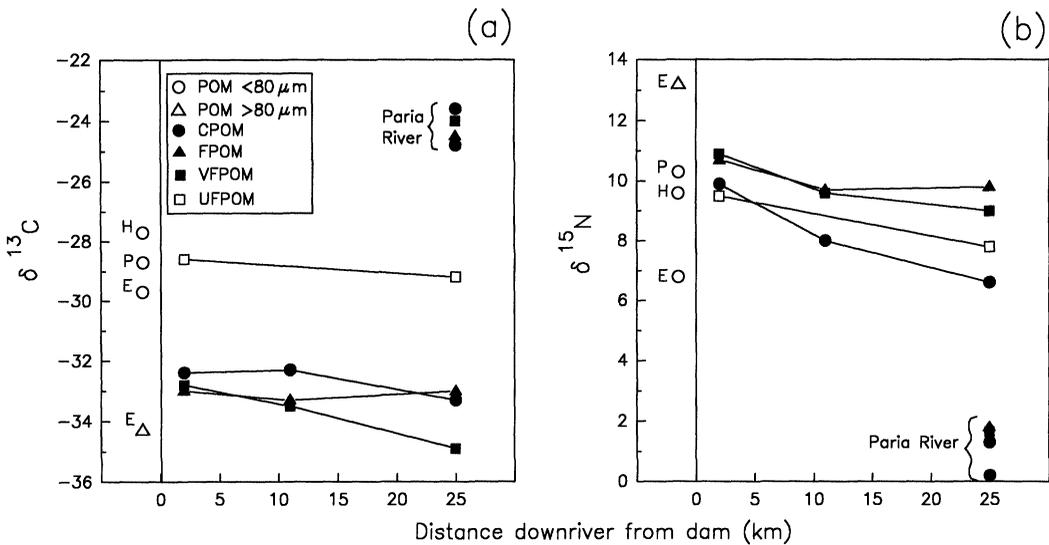


FIG. 4. Variation in $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) of seston with distance downriver from Glen Canyon Dam. Values are expressed as parts per thousand (‰). Vertical line indicates location of the dam. Letters adjacent to points refer to hypolimnion (H), epilimnion (E), and penstock (P) sample locations in Lake Powell.

tance downriver from the dam were detected for $\delta^{15}\text{N}$ values of FPOM, VFPOM, and UFPOM (Fig. 4). $\delta^{15}\text{N}$ values of CPOM decreased the most, about 3.3‰ over the 23 km (CR02 to CR25).

Glen Canyon consumers

Primary consumers (benthic macroinvertebrates) in Glen canyon had $\delta^{13}\text{C}$ values between -31 and -34 ‰ (Fig. 5a). There was no ^{13}C -enrichment of lotic primary consumers over primary producers. Secondary consumers (fish) were $+2.5$ to $+6$ ‰ ^{13}C -enriched (> -30 ‰) compared with macroinvertebrates. Trout fry were 1.5 to 2 ‰ ^{13}C -depleted compared with adult trout and suckers. Enrichment in ^{15}N per trophic level was $+2$ to $+4$ ‰ for macroinvertebrates versus lotic algae, and $\sim +5$ ‰ for fish versus macroinvertebrates (Fig. 5a). A sample of *Gammarus* had a $\delta^{34}\text{S}$ value similar to algae (~ -7 ‰). Trout and flannelmouth sucker were ~ 1.5 ‰ ^{34}S -depleted compared to *Gammarus*.

Fishes of Grand Canyon tributaries

Fishes collected in Grand Canyon tributaries, especially speckled dace, occupied a broad range of isotopic positions compared with Glen Canyon fishes (Fig. 6). Isotopic separation among

sample sites was greater for ^{15}N than for ^{13}C . Fish from Nankoweap Creek were more ^{15}N -enriched and generally more ^{13}C -depleted than fish collected elsewhere in Grand Canyon, and were similar, isotopically, to Glen Canyon fishes (Fig. 6). Rainbow trout fry and speckled dace from the Paria River, Deer Creek, Bright Angel Creek, and Crystal Creek had variable isotope values and generally lacked unique signatures (Fig. 6). Speckled dace from Shinumo Creek were isotopically distinct (^{13}C -enriched and ^{15}N -depleted) from dace collected elsewhere.

Discussion

Dissolved inorganic carbon

The $\delta^{13}\text{C}$ value of DIC (dissolved CO_2 and HCO_3^-) in freshwater depends on the extent to which it is in equilibrium with air ($\delta^{13}\text{C}$ of atmospheric $\text{CO}_2 = -7$ to -8 ‰, $\delta^{13}\text{C}$ of DIC of water in equilibrium with air is ~ 0 ‰), the rates of photosynthesis and respiration, and the contribution from dissolution of ^{13}C -enriched carbonate rock (Oana and Deevey 1960, Quay et al. 1986, Boutton 1991). Lake Powell is generally stratified by April, when samples were collected, and the phytoplankton biomass of the epilimnion (as indicated by particulate chlorophyll

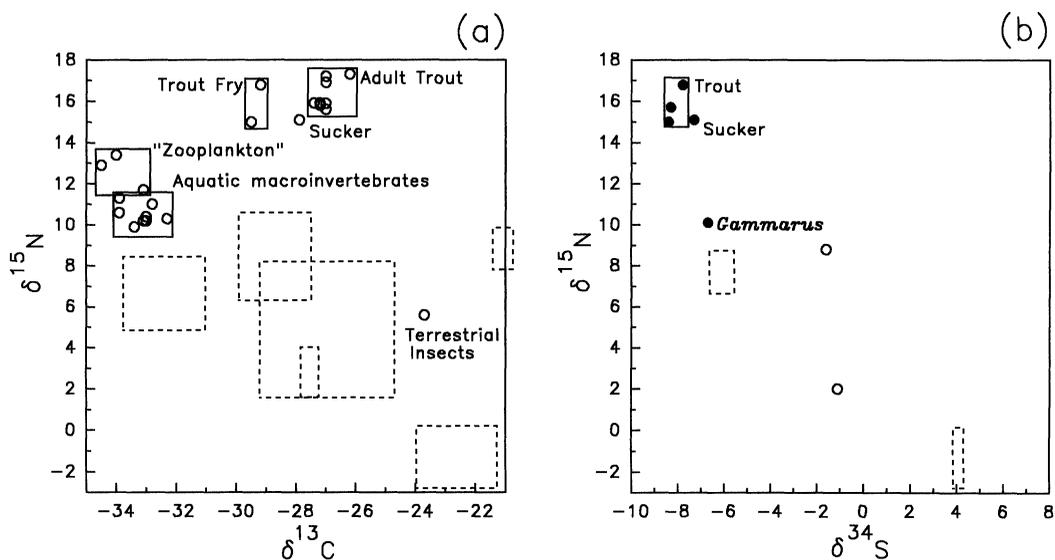


FIG. 5. Dual isotope plots for Glen Canyon consumers. In (a), $\delta^{15}\text{N}$ is plotted against $\delta^{13}\text{C}$. In (b), $\delta^{15}\text{N}$ is plotted against $\delta^{34}\text{S}$. Values are expressed as parts per thousand (‰). Unlabelled boxes and open circles (in plot b) correspond to primary producers plotted in Fig. 2. "Zooplankton" is Lake Powell POM $>80\ \mu\text{m}$ (as in Fig. 3) and a sample of cladocerans from a trout stomach (see Appendix 1). Aquatic macroinvertebrates includes *Gammarus lacustris*, chironomids, and oligochaetes. Each point represents a single sample. Means are given in Appendix 1.

a concentration) is more than twice that of the hypolimnion at penstock depth (T. R. Angradi, unpublished data). Photosynthesis increases the $\delta^{13}\text{C}$ of DIC as isotopically light (i.e., ^{12}C -enriched) dissolved CO_2 is selectively incorporated into phytoplankton (Quay et al. 1986). Hypolimnetic and river DIC are probably more ^{13}C -depleted than epilimnion DIC as a result of contributions of dissolved CO_2 from respiration of plankton (Oana and Deevey 1960). The ^{13}C -enriched condition of Paria River DIC probably results from dissolution of carbonate rock ($\delta^{13}\text{C} = \sim 0\text{‰}$, Deevey and Stuiver 1964). The concentration of bicarbonate ions in the Paria River (3.5 meq/L) exceeds that of the Colorado River (2.8 meq/L, Kubly and Cole 1979).

$\delta^{13}\text{C}$ values of Glen Canyon DIC were not sufficiently variable to produce spatial variation in $\delta^{13}\text{C}$ values of lotic epilithic algae as has been reported to occur elsewhere (Rounick and Winterbourn 1986, Keeley and Sandquist 1992). Vertical variation in $\delta^{13}\text{C}$ values for reservoir DIC might produce seasonal changes in DIC associated with reservoir processes (discussed later in "Glen Canyon consumers").

Primary producers

Litter from Paria River flood-deposits had $\delta^{13}\text{C}$ values similar to published $\delta^{13}\text{C}$ values for leaves and twigs of one-seed juniper (*Juniperus monosperma*), Utah juniper (*Juniperus osteosperma*), and pinyon (*Pinus edulis*) collected in Arizona (-20 to -23‰ , Leavitt and Long 1982, 1986). The mean value for terrestrial C_3 plants is $\sim -28\text{‰}$ (Peterson and Fry 1987); most stable isotope studies of terrestrial inputs of C_3 plants to freshwater ecosystems report a 2 to 4‰ range in $\delta^{13}\text{C}$ values for terrestrial organic matter sources (e.g., Rau 1980, Rounick et al. 1982, Bunn et al. 1989, Rosenfeld and Roff 1992, Angradi 1993). The enriched values for upland vegetation ($> -25\text{‰}$) account for the larger $\delta^{13}\text{C}$ range reported here ($\geq 7\text{‰}$). The underlying reason for the difference in $\delta^{13}\text{C}$ values between upland ($> -25\text{‰}$) and riparian plants ($\leq 25\text{‰}$) may be related to the effect of soil water availability on isotopic discrimination by the plants. Plants growing on drier slope sites have higher $\delta^{13}\text{C}$ values than do plants growing on wetter sites (Ehleringer and Cooper 1988).

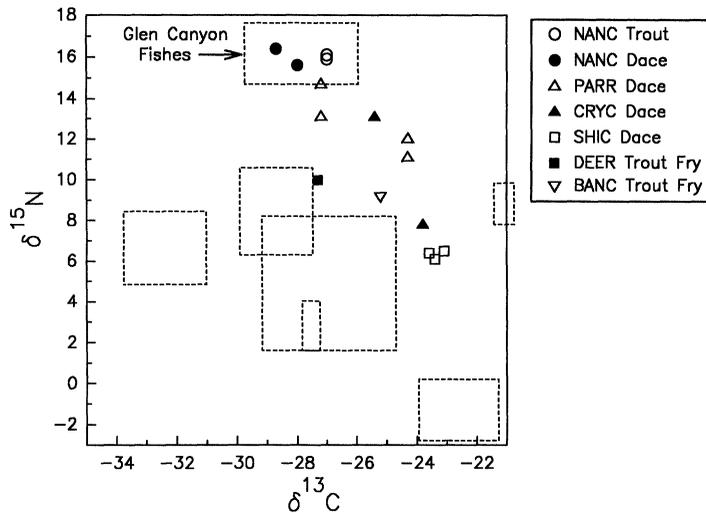


FIG. 6. $\delta^{15}\text{N}$ plotted against $\delta^{13}\text{C}$ for rainbow trout and speckled dace from Grand Canyon tributaries. Values are expressed as parts per thousand (‰). Unlabelled boxes correspond to primary producers plotted in Fig. 2. Each point represents a single sample. Means are given in Appendix 1. Site codes are as in Fig. 1.

The relatively enriched $\delta^{15}\text{N}$ value for *Oscillatoria* (8.8‰) was unexpected since nitrogen-fixing algae usually have a $\delta^{15}\text{N}$ value near 0‰ (Estep and Macko 1985, Fry 1991) or are at least relatively ^{15}N -depleted ($\delta^{15}\text{N}$ values of 2 to 4‰, Estep and Vigg 1985, Angradi 1993). Possible explanations are that non-heterocystous *Oscillatoria* does not fix nitrogen (although it has been reported to do so in unialgal cultures, Stewart 1973) or, more likely, that the high $\delta^{15}\text{N}$ value is an artifact since *Oscillatoria* was found in a matrix of sediment and detritus of unknown composition; the $\delta^{15}\text{N}$ value of the bulk sample probably represented a mixture of *Oscillatoria* and other N-containing materials (e.g., diatoms).

Dual isotope plots reveal that lotic algae, riparian vegetation, and upland vegetation had distinct isotope signatures. Of the isotopes used in this study, $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ were most suitable for distinguishing between terrestrial or aquatic origins for organic matter sources. $\delta^{15}\text{N}$ may be useful for distinguishing upland vegetation from riparian and aquatic material. The dual isotope range ($\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$) for Lake Powell "phytoplankton" (POM <80 μm) overlapped with that of riparian vegetation (Fig. 2), although the actual values did not. This overlap is discussed further in the next section.

Seston

The co-plotted $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ and $\delta^{15}\text{N}$ versus $\delta^{34}\text{S}$ ranges of CPOM from CR02, and FPOM and VFPOM from all Glen Canyon sites (Fig. 4) reflect a mixture of lotic algae and Lake Powell POM >80 μm (Figs. 3, 6). The isotope signature of CPOM from CR11 and CR25 reflect an algal origin. Glen Canyon macroinvertebrates were very similar isotopically to Glen Canyon seston. However, visual inspection of samples showed that drifting macroinvertebrates were rare in samples and largely confined to CPOM which was the seston fraction most *unlike* macroinvertebrates isotopically. An alternate explanation for the enrichment of seston over algae is that rather than reflecting the presence of ^{15}N -enriched plankton, the algal particles were colonized by microbes that substantially enriched the $\delta^{15}\text{N}$ value (as described for marsh detritus by Macko and Estep 1984) or that ^{15}N -depleted compounds were leached out of particles before they were entrained as seston. These interpretations would contradict the results of litter-bag experiments conducted in rivers which have shown little alteration in isotope values of autochthonous material incubated in situ (this study; Angradi 1993). CPOM, FPOM, and VFPOM samples from the site nearest the dam

(CR02) were the most ^{15}N -enriched (Appendix 1, Fig. 4). However, autochthonous material from this site would most likely be the *least* processed, because it was collected closer to its point of origin than seston from any other site (virtually no material is exported from sites upstream of the 300 km long reservoir). Finally, seston from CR02 would be expected to include the highest proportion of zooplankton relative to cumulative lotic inputs, since the amount of reservoir zooplankton remains rather constant through Glen Canyon (Haury 1988). Interestingly, only CPOM from the site nearest the dam (CR02) had $\delta^{13}\text{C}$ values suggestive of a zooplankton contribution. Ward (1975) also showed that large (i.e., CPOM-sized) zooplankters, especially cladocerans, disappeared from the seston 2.5–5 km downriver from a hypolimnetic release reservoir.

The dual-isotope range of Glen Canyon UFPOM lies within the dual isotope range for reservoir POM $<80\ \mu\text{m}$. There is some overlap in the isotope ranges of UFPOM and riparian vegetation (Fig. 3). Riparian vegetation probably does not contribute much organic matter to the UFPOM fraction, however, because it is unlikely that the finest riparian-derived particles would be significant in the seston when the coarser particles are not. The uniqueness of the $\delta^{13}\text{C}$ range of UFPOM compared with larger size fractions of seston, and its dual-isotope similarity to reservoir POM $<80\ \mu\text{m}$ (Figs. 3, 4), suggests that this fraction is dominated by material exported from the reservoir. I did observe CPOM of riparian origin (e.g., tree limbs, tamarisk litter) in the seston, but only during seasonal peak dam releases when particles were entrained by floodplain capture.

The dual isotope ranges of Paria River seston reveal that it is a mixture of particles derived from upland and riparian vegetation and is probably dominated by the latter (Fig. 3). A sample of large CPOM ($>3\ \text{mm}$) collected during a spate was most similar, isotopically, to upland vegetation (Fig. 3).

Glen Canyon consumers

Dual-isotope plots (Fig. 5) reveal three aquatic trophic levels in Glen Canyon: algae, benthic macroinvertebrates, and fish. Trout in Glen Canyon also forage on zooplankton passing through the dam (Maddux et al. 1987; T. R. An-

gradi, unpublished data). The relatively large ^{15}N enrichment of trout over macroinvertebrates (+5 to +6‰) and the intermediate position of zooplankton (Fig. 5) suggests some assimilation of reservoir-derived zooplankton by the trout analyzed for this study. There is a contradiction with the $\delta^{13}\text{C}$ values of trout which are too ^{13}C -enriched for trout to be eating zooplankton or macroinvertebrates. This anomaly is resolved with the use of the third isotope, ^{34}S (see below). Although zooplankton is generally present in much lesser amounts in Glen Canyon trout stomachs than are lotic macroinvertebrates and algae (e.g., Maddux et al. 1987), the high digestibility of plankton may lead to an underestimation of its dietary importance.

Plankton and terrestrial organic matter were not important in the diet of *Gammarus* or other macroinvertebrates in Glen Canyon (Fig. 5). The relative importance of diatoms versus *Cladophora* in the food web could not be determined using stable isotopes (e.g., Fig. 3). *Gammarus* in Glen Canyon probably do not graze *Cladophora* but rather forage on epiphytic diatoms (Pinney 1991).

Higher fish $\delta^{13}\text{C}$ values, $\geq +4\text{‰}$ in the case of adult trout, relative to the benthic invertebrates and zooplankton exceeded the expected +1 or +2‰ enrichment. Three explanations for this are (1) that there was an unmeasured, ^{13}C -enriched trout food source, (2) that trout actually fractionated $^{13}\text{C} >4\text{‰}$, or (3) that the enriched $\delta^{13}\text{C}$ values for fish reflect slower turnover of fish-tissue carbon relative to isotopic shifts at lower trophic levels (algae). The first explanation seems least likely. Although feeding extensively on terrestrial insects with $\delta^{13}\text{C}$ values similar to riparian vegetation could account for the unexpectedly high $\delta^{13}\text{C}$ values, no study of trout diet in Glen and Grand canyons found that terrestrial organisms were a major component of the diet (Maddux et al. 1987, Carothers and Minckley 1981; T. R. Angradi, unpublished data). Terrestrial insects from the stomach of a trout had a depleted $\delta^{15}\text{N}$ value and an enriched $\delta^{13}\text{C}$ value suggesting an insect diet of upland rather than riparian vegetation (Appendix 1, Fig. 5). Furthermore, the isotopic signature of the flannelmouth sucker was similar to that of adult trout (Fig. 5), and the sucker is a benthic forager whose reported food habits do not include terrestrial animals (Minckley 1991). Large $\delta^{13}\text{C}$ shifts with trophic level are not with-

out precedent (e.g., Hesslein et al. 1991 reported a 1 to 7‰ depletion of lake trout [*Salvelinus namaycush*] tissue over its presumed prey that they could not explain), but are not corroborated by most other studies.

I consider it most likely that seasonal shifts in $\delta^{13}\text{C}$ values of lower trophic levels account for the anomaly in $\delta^{13}\text{C}$ values of fish. Isotope values of aquatic plants can be highly variable (Rounick and Winterbourn 1986). For example, I found that summer-collected periphyton samples were +3 to +4‰ more ^{13}C -enriched than winter or spring samples in a regulated Idaho river (Angradi 1993). In Lake Powell, epilimnion DIC was 2‰ higher than hypolimnion DIC (Appendix 1). A decrease in penstock intake depth in the drawn-down reservoir in late summer and fall could result in partial epilimnetic discharge (USDI 1994) and provide a supply of ^{13}C -enriched DIC to algae in the river.

The turnover rate of carbon in animal tissue is fastest in growing animals (Fry and Arnold 1982). Fish, which grow more slowly than invertebrates, would have slower carbon turnover rates; they would respond more slowly, isotopically, to a seasonal change in the $\delta^{13}\text{C}$ of the diet (e.g., macroinvertebrates that feed on diatoms) caused by an altered $\delta^{13}\text{C}$ value of the DIC supply and its effect on the $\delta^{13}\text{C}$ values of algae. Trout fry, which grow faster than adults, had $\delta^{13}\text{C}$ values closer to the expected range (+1 or +2‰ enriched relative to food). Thus, the measured $\delta^{13}\text{C}$ of adult trout in Glen Canyon may reflect the isotopic structure of its prey of past seasons.

The $\delta^{34}\text{S}$ data support this explanation. The $\delta^{34}\text{S}$ range of Glen Canyon algae and *Gammarus* was similar to that of trout and suckers (~1.5‰ depleted) (Fig. 5b). ^{34}S may be less variable than ^{13}C as a tracer of autochthonous production through food webs—it is not sensitive to seasonal or spatial changes in CO_2 sources—and should be useful for examining unexpected variation in $\delta^{13}\text{C}$ values (see also Hesslein et al. 1991).

Several studies of adult trout diets in Glen and Grand canyons have found that *Cladophora* filaments are the predominant food item by weight and volume followed by *Gammarus lacustris* and aquatic diptera (Carothers and Minckley 1981, Maddux et al. 1987, Leibfried 1988). Leibfried (1988) concluded that trout consume large amounts of *Cladophora* inten-

tionally for the nutritional value of lipid-rich diatom epiphytes. The +7 to +9‰ enrichment in $\delta^{15}\text{N}$ values of trout over algae (Fig. 5a) suggests an intermediate trophic level: aquatic macroinvertebrates and zooplankton. Apparently, trout assimilate little *Cladophora* N directly. My findings corroborate Liebfried (1988), who showed that little protein (the source of tissue N) derived from *Cladophora* or diatoms was assimilated into trout tissue. Algae consumed by trout may provide some energy for maintenance; it seems unlikely that trout can grow on a diet dominated by algae.

Fishes in Grand Canyon tributaries

The similarity in the stable isotope ranges of Colorado River and Nankoweap Creek fishes suggests either (1) fish from Nankoweap Creek had assimilated C and N from the Colorado River (*Gammarus* are rare in the tributaries [Carothers and Minckley 1981, Hofknecht 1981], and *Cladophora* is scarce or absent [Carothers and Minckley 1981].), or (2) autotrophy in Nankoweap Creek supports a food web with secondary consumer isotope values the same as in Glen Canyon. Examination of lower trophic levels at Nankoweap Creek would answer this question.

The dual-isotope range of speckled dace from Shinumo Creek (Fig. 6) suggests that the food web there was more strongly based on organic matter derived from upland vegetation than were the food webs of other tributaries. Hofknecht (1981) found that the macroinvertebrate biomass, abundance, and diversity in Shinumo Creek was less than in Bright Angel, Crystal, and Deer Creeks. Lower Shinumo Creek is in a deep canyon and has a poorly developed riparian zone. Hofknecht (1981) partially attributed the relatively depauperate fauna of Shinumo Creek to the low allochthonous and autochthonous inputs. The same explanation may apply to the food web in general: local algal and riparian inputs are minimal, so the isotope values of the speckled dace reflect a macroinvertebrate fauna dependent largely on detritus exported from upland areas.

Isotope values of Paria River speckled dace suggest a closer linkage to riparian vegetation than to upland vegetation (Fig. 6). Autotrophy is very limited in the Paria River due to high turbidity, unstable substrate, and frequent spates

be possible to resolve relatively fine-scale differences in the sources of organic matter in tributaries (e.g., upland versus riparian vegetation) because seasonal and spatial variation in detritus derived from terrestrial C_3 vegetation is less variable than for aquatic plants (Fry and Sherr 1984).

Perspective

Isotopic separation among organic matter sources—lotic algae, riparian vegetation, upland vegetation, and reservoir plankton—was adequate for addressing the questions posed in the introduction using ^{13}C , ^{15}N , and ^{34}S , and permits construction of a qualitative model depicting the important trophic linkages in the Glen Canyon ecosystem, including Lake Powell and the Paria River (Fig. 7). This study is the first attempt to determine the important trophic linkages in the Colorado River below Glen Canyon Dam. I hope my model (Fig. 7) is considered a working hypothesis to be tested using other methods and to be compared with downriver reaches and other reservoir tailwaters. Relatively unambiguous determinations of organic matter origin and trophic position were possible in this study (c.f., Peterson et al. 1986, Rosenfeld and Roff 1992), largely because of the strong effects of flow regulation on patterns of organic matter flux (Angradi 1993) and faunal complexity.

Acknowledgements

Jeff Sorensen, Diane Parmley, and Jim Coligan assisted in the field and in the laboratory. Bob Michener and Kris Tholke performed the mass spectrometry. Dean Blinn identified the alga *Ulothrix tenuissima*. Rosemary Mackay, Fred Benfield, Dennis Kubly, Bret Harvey, Beth Adams, and three anonymous reviewers provided useful comments on the manuscript. This study was funded by the United States Bureau of Reclamation; support for the completion of the study was provided by the United States Forest Service.

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Received: 15 October 1993

Accepted: 22 August 1994

APPENDIX 1. Stable isotope values (‰) for dissolved inorganic carbon (DIC), aquatic and terrestrial primary producers, seston, invertebrates, and fish in Glen Canyon and in Grand Canyon tributaries. Site codes are LAKP, Lake Powell; GLCD, Glen Canyon Dam; PARR, Paria River; CR02, CR11, etc., Colorado River 2 and 11 km downriver from the dam, etc.; GRCN, Grand Canyon; NANC, Nankowap Creek; BANC, Bright Angel Creek; DEER, Deer Creek; SHIC, Shinumo Creek; CRYC, Crystal Creek. Mean value given in parentheses when $n = 2$; mean ± 1 SE given when $n = 4$ or $n = 3$ (speckled dace from SHIC only). All dates were in 1992.

	Date	Site	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
DIC (epilimnion)	7 April	LAKP	-5.3, -5.0 (-5.1)		
DIC (hypolimnion)	7 April	LAKP	-7.2, -7.0 (-7.1)		
DIC (penstock)	8 April	GLCD	-7.4, -7.2 (-7.3)		
DIC	9 April	CR02	-6.8, -7.1 (-7.0)		
DIC	9 April	CR11	-7.0, -6.9 (-7.0)		
DIC	9 April	CR25	-6.9, -6.9 (-6.9)		
DIC	13 April	PARR	-3.0, -2.8 (-2.9)		
<i>Cladophora</i> with epiphytes	12 April	CR02	-33.4, -33.5 (-33.5)	7.0, 7.0 (7.0)	-5.9
<i>Cladophora</i> with epiphytes	26 April	CR22	-31.2, -31.4 (-31.3)	8.8, 8.2 (8.5)	-6.3
<i>Cladophora</i> with epiphytes 25 d in situ	20 May	CR02	-33.8	6.7	
<i>Cladophora</i> with epiphytes 53 d in situ	17 June	CR02	-33.0	6.6	
<i>Cladophora</i> without epiphytes	26 April	CR02	-33.2, -33.2 (-33.2)	5.2, 5.2 (5.2)	
<i>Cladophora</i> without epiphytes	26 April	CR22	-33.2, -33.4 (-33.3)	8.0, 8.0 (8.0)	
<i>Cladophora</i> without epiphytes	20 May	CR02	-32.8	4.6	
<i>Cladophora</i> without epiphytes 25 d in situ	17 June	CR22	-32.6	5.7	
<i>Cladophora</i> without epiphytes 53 d in situ	27 April	CR22	-33.4, -33.5 (-33.5)	6.9, 7.1 (7.0)	
Epiphytes stripped from <i>Cladophora</i>	30 April	CR01	-31.3	9.0	
<i>Ulothrix tenuissima</i>	22 April	GRCN	-21.2, -21.0 (-21.1)	9.5, 8.1 (8.8)	-1.6
<i>Oscillatoria</i> sp.	12 April	CR11	-25.6	8.0	
Tamarisk	8 April	CR02	-27.6, -27.5 (-27.6)	3.7, 3.7 (3.7)	
Tamarisk litter	12 April	CR11	-29.0, -29.0 (-29.0)	5.0, 5.0 (5.0)	
Willow	12 April	CR11	-24.9	7.4	
Equisetum	30 March	PARR	-27.6	2.0	-1.1
Cottonwood litter	30 March	PARR	-23.8	-2.5	4.1
Floodplain litter	13 April	PARR	-23.2	-0.1	
Floodplain litter	6 April	LAKP	-29.7	6.8	
POM <80 μm (epilimnion)	6 April	LAKP	-27.7	9.6	
POM <80 μm (hypolimnion)	6 April	LAKP	-34.5, -34.0 (-34.3)	12.9, 13.4 (13.2)	
Zooplankton (POM >80 μm , epilimnion)	30 April	CR01	-33.1	11.7	
Zooplankton (trout stomach)	7 April	GLCD	-28.5	10.3	
POM (penstock)	9 April	CR02	-32.4, -32.3 (-32.4)	9.6, 10.3 (9.9)	
CPOM	9 April	CR11	-33.4, -31.1 (-32.3)	7.5, 8.5 (8.0)	

APPENDIX 1. Continued.

	Date	Site	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
CPOM	9 April	CR25	-33.1, -33.4 (-33.3)	6.7, 6.4 (6.6)	
CPOM	13 April	PARR	-24.8	1.3	
CPOM (>3 mm)	30 March	PARR	-23.6	0.2	
FPOM	9 April	CR02	-32.9, -33.0 (-33.0)	10.8, 10.6 (10.7)	-7.0
FPOM	9 April	CR11	-33.2, -33.3 (-33.3)	9.4, 10.0 (9.7)	
FPOM	9 April	CR25	-32.7, -33.2 (-33.0)	10.0, 9.5 (9.8)	-5.2
FPOM	13 April	PARR	-24.8, -24.7 (-24.8)	1.8, 1.6 (1.7)	-1.6
VFPOM	9 April	CR02	-32.9, -32.6 (-32.8)	11.1, 10.6 (10.9)	
VFPOM	9 April	CR11	-33.6, -33.3 (-33.5)	9.5, 9.7 (9.6)	
VFPOM	9 April	CR25	-34.8, -34.7 (-34.8)	9.0, 9.0 (9.0)	
VFPOM	13 April	PARR	-24.6, -24.8 (-24.7)	2.2, 1.1 (1.7)	
UFPOM	9 April	CR02	-28.6	9.5	
UFPOM	9 April	CR25	-29.2	7.8	
<i>Gammarus lacustris</i>	12 April	CR02	-32.8, -33.0 (-32.9)	11.0, 10.4 (10.7)	
<i>Gammarus lacustris</i>	12 April	CR11	-33.9, -33.9 (-33.9)	10.6, 11.3 (11.0)	
<i>Gammarus lacustris</i>	12 April	CR22	-33.1, -33.4 (-33.2)	10.2, 9.9 (10.1)	-6.7
Oligochaetes	12 April	CR11	-33.0	10.2	
Chironomids (trout stomach)	30 April	CR01	-32.3	10.3	
Terrestrial insects (Orthoptera, Lepidoptera)	30 April	CR01	-23.7	5.6	
Rainbow trout adult	30 April	CR01	-27.0 \pm (0.3)	16.8 \pm (0.3)	-7.8
Rainbow trout adult	1 May	CR19	-27.2 \pm (0.1)	15.7 \pm (0.1)	-8.3
Rainbow trout adult	14 April	NANC	-27.0, -27.0 (-27.0)	15.9, 16.0 (16.0)	
Rainbow trout fry	18 April	CR02	-29.2	16.8	
Rainbow trout fry	28 April	CR25	-29.5	15.0	-8.4
Rainbow trout fry	16 April	BANC	-25.2	9.2	
Rainbow trout fry	19 April	DEER	-27.3	10.0	
Speckled dace	30 March	PARR	-25.8 \pm (0.8)	12.8 \pm (0.8)	
Speckled dace	14 March	NANC	-28.0, -28.7 (-28.4)	16.4, 15.6 (16.0)	
Speckled dace	17 March	CRYC	-23.8, -25.4 (-24.6)	7.8, 13.1 (10.5)	
Speckled dace	18 March	SHIC	-23.4 \pm (0.2)	6.3 \pm (0.1)	
Flannelmouth sucker	01 May	CR19	-27.9	15.1	-7.3