Basal Resources in Backwaters of the Colorado River Below Glen Canyon Dam—Effects of Discharge Regimes and Comparison with Mainstem Depositional Environments

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Cover: Photograph of Grand Canyon backwater treated with nontoxic dye, which scientists use to determine water turnover rates for backwater habitats. (Photograph courtesy of Brian Dierker, Humphreys Summit Support.)

Prepared in cooperation with the University of Wyoming

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By Kathrine E. Behn, Theodore A. Kennedy, and Robert O. Hall, Jr.

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Basal Resources in Backwaters of the Colorado River Below Glen Canyon Dam—Effects of Discharge Regimes and Comparison with Mainstem Depositional Environments

By Kathrine E. Behn[1], Theodore A. Kennedy[2], and Robert O. Hall Jr.[1]

Abstract

Eight species of fish were native to the Colorado River before the closure of Glen Canyon Dam, but only four of these native species are currently present. A variety of factors are responsible for the loss of native fish species and the limited distribution and abundance of those that remain. These factors include cold and constant water temperatures, predation and competition with nonnative fish species, and food limitation. Backwaters are areas of stagnant flow in a return-current channel and are thought to be critical rearing habitat for juvenile native fish. Backwaters can be warmer than the main channel and may support higher rates of food production. Glen Canyon Dam is a peaking hydropower facility and, as a result, has subdaily variation in discharge because of changes in demand for power. Stable daily discharges may improve the quality of nearshore rearing habitats such as backwaters by increasing warming, stabilizing the substrate, and increasing food production.

To evaluate whether backwaters have greater available food resources than main-channel habitats, and how resource availability in backwaters is affected by stable flow regimes, we quantified water-column and benthic food resources in backwaters seasonally for 1 year using both standing (organic matter concentration/density; chlorophyll *a* concentration/density; zooplankton concentration; benthic invertebrate density and biomass) and process measurements (chamber estimates of ecosystem metabolism). We compared backwater resource measurements with comparable data from main-channel habitats, and compared backwater data collected during stable discharge with data collected when there was subdaily variation in discharge. Rates of primary production in backwaters (mean gross primary production of 1.7 g $O_2/m^2/d$) and the main channel (mean gross primary production of 2.0 g $O_2/m^2/d$) were similar. Benthic organic matter standing stock (presented as ash-free dry mass—AFDM) was seven times higher in backwaters relative to main-channel habitats (median value of 210 g AFDM/m^2 versus 27 g AFDM/m^2); this likely reflects greater retention of tributary-derived organic matter in backwaters relative to main-channel habitats. Water-column and benthic organic matter were higher during periods of steady discharge relative to periods of fluctuating discharge. However, our steady-discharge data collection was confounded by tributary activity. Flooding tributaries contribute substantial quantities of sediment and organic matter to the Colorado River; there were two large

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tributary floods during our steady-discharge data collection but none during our fluctuating-discharge data collections. Although only preliminary data on invertebrate biomass are available at this time, invertebrate biomass in backwaters (range 2–27 mg AFDM/m^2) appears low relative to previously published data from main-channel habitats (~100 mg AFDM/m^2).

The rate of water turnover in backwaters may be a master variable that affects both physical (for example, warming) and biological (for example, primary production) processes in backwaters. We used dye tracer studies to estimate turnover rates in backwaters across flow regimes. Turnover took considerably longer when discharge was stable compared to when there was subdaily variation in discharge (613 minutes versus 220 minutes). Our results indicate that backwaters may represent a sink for organic matter that enters from the main channel and that stable discharge, by lengthening water turnover times, will likely increase organic matter retention.

Introduction

Closure of the gates of Glen Canyon Dam changed the Colorado River through Grand Canyon from a highly turbid river with large variation in annual discharge and temperature to one of relatively constant discharge, constant low temperature and much lower overall sediment load. Annual discharge narrowed from a range of ~14–5,700 m^3/s to ~140–1,275 m^3/s. Daily fluctuation currently ranges up to 225 m^3/s because of hydropower generation (Topping and others, 2003). Water temperatures which once ranged from 0–30°C currently range from 9–15°C at the foot of the dam (Voichick and Wright, 2007). Suspended sediment loads are now less than 10 percent of pre-dam levels (Topping and others, 2000). Before the construction of Glen Canyon Dam, eight species of fish were native to Grand Canyon (Gloss and Coggins, 2005), but only four of these native species presently occur there: humpback chub (*Gila cypha*), bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*Catostomus latipinnis*), and speckled dace (*Rhinichthys osculus*).

In the Colorado River in Grand Canyon a “backwater” is the condition of stagnant flow in a return-current channel in the lee of an emergent reattachment sandbar or tributary debris fan. Backwater habitats have been hypothesized to offer benefits to endangered humpback chub and other native fishes because of greater food availability and warmer water temperatures relative to mainstem habitats (Gloss and Coggins, 2005). For example, Converse and others (1998) found higher densities of subadult humpback chub in low-velocity habitats, such as occur in backwaters. Protected backwater habitats constitute a small portion (approximately 5 percent or less, depending on conditions and flows) of the nearshore habitat in the Colorado River in Marble and Grand Canyons (Grams and others, 2010). The relatively shallow, isolated backwater habitats warm more than the mainstem during summer months (J. Korman; Ecometric Research, Inc.; written commun.; 2006). When backwaters are warm, they may offer advantages to humpback chub and other native fishes for increased growth because they foster both higher metabolic and growth rates (see, for example, Petersen and Paukert, 2005). Stable daily discharges may improve the quality of nearshore rearing habitats such as backwaters by increasing warming, stabilizing the nearshore substrate, and increasing food production in nearshore environments (U.S. Department of the Interior, 2008a). Furthermore, it is thought that the degree of warming in backwaters increases when discharge is stable because of the increased physical isolation of these habitats relative to when discharge fluctuates on a daily basis because of hydropower generation (J. Korman; Ecometric Research, Inc.; written commun.; 2006). The advantages that backwaters confer to native fishes may be so important that these ephemeral habitats are of high value despite their limited distribution. Figure 1 illustrates the physical factors that differentiate backwaters from the mainstem river and how these may be beneficial habitat for small-bodied fish in particular. It is not known what the effects of velocity are on temperature, primary production, and invertebrates; however, it is hypothesized that lower velocity results in higher temperature. This question of backwater temperature is currently being investigated by U.S. Geological Survey (USGS) scientists in Flagstaff, but data were unavailable at the time of this report.

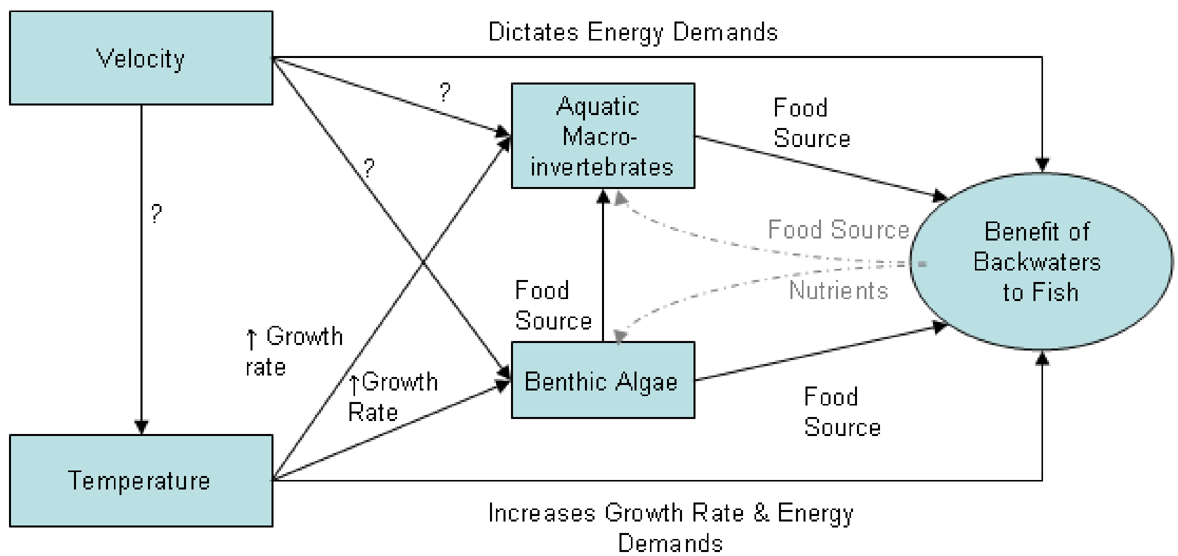


Figure 1. A schematic showing the two main factors that differentiate backwaters from the mainstem river (velocity and temperature) and how they may affect primary and secondary resources and fish.

The goals of this study were to assess (1) how much the availability of food resources for fish in backwaters differs from the availability of food resources in main-channel habitats and (2) whether this resource availability in backwaters was higher during steady discharges relative to when discharge fluctuated on a daily basis. We quantified water-column and benthic food resources in backwaters seasonally for 1 year using both standing (organic matter concentration/density; chlorophyll *a* concentration/density; zooplankton concentration; benthic invertebrate density and biomass) and process measurements (chamber estimates of ecosystem metabolism). We compared these measures with comparable data collected in main-channel habitats as part of the ongoing USGS food-base research project. During the period in which we sampled backwater habitats (April 2008 to January 2009), a flow experiment was conducted as prescribed in the 2008 environmental assessment on operation of Glen Canyon Dam (U.S. Department of Interior, 2008b). Glen Canyon Dam is a peaking hydropower facility, and discharge usually fluctuates on a daily basis to meet changes in demand for power. In the 2008 final biological opinion on the operation of Glen Canyon Dam, it is stated that discharge from Glen Canyon Dam will be steady during September and October from 2008 to 2012 (U.S. Department of Interior, 2008a). In 2008 discharge during September and October was ~350 m^3/s. To evaluate the effects of this stable discharge regime, we compared the availability of food resources during steady discharges (September 2008) with data collected when discharge fluctuated on a daily basis (April 2008, June 2008, and January 2009). Backwaters are partly hydrologically isolated from the main channel, which allows for warming of water, a key constraint on algae, invertebrate, and fish growth rates in the ecosystem, and stable discharge is thought to increase the degree of isolation. Thus, the rate of water exchange between backwaters and the main channel may be a master variable that affects physical (for example, warming) and biological (for example, rates of primary production) processes in backwater habitats. We therefore quantified the rate of exchange of water between backwaters and the river across flow regimes using dye-tracer experiments. Processing of some types of samples (benthic invertebrate and zooplankton) is ongoing, so this report represents a summary of our preliminary findings.

We note that, along with the temperature data, other data collections concerning the question of value to backwaters to fish are ongoing under other USGS-funded projects. Information on movement in and out of backwaters by native and nonnative fish and diet analysis of fish caught in backwaters are both key datasets that, along with our findings, will shed more light on the role of these habitats in Grand Canyon.

Methods

By convention, river mile (RM) is used to describe distance along the Colorado River in Grand Canyon: Lees Ferry (located 15.7 miles downstream of Glen Canyon Dam) is the starting point, as RM 0, with mileage measured for both upstream (-) and downstream directions. Sampling of backwaters was done in conjunction with existing food-base research project river trips, so backwater activities were generally restricted to the timing of those trips (April, June, and September of 2008 and January 2009) and to the immediate vicinity of food-base study reaches: Lees Ferry (RM 0), Marble Canyon (RM 30), downriver of the Little Colorado River confluence (RM 62), Randy’s Rock (RM 127), National Canyon (RM 167), and Diamond Creek (RM 225) (fig. 2). Additional nights were added to the food-base river trips starting in June 2008 to allow for additional backwater data collection at locations other than food-base reaches, including Eminence backwater (RM 44.6) and others in that vicinity, and also backwaters in the western Grand Canyon (RM 190–205). Additional backwater sampling occurred during the 5 days of steady discharge in late May 2009 (226 m^3/s, associated with collection of aerial imagery) and October 2009 (289 m^3/s, fall steady-flow experiment). We launched a river trip in October 2009 with the intention of collecting data on fish abundance in backwaters and water-exchange measurements during steady flows, but because of equipment failure we were unable to collect a single water-exchange measurement on this trip. However, we did make two estimates of water exchange for backwaters between RM 0 and RM 8 in late October thanks to the assistance of Grand Canyon National Park staff. An inventory of the backwater sites sampled is presented in table 1. Exact sampling dates and associated data on the range of discharge for the Colorado River at Lees Ferry; discharge of the Little Colorado River, a major tributary to the Colorado River; and suspended sediment concentrations of the Colorado River at RM 225 are presented in table 2.

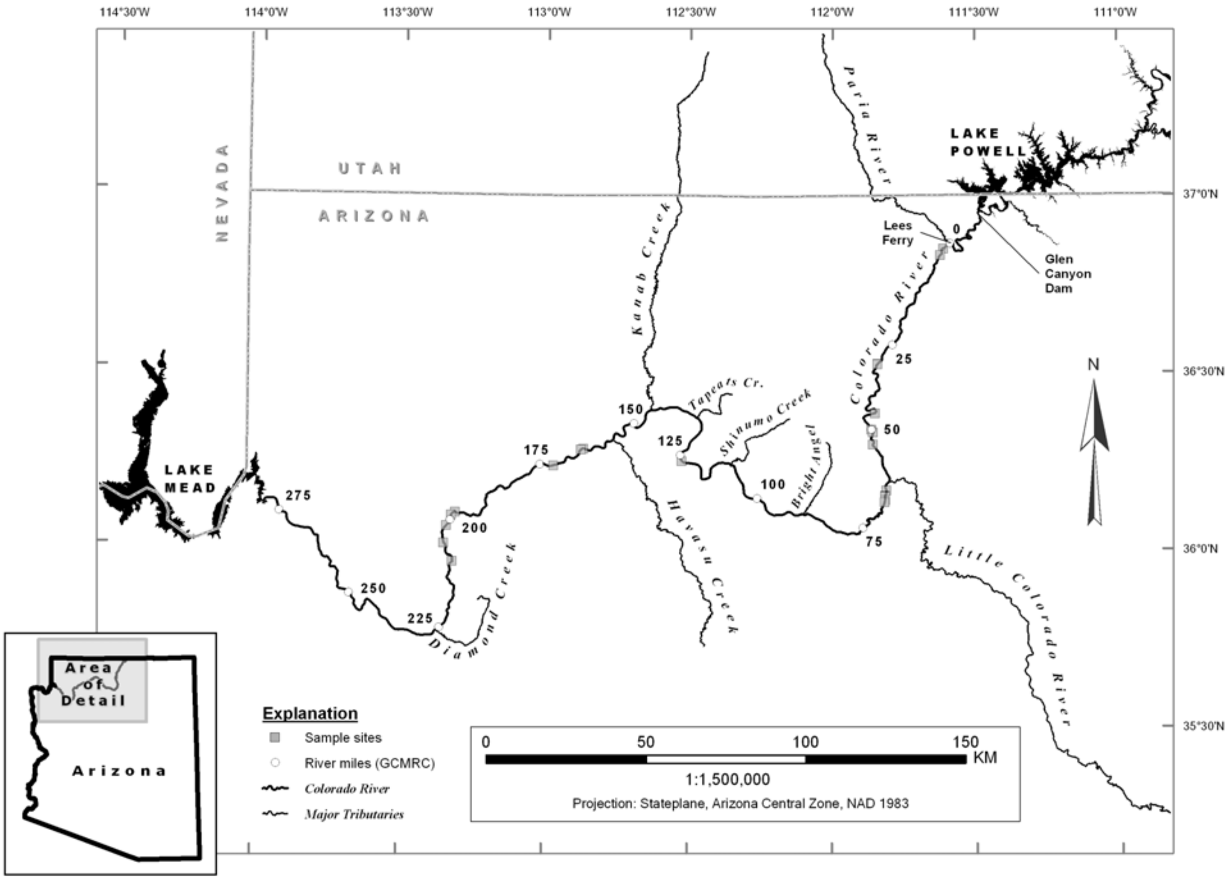


Figure 2. A map of the Colorado River through Grand Canyon, northwestern Arizona, U.S.A., showing the customary river miles downstream from a start point at Lees Ferry as measured by the Grand Canyon Monitoring and Research Center (GCMRC) (U.S. Geological Survey, 2006). Distance downstream from Lees Ferry is noted in 25-mile increments by outlined circles, while the backwater sampling sites are noted by grey boxes.

Table 1. Summary of backwaters sampled and data collected in the Colorado River in Grand Canyon from April 2008 to October 2009.

[--, no data.]

Colloquial name (if known)	River mile (left or right, facing downstream)	Month sampled	Year sampled	Data Collected: Water column and benthic resources	Data Collected: Metabolism	Data Collected: Water exchange rate
Secret Beach	1.7 (R)	October	2009	--	--	X
	3.4 (L)	October	2009	--	--	X
	30.05 (R)	June	2008	X	--	X
The Dune	30.75 (R)	April	2008	X	--	X
Eminence	44.6 (L)	April	2008	X	X	--
		June		X	X	X
		September		X	X	X
		January	2009	X	X	X
		May				X
	50 (L)	April	2008	X	--	--
	50.6 (L)	April	2008	X	--	--
Lower Nankoweap	53.3 (R)	June	2008	X	--	--
	63.9 (L)	April	2008	X	X	X
		June		X	X	--
	64.95 (L)	September	2008	X	X	--
Carbon	65.1 (R)	April	2008	X	X	--
		June		X	X	X
		August		X	X	X
		January	2009	X	--	--
Lava-Chuar	65.8 (L)	April	2008	X	X	X
		June		X	X	X
Palisades	66.2 (L)	January	2009	X	X	--
Forster	123.7 (R)	June	2008	X	--	--
		September		X	X	X
		January	2009	X	--	X
	164.5 (L)	June	2008	X	X	X
		September		X	X	X
Tuckup	165.0 (R)	January	2009	X	X	X
	198 (L)	September	2008	X	X	X
	199 (R)	September	2008	X	X	--
Mohawk	172.1 (L)	April	2008	X	X	--
	201.4 (R)	June	2008	X	X	X
	205.1 (L)	June	2008	X	--	--
Granite Park	209.6 (L)	April	2008	X	--	X
		June		X	X	--
		January	2009	X	--	--

Table 2. Backwater sampling dates and associated data on range of discharge for the Colorado River at Lees Ferry, range of discharge for the Little Colorado River, and suspended sediment data measured at river mile 225 on the Colorado River.

[Suspended sediment data can be accessed at http://www.gcmrc.gov/products/other_data/gcmrc.aspx.]

Dates of backwater sampling events	Range of discharge (m^3/s) for Colorado River at Lees Ferry (USGS Gage 09380000)	Range of discharge (m^3/s) for Little Colorado River (USGS Gage 09402300)	Concentrations of silt and clay (mg/L) measured at Colorado River at river mile 225
April 18–28, 2008	270–448	7.3–9 .7	66.5–366 avg.=98.0
June 15–28, 2008	286–464	6.5–7.8	83.9–161 avg.=115
August 17–22, 2008	297–530	7.1–83.0	1,110–5,160 avg.=2,650
September 15–25, 2008	346–357	6.1–11.5	99.4–2870 avg.=637
January 10–19, 2009	267–481	6.1–6.6	8.70–50.2 avg.=68.5
May 22–23, 2009	225–249	6.1–64.3	53.6–94.8 avg.=76.4
October 29–30 2009	292–297	6.2–6.3	2.52–113 avg.=35.1*

*Used measurements at river mile 30, because all samples during this period were taken above the Little Colorado River

Because of the logistical constraints of combining river trips with the food-base group, we employed two different sampling strategies. If time was limited, we sampled backwaters for only water-column and benthic resources. If time permitted, we conducted a more complete assessment that also included chamber measurements of ecosystem metabolism (gross primary production, ecosystem respiration, net ecosystem production) and water exchange rates. Water-column resources were sampled first, so as not to disturb benthic organic matter or sediment. During ecosystem metabolism measurements or water exchange measurements, benthic resources were sampled. Three replicates of each type of water-column measurement were collected from the middle of the backwater. We also collected three replicate samples of each benthic resource and our sampling effort was spatially stratified, with one sample collected near the mouth, one from the middle, and one near the back of the backwater. All benthic samples were collected at depths greater than one-half the maximum depth for that spatial location in the backwater.

We measured three water-column parameters that are indicators of resource availability in backwaters: organic matter of fine suspended particulates, fine suspended chlorophyll *a* concentration, and zooplankton concentration. For determining suspended organic matter and chlorophyll *a*, water was first poured through a sieve with a mesh size of 0.25 mm to remove coarse particles. A known quantity (0.04–4 liters, depending on water conditions) of this water was then filtered through a precombusted glass fiber filter (GF/F filters, Whatman, Kent, U.K.; pore size ~0.7 µm). Filters for organic-matter samples were preweighed so that we could also estimate percent organic matter. Organic matter filters were air-dried in the field, and then, back in the lab, samples were oven dried, weighed, combusted at 500ºC for 2 hours, and reweighed. Ash-free dry mass (AFDM) was estimated by subtracting ash weight from the oven-dry weight. Percent organic matter was estimated by dividing AFDM by the oven-dry weight of the sample. Chlorophyll *a* was extracted from filters using a cold ethanol extraction, and then a sample of the extract was analyzed using the fluorometer method (Holm-Hansen and others, 1965) using an *Aqua*fluor® field fluorometer (Turner Designs, Sunnyvale, Calif.). Zooplankton were sampled by passing 100 L of water through a 63-µm sieve or plankton net. The filtrand was preserved in 95-percent ethanol, and zooplankton were enumerated using standard methods (Wetzel and Likens, 2000). Comparable water-column samples were collected from the mainstem Colorado River within 5 miles of backwater collections and processed in the same manner as described above. On a few occasions we were unable to collect mainstem samples from within 5 miles of the backwater because of time constraints; we therefore used mainstem water-column data from the nearest food-base site for comparison. Zooplankton sample processing is ongoing, so no data are presented in this report of preliminary findings.

We sampled the benthos of backwaters using a Standard Ponar Dredge (Wildlife Supply Company, Buffalo, N.Y.) with a sampling area of 0.052 m^2 or, alternatively, a 0.031- or 0.053-m^2 stovepipe style corer made from either 8- or 20-L buckets with the bottoms removed, which were nested to attain the appropriate height. We pushed the corer 20 cm into the sediments, stirred the sediments 10 cm deep, and then bailed the contents of the corer into one or more 20-L graduated buckets until the corer was dry or until all suspended benthic material had been evacuated. Ponar samples were collected and then emptied into a tub. The volume of the sample was measured, the sample was mixed, and then subsampled (~250 mL) for chlorophyll *a* content. Subsamples for chlorophyll *a* were filtered onto a glass-fiber filter and processed in the same manner as the water column samples; this was the same approach taken by the food-base project for depositional habitats in the mainstem. Chlorophyll *a* content of the entire sample was estimated by multiplying the measured concentration of the subsample by the total volume of the sample. Benthic chlorophyll *a* density was then estimated by dividing this value by the area of the sampler. We estimated fine benthic organic matter (FBOM; <0.25 mm) by subsampling the filtrate that passed through a 0.25-mm sieve and processing as above for water-column AFDM. The remaining benthic slurry was passed through a 0.25-mm sieve, and the filtrand was preserved in 95 percent ethanol for determination of invertebrate abundance, biomass, and AFDM of coarse material (>0.25 mm). In the lab, samples were split into two size fractions—greater than 1 mm and less than 1 mm but greater than 0.25 mm—by placing the entire sample into nested sieves, then washing vigorously with water for several minutes. Both of these size fractions were then quantitatively subsampled using a sample splitter and examined under a dissecting microscope using 10–15X magnification. Invertebrates were identified to the lowest practical taxonomic unit, counted, and their lengths measured to the nearest millimeter (Cross and others, 2010). After invertebrate counts were completed, the subsamples were returned to their corresponding size fraction and each size fraction was dried, weighed, combusted at 500ºC, and reweighed for determination of AFDM. Biomass of the recorded invertebrates was determined by using published length-mass regressions (Benke and others, 1999). Processing of backwater invertebrate and coarse benthic organic matter is ongoing, so we present complete data on fine benthic AFDM and chlorophyll *a*, but limited data on benthic invertebrates and no data on coarse benthic organic matter. We compared backwater benthic organic matter and chlorophyll values to comparable data from depositional environments in the main channel.

Metabolism was measured using two different types of Plexiglas chambers, depending on depth and substrate of the backwater. Open-bottom chambers were 30x30 cm by 75 cm tall and had a hinged lid that allowed air bubbles to be removed before incubations were started. These chambers were pushed into the sand with the lid open, and then the lid was closed. Five depth measurements (one at each corner and one at the center) were recorded. In rocky or shallow backwaters, cobbles or cores of sand were transferred to watertight containers (total volume 4 L), and then the chambers were filled with a known volume of water. Within 10 minutes we measured initial dissolved oxygen concentration in the chamber using a YSI 550A dissolved oxygen meter (Yellow Springs Inc, Yellow Springs, Ohio) and the measurement port was closed. Following a 2-hour incubation we remeasured dissolved O_2. We then covered chambers with opaque plastic, incubated them 2–4 hours further, and remeasured dissolved O_2.

Net ecosystem production (NEP; g $O_2/m^2/d$) was calculated as follows:

$$\text{NEP (g O}_2\text{/m}^2\text{/d)} = \left[\frac{[\text{Initial O}_2 \text{ (g/m}^3) - \text{Final O}_2 \text{ (g/m}^3)] * \text{depth (m)}}{\text{Incubation time (hours)}}\right] \frac{\text{\# of hours daylight}}{24}$$

Ecosystem respiration (ER; g $O_2/m^2/d$) was final oxygen reading of light-exposed incubation minus final dark-exposed oxygen measurement multiplied by depth, divided by incubation time, and extrapolated to a daily value by multiplying by 24. Gross primary production (GPP) was calculated by subtracting ecosystem respiration (a negative value) from net ecosystem production (Bott, 2006). We compared gross primary production values from backwaters with gross primary production estimates from the mainstem that were obtained using an open-channel metabolism approach (Van de Bogert and others, 2007; Hall and others, in press).

Water residence time was estimated using rhodamine WT (RWT) tracer dye releases. After completing water-column measurements, an on-site calibrated SCUFA® in-place logging fluorometer (Turner Designs, Sunnyvale, Calif.) was installed near the mouth of the backwater with a small concrete anchor and a float and programmed to record RWT concentration every 10 or 30 seconds. The approximate volume of the backwater was then estimated by a cursory visual survey. We added enough concentrated RWT dye (5 percent RWT by weight, Bright Dyes, Miamisburg, Ohio) in a 20-L bucket to obtain an initial peak concentration of at least 150 µg/L in the backwater. The bucket was then filled to the rim with river water in order to dilute the dye, which allowed for a more even distribution of dye in the backwater. The diluted dye was distributed throughout the backwater using a small cup and gentle mixing using boat paddles. The fluorometer was deployed for as long as logistically possible. For two samplings, the dye had not completely left the backwater before we needed to move on to the next food-base sampling reach, and we were not able to estimate the evacuation time for these backwaters (see below). The decline in RWT concentration through time is a measure of the rate of backwaters' water exchange with the mainstem; longer residence times represent less mixing with the mainstem, or more isolation, relative to shorter turnover times. We modeled this rate of turnover in two different ways. The first calculates residence time and half-life time by assuming a perfectly mixed backwater where the loss depends on the concentration as described in the following equation:

$$\ln C_0 = \ln C_t - k * t,$$

where ln is the natural logarithm, C_0 is concentration of dye at time=0, C_t is the concentration of dye at time=t (minute), and k is the empirically fitted rate of decay (units of 1/minute). Residence time is the inverse of k and half-life time is ln (0.5)/k. The second approach for modeling these data, evacuation time, does not assume the backwater is perfectly mixed and represents the time required to go from peak concentration to the baseline concentration reading that was measured before dye was added. Because of the exponential decay pattern seen in most of our data, these evacuation times tend to be much longer than estimates of residence time.

Statistical Analyses

Triplicate water-column, benthic, and metabolism estimates for each backwater or mainstem location were averaged for habitat and flow comparisons to yield a single value for each backwater or mainstem location and sampling event. Because we sampled many backwaters, we did not compare variation between backwaters and main channel to the variation within backwaters for any one measure. Rather we compared the entire population of backwater measurements to focus on the question of backwaters as a whole. Water-column (percent AFDM, AFDM concentration, chlorophyll *a*), benthic (AFDM concentration, chlorophyll *a*), and metabolism (gross primary production) data were log-transformed to meet assumptions of normality, then statistically compared to mainstem values by calculating the difference between a backwater value and comparable mainstem value and then conducting a one-sample *t*-test to determine if the values were significantly different from zero. The advantage of this approach is that it accounted for seasonal effects that were observed in the mainstem measurements. Of the three measures of metabolic activity, only GPP data are available from the main channel. We compared our chamber estimates of GPP with main-channel estimates of GPP for the most proximate food-base study reach (Robert O. Hall Jr., University of Wyoming, written commun., October 2009)

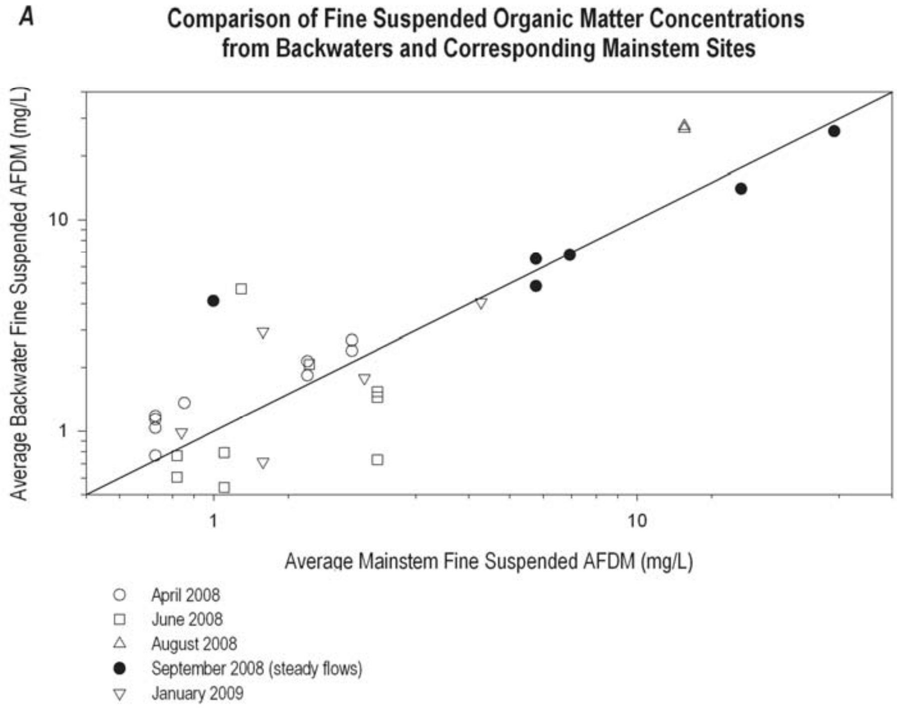
We also evaluated whether backwater resources differed during the steady discharges of September 2008 relative to the fluctuating discharges that occurred during other seasons by comparing the respective means with either a t-test or, when data were non-normally distributed, with a Wilcoxon rank-sum test.

Processing of zooplankton and benthic invertebrate samples is ongoing. In this report of preliminary findings we present limited data on benthic invertebrate abundance and biomass and no data on zooplankton.

Results

Water-Column and Benthic Resources

Concentrations of suspended organic matter in backwaters were not significantly different relative to mainstem concentrations (fig. 3*A*, table 3), and flow did not affect the backwater suspended organic matter concentrations when compared to the mainstem (fig. 3*A*,*B*). Organic matter represented a 40-percent greater portion of suspended particles in backwaters relative to mainstem habitats across all flow regimes (p=0.002; fig. 4*A*, table 3). However, flow regime was not related to any changes in percentage of organic matter of the total suspended particulate load (fig. 4*A*,*B*). Fine suspended chlorophyll *a* levels in backwaters were 47 percent lower relative to the main channel (p=0.001; fig. 5*A*, table 3). Still, suspended chlorophyll in backwaters was unrelated to flow regime (fig. 5*A*,*B*).



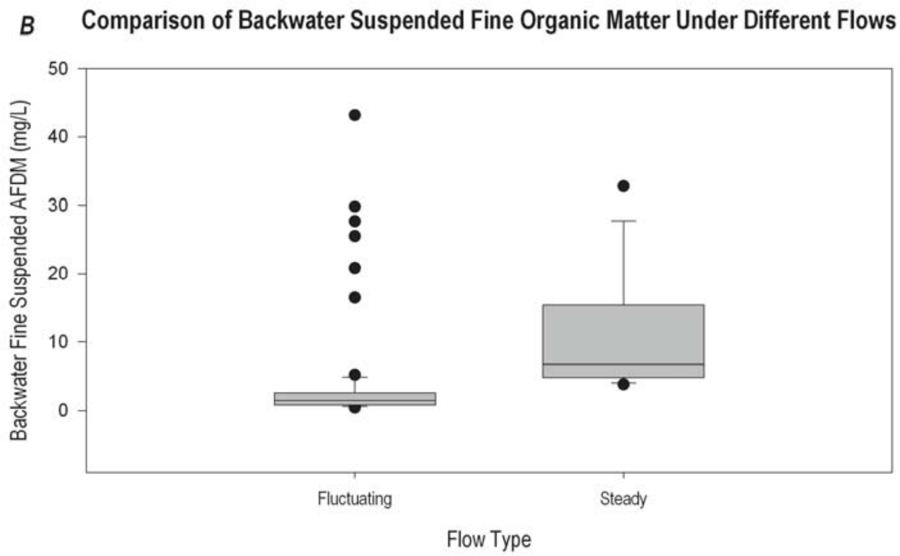
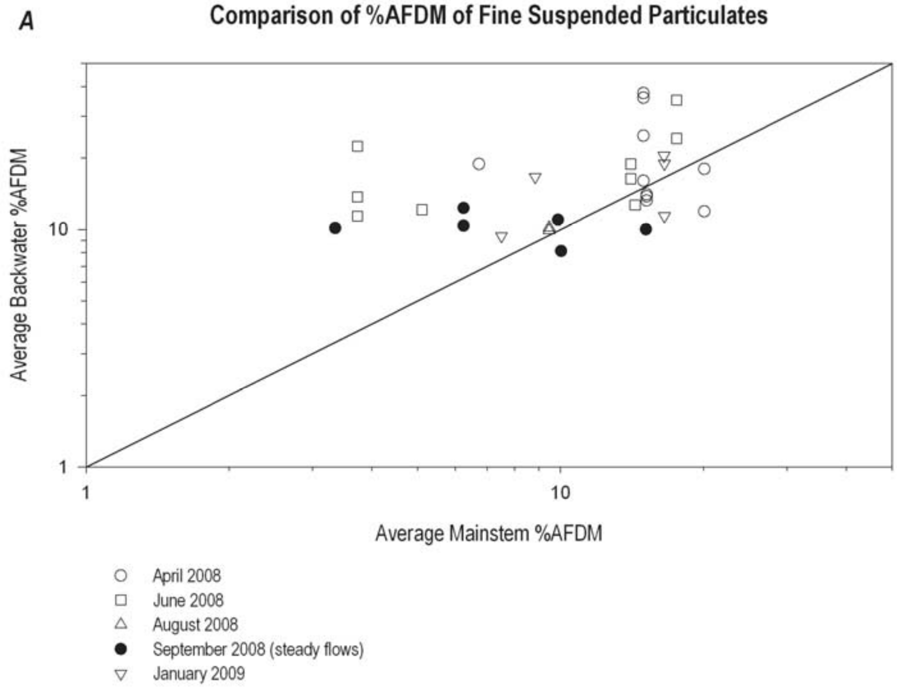


Figure 3. Comparisons of fine (<0.25 mm) suspended organic matter concentration as ash-free dry-mass (mg AFDM)/L. *A*, Grand Canyon backwaters versus corresponding mainstem sites. Line is 1:1 line that indicates equality between the backwater and main channel samples. *B*, Grand Canyon backwaters during fluctuating flows versus steady flows. Boxplot with whiskers from the 10th percentile to the 90th percentile.

Table 3. Results of Grand Canyon backwater (BW) and mainstem (MS) resource comparisons.

[Mean BW-MS is the log-transformed BW average minus the corresponding log-transformed MS average. Positive values indicate the backwater values were greater than mainstem resources. P-values less than 0.05 indicate the distribution of these values is significantly different from zero]

Measure	Mean log-transformed BW-MS (Std Dev)	Test statistic	Degrees of freedom	P-value
Water-column AFDM (mg/L)	0.040 (0.23)	t=0.912	28	0.369
Water-column % AFDM	0.153 (0.24)	t=3.496	29	0.002
Water-column Chlorophyll *a* (µg/L)	-0.166 (0.26)	t=-3.558	29	0.001
Benthic AFDM (g/m^2)	0.858 (0.75)	t=6.25	29	<0.0001
Benthic Chlorophyll *a* (mg/m^2)	0.812 (0.72)	t=5.41	22	<0.0001
Gross Primary Production ($g\ O_2/m^2/d$)	-0.065 (0.25)	t=-0.941	11	0.378



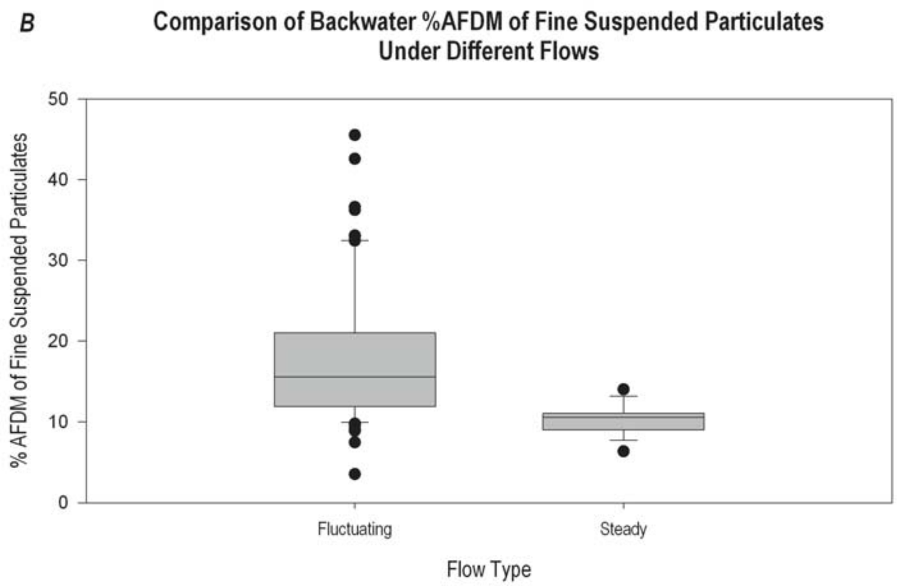


Figure 4. Comparison of percent organic matter of fine (<0.25 mm) particulates as ash-free dry-mass (AFDM). *A*, Grand Canyon backwaters versus corresponding mainstem sites. Line is 1:1 line that indicates equality between the backwater and main channel samples. *B*, Grand Canyon backwaters during fluctuating flows versus steady flows. Boxplot with whiskers from the 10th percentile to the 90th percentile.

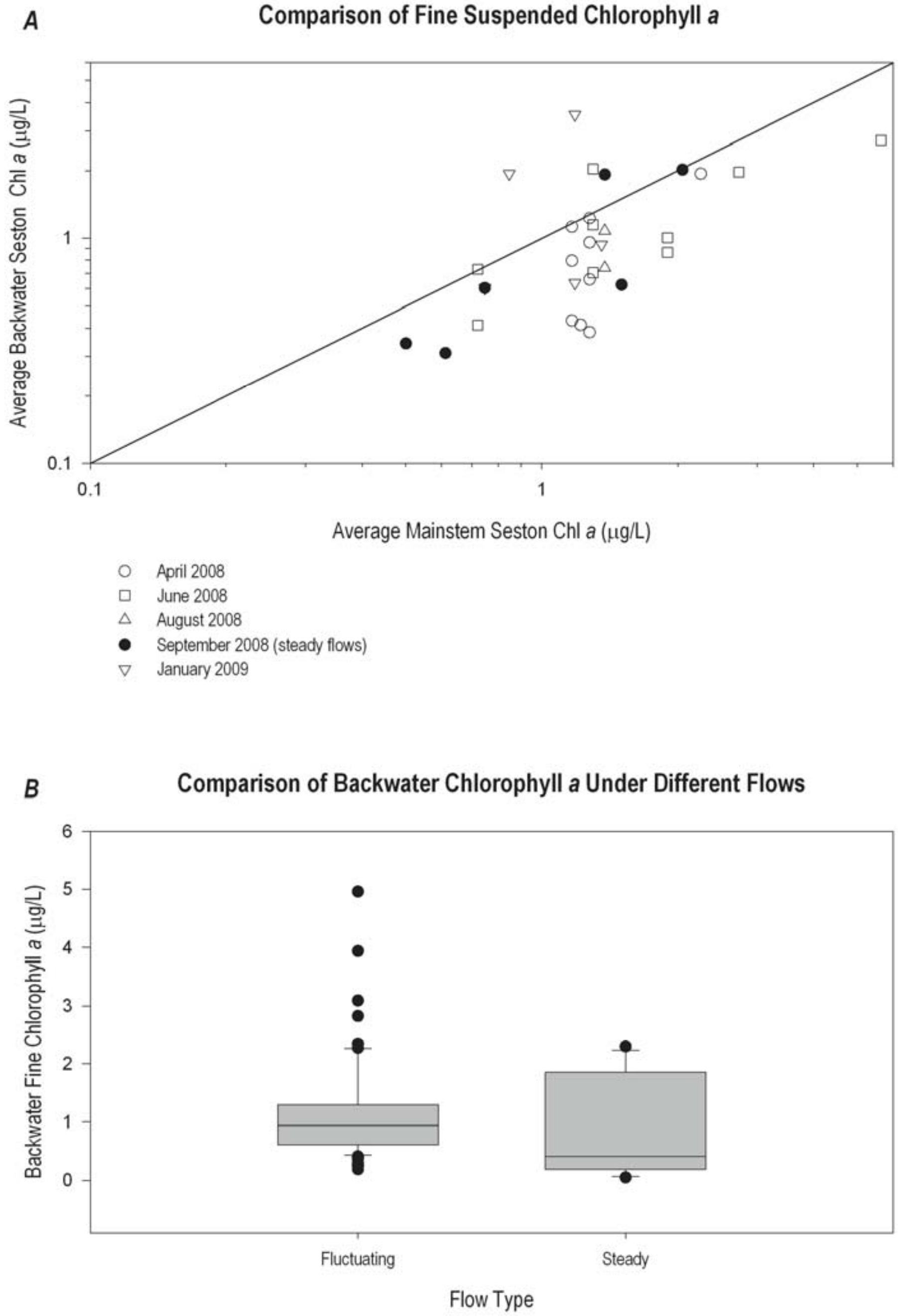


Figure 5. Comparison of fine (<0.25 mm) suspended chlorophyll *a*. *A*, Grand Canyon backwaters versus corresponding mainstem sites. Line is 1:1 line that indicates equality between the backwater and main channel samples. *B*, Grand Canyon backwaters during fluctuating flows versus steady flows. Boxplot with whiskers from the 10th percentile to the 90th percentile.

The standing stock of benthic organic matter in backwaters was seven times higher relative to main-channel depositional areas across all flow regimes ($p<0.0001$; fig. 6*A*; table 3). There was no effect of steady flow on backwater fine benthic organic matter (fig. 6*A*,*B*). Benthic chlorophyll *a* density was 6.5 times higher in backwaters relative to main-channel habitats ($p<0.0001$; fig. 7*A*, table 3), but benthic chlorophyll levels in backwaters were unrelated to flow regime (fig. 7*A*,*B*, table 3).

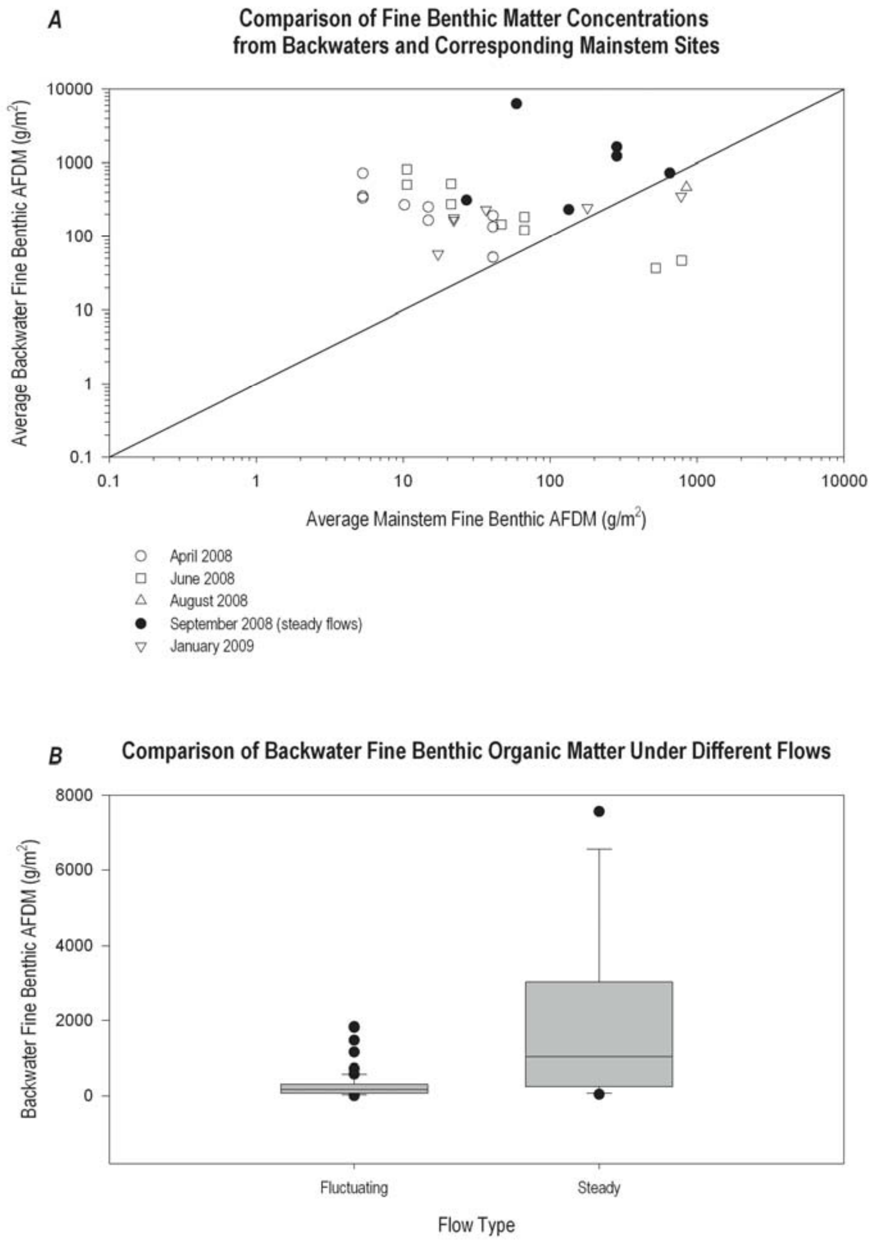


Figure 6. Comparison of fine (<0.25 mm) benthic organic matter as ash-free dry-mass (AFDM). *A*, Grand Canyon backwaters versus corresponding mainstem sites. Line is 1:1 line that indicates equality between the backwater and main channel samples. *B*, Grand Canyon backwaters during fluctuating flows versus steady flows. Boxplot with whiskers from the 10th percentile to the 90th percentile.

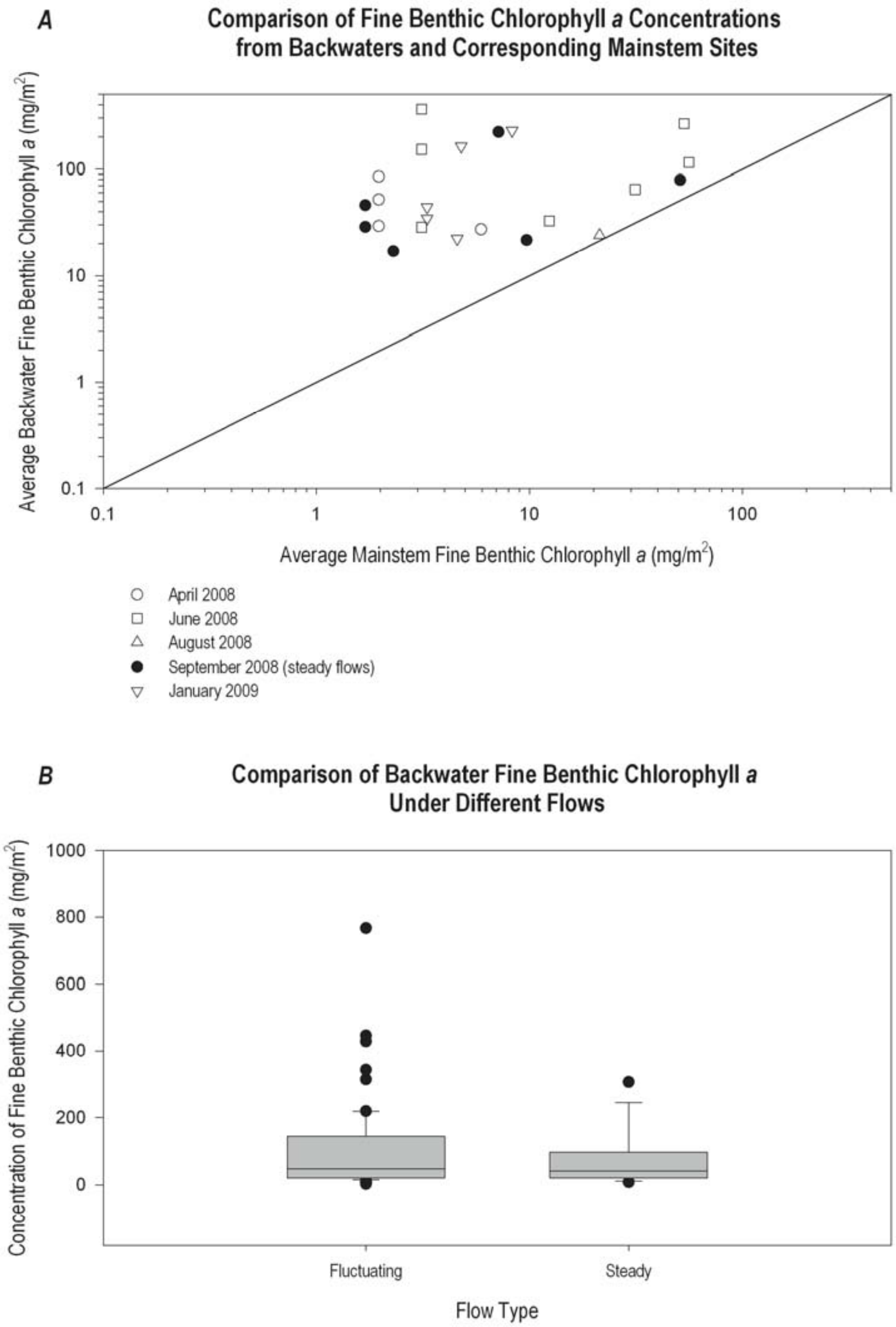


Figure 7. Comparison of fine (<0.25 mm) benthic chlorophyll *a*. *A*, Grand Canyon backwaters versus corresponding mainstem sites. Line is 1:1 line that indicates equality between the backwater and main channel samples. *B*, Grand Canyon backwaters during fluctuating flows versus steady flows. Boxplot with whiskers from the 10th percentile to the 90th percentile.

Ecosystem Metabolism

Rates of GPP in backwater habitats were comparable to those measured in the mainstem river (fig. 8*A*, table 3); both had median values near 2 g $O_2/m^2/d$. Rates of GPP in backwaters were unrelated to flow regime (fig. 8*A*,*B*). Other measures of ecosystem metabolism (ER, NPP, and the ratio of production to respiration—P:R) in backwaters were also unrelated to flow regime (fig. 9*A*–*C*). There was a trend towards lower P:R during steady discharge relative to fluctuating discharge (median value of 0.7 for steady versus median of 3 for fluctuating), but the difference was not statistically significant ($p=0.07$).

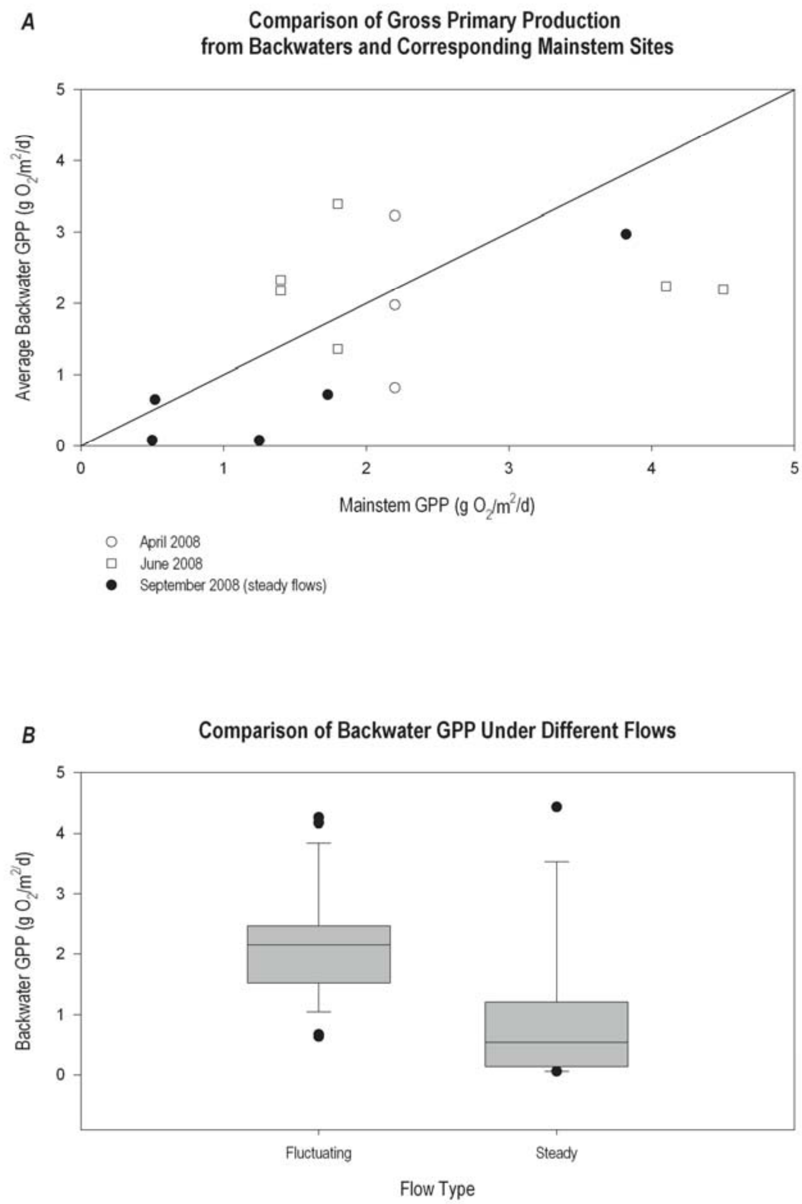


Figure 8. Comparison of gross primary production (GPP, in units of g $O_2/m^2/d$). *A*, Grand Canyon backwaters versus corresponding mainstem sites. Line is 1:1 line that indicates equality between the backwater and main channel samples. *B*, Grand Canyon backwaters across flow regimes. Boxplot with whiskers from the 10th percentile to the 90th percentile.

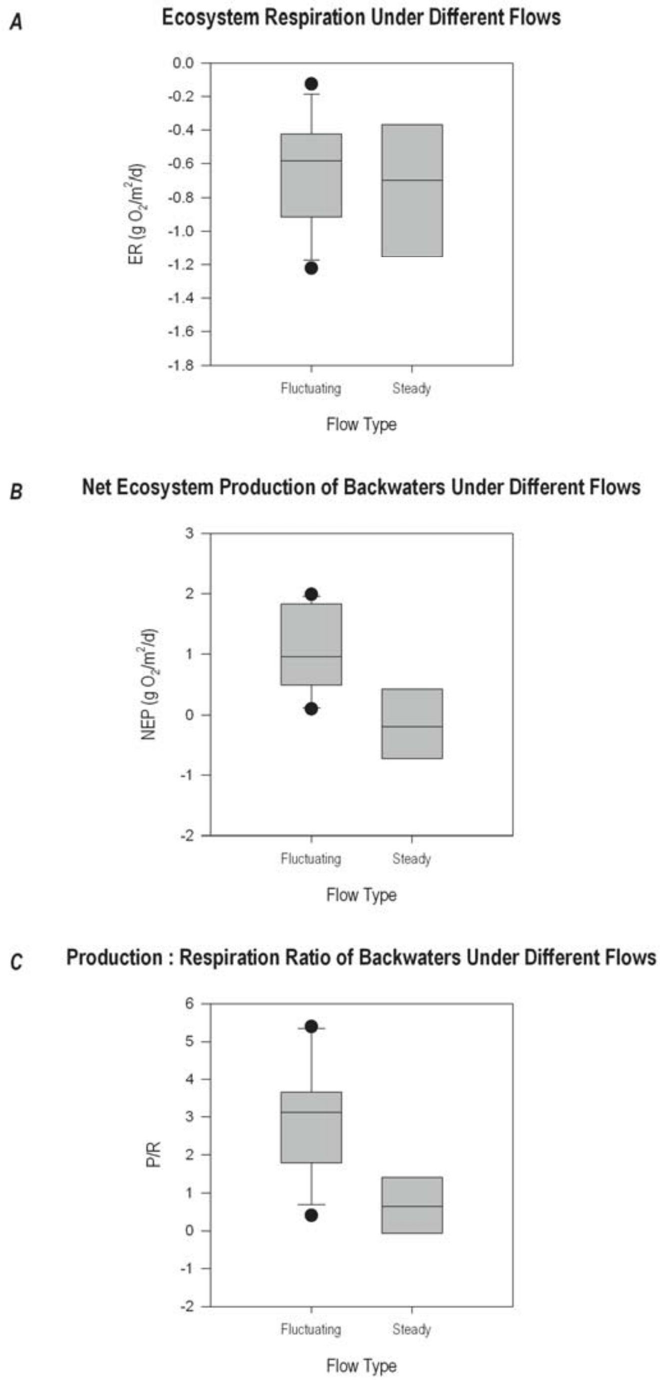


Figure 9. Comparison of (*A*) ecosystem respiration (ER), (*B*) net ecosystem production (NEP), and (*C*) Production:Respiration (P/R) of Grand Canyon backwaters during fluctuating and steady flows. Boxplots with whiskers from the 10th percentile to the 90th percentile.

Benthic Invertebrates

Processing of benthic invertebrate samples for both backwaters and mainstem habitats is still ongoing, but preliminary data (density and biomass) for the four most abundant taxa (New Zealand mudsnails—*Potamopyrgus antipodarum*; Chironomidae midges; *Gammarus lacustris*; and tubificid oligochaetes) from the backwater samples collected during September 2008 are presented in figure 10. Tubificid worms were present in large numbers relative to other taxa in a third of the backwaters sampled, with densities ranging from 50 individuals/m^2 to 16,500 individuals/m^2 compared to 0–3,300 individuals/m^2 for chironomids, the next most abundant taxa. Invertebrate biomass densities followed this trend, with a calculated range of 2.5 mg/m^2 to 1,000 mg/m^2 for tubificids compared to 0 mg/m^2 to 200 mg/m^2 for chironomids. Invertebrate abundance appears to decline with distance downriver (fig. 10*A*). Biomass also appeared to follow this trend, with the exception of RM 123.7, which had high invertebrate biomass relative to other sites in that vicinity. The sampled backwaters farthest downriver had considerably lower invertebrate abundance and biomass relative to those in Marble Canyon (for example, 5.1 mg/m^2 at RM 199 versus 1,073.6 mg/m^2 at RM 44.6).

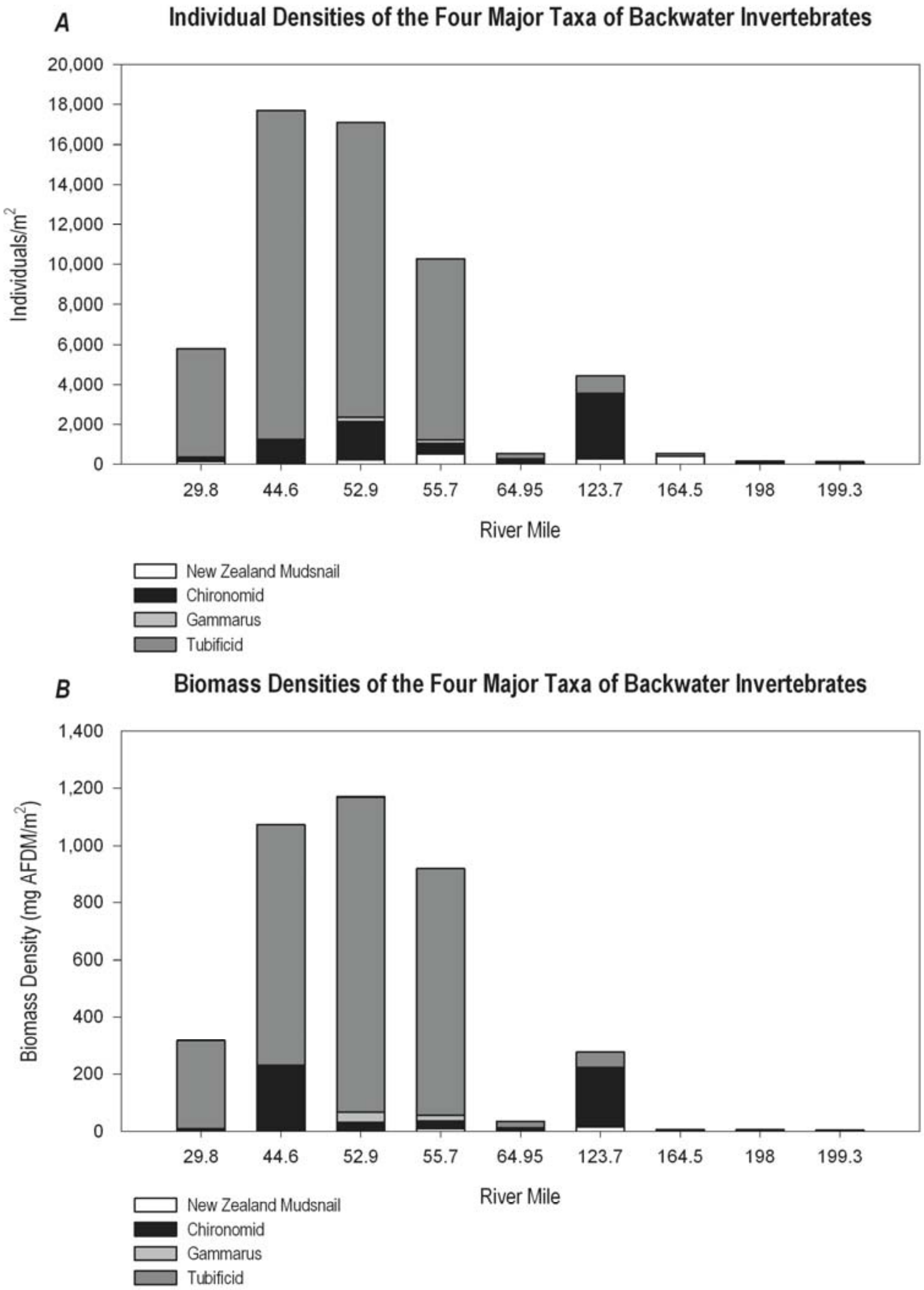


Figure 10. Bar graphs showing invertebrate density of (*A*) individuals/m^2 and (*B*) biomass as mg ash-free dry mass (AFDM)/m^2) of the four most common benthic invertebrates (New Zealand mudsnail (*Potamopyrgus antipodarum*), chironomids, *Gammarus lacustris*, and tubificid worms) found in Grand Canyon backwaters during September 2008 as a function of river mile.

Water Turnover Rates

The dye tracer experiments indicated that backwaters retained water significantly longer in steady flows than in fluctuating flows, regardless of which approach was used (p-values <0.05 for all measures; fig. 11 and table 4). Calculated residence time during fluctuating discharge ranged from less than 5 minutes in small, shallow backwaters to 28 hours in a large, deep backwater with complex geometry (Eminence site). Under a steady flow regime, calculated residence time had the same upper bound of 28 hours as fluctuating flows but the minimum was 4.6 hours. Average residence time was 220 minutes during fluctuating flows and 613 minutes during steady flows. These data indicate an estimated 2.3 and 6.5 turnovers per day for fluctuating flows and steady flows, respectively. On the whole, steady discharge led to a 2.7-fold to 4.7-fold increase in the average turnover time, depending on the measure of turnover.

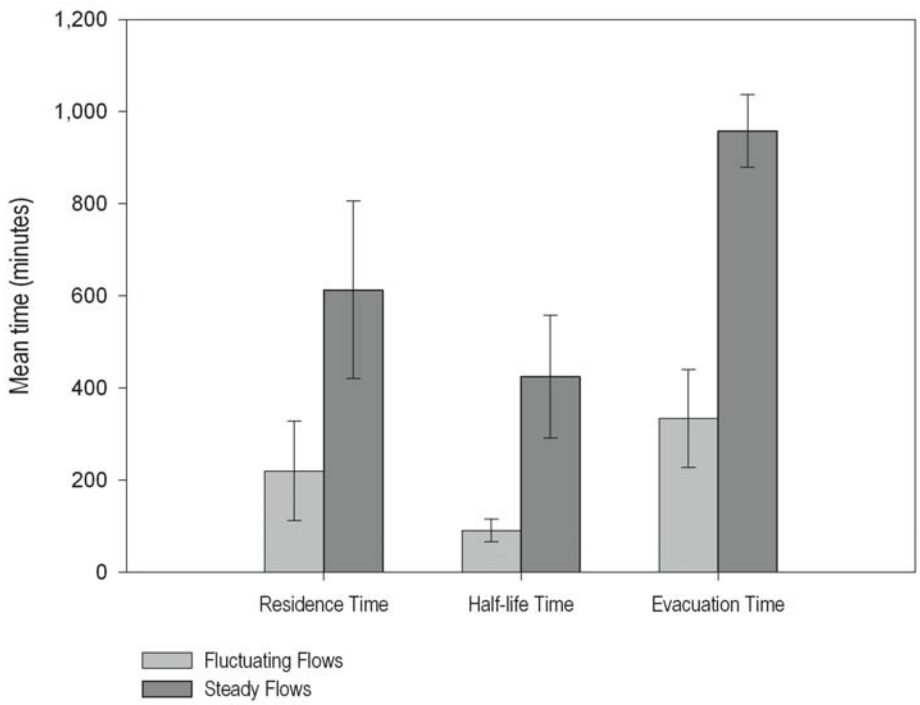


Figure 11. Bar graph showing the average turnover time of water in backwaters of Grand Canyon under fluctuating and steady flow regimes between April 2008 and October 2009. Error bars are ± one standard error. Residence time refers to the duration of the dye's presence in the backwater calculated with the formula: $\ln C_0 = \ln C_t - k*t$ where C_0 is concentration of dye at time=0, C_t is the concentration of dye at time=t (minutes), and k is the empirically fitted rate of decay (units of 1/minute). Half-life time uses the same equation as above, but refers to the duration until one half of the dye is left in the backwater. Evacuation time refers to the observed duration of dye's presence as read by the fluorometer.

Table 4. Results of statistical comparison of water turnover rates under steady and fluctuating flow regimes between April 2008 and October 2009 in Grand Canyon backwaters.

[Residence time refers to the duration of the dye's presence in the backwater calculated with the formula: $\ln C_0 = \ln C_t - k*t$ where C_0 is concentration of dye at time=0, C_t is the concentration of dye at time=t (minutes), and k is the empirically fitted rate of decay (units of 1/minute). Half-life time uses the same equation as above, but refers to the duration until one half of the dye is left in the backwater. Evacuation time refers to the observed duration of dye's presence as read by the fluorometer]

Response	Mean minutes steady (SE)	Mean minutes fluctuating (SE)	Sample size steady/ fluctuating	Test	Statistical value	P-value
Residence time	613 (193)	220 (108)	7/15	*t*-test	$t = 0.0015$	0.0007
Half-life time	901 (133)	425 (24)	7/15	Wilcoxon	$\chi^2 = 0.0067$	0.0074
Evacuation time	958 (79)	335 (106)	6/13	Wilcoxon	$\chi^2 = 0.0085$	0.0096

Discussion

Food resources for invertebrates were found to be greater in backwaters than adjoining mainstem areas for all of the standing measures (organic matter concentration/density, chlorophyll *a* concentration/density). This finding, along with the assumption that backwaters provide an environment of lower energy demands, suggests that they provide an environment beneficial to fish compared to their depositional, mainstem counterparts even during times of discharge variability. Certain patterns in our data (particulate settling, no difference in gross primary production), lead us to hypothesize that these benefits to fish are mainly attributable to the primary physical factors that determine a backwater instead of to any primary or secondary production increase based on these physical factors. Without complete invertebrate data and fish-diet analysis, this conclusion is far from certain. Additionally, because our data from steady flows were confounded by tributary inputs, we were not able to draw any conclusions on the benefits of steady flows and whether they would create an environment suitable for the development of internally driven primary and secondary production. Comparable data from either a relatively long period of steady flows or a collection during periods of high tributary input under fluctuating flows would help to answer these questions.

Some water-column measures in backwaters differed from main-channel values. The percent, but not the concentration, of organic matter in suspension was higher in backwaters relative to the mainstem river, which could simply be a result of differential settling of denser inorganic particles. The finding of fine suspended chlorophyll *a* concentration being only half as much in the backwater compared to the mainstem is difficult to explain, given that there was no difference in the concentration of suspended organic matter and the high rates of water exchange we documented.

Rates of gross primary production in backwaters were comparable to the mainstem river. Algae are a high-quality food resource for invertebrates and some fish (Thorp and Delong, 1994), and GPP is one measure of its availability. Primary producer biomass (as indicated by benthic chlorophyll *a*) was higher in backwaters relative to depositional habitats in the main channel, so finding that GPP was comparable across habitats was surprising. However, our main-channel rates of GPP were estimated using open-channel methods, so they represent an integrated value that includes both the low rates of production that are likely in deep, depositional habitats and the higher rates that are likely in shallow, cobble habitats. Finding comparable GPP in backwaters supports the conclusion that higher amounts of benthic organic matter results from settling and/or retention of matter instead of higher rates of organic matter creation through algae or aquatic macrophytes.

The preliminary data we present give an estimate of benthic invertebrate biomass that is low compared to previously published estimates of invertebrate biomass from main-channel habitats (Stevens and others, 1997). Although the habitats sampled are unknown, Stevens and others (1997) reported that invertebrate biomass for main-channel habitats below the Little Colorado River confluence averaged around 100 mg/m^2, whereas the highest value we measured was 27 mg/m^2 and several of our values were less than 10 mg/m^2. However, our data are for only one season, and biomass estimates may change as additional invertebrate data become available.

The lack of an effect of flow regime on the comparison of backwater resource versus mainstem resources was surprising. However, it is important to note that the steady-flow portion (September 2008) of our observations was confounded by tributary inputs of sediment and organic matter from the Little Colorado River. Discharge of the Little Colorado River, which has a baseflow discharge of around 7 m^3/s, peaked at 36 m^3/s on September 3, 2008, and a second freshet on September 13 peaked at more than 25 m^3/s. Concentrations of sediment (>100,000 mg/L) and organic matter (as much as 10,000 mg/L) in tributaries during flooding conditions are extremely high (U.S. Geological Survey, unpub. data, 2009). Concentrations of suspended sediment in the Colorado River are highly correlated with concentrations of suspended organic matter (U.S. Geological Survey, unpub. data, 2009). The suspended sediment data for the Colorado River at RM 225 that are presented in table 2 indicate that the supply of organic matter was higher during our September sampling relative to the other times we collected biological data from backwaters. It is likely that a greater supply of tributary-derived organic matter accounts for the higher water-column and benthic organic matter we documented during the steady discharge experiment. Indeed, the higher percentage of sediment (lower percentage of organic matter) in suspension in backwaters during stable discharge is consistent with this assertion.

Stable discharge increased residence time of water in backwaters. Depending on the measure of exchange, residence times were seven times longer during steady discharge relative to fluctuating discharge. However, even during steady discharge backwaters were completely turning over 1.5 to 3.4 times per day. Given these turnover rates, it seems unlikely that water-column resources in backwaters, such as zooplankton, could ever become substantially higher than in the mainstem river. Benthic resources are undoubtedly less susceptible to export from the backwater than water-column resources; however, because turnover rates for virtually all backwaters exceeded once per day, the rate of exchange may influence the accumulation of benthic organic matter and invertebrates.

Collectively, these preliminary findings indicate that the availability of autochthonous resources in backwaters is comparable to that in mainstem habitats and the availability of detrital resources in backwaters exceeds that of mainstem habitats. We were unable to draw any definitive conclusions about the influence of steady discharge on resource availability in backwaters because tributary floods occurred during the period of steady-discharge sampling but not during fluctuating-discharge sampling. However, the effects of stable discharge on backwaters are likely context dependent. If stable discharges occur during times of clear water, it is possible that rates of primary production will increase relative to fluctuating flows because longer turnover times will allow for warmer water temperatures and greater retention of benthic algae biomass. If, however, stable discharges occur during times of tributary activity, suspended inorganic sediment will make backwaters turbid, and primary production will be low. In that case, the supply of tributary-derived organic matter to backwaters will be high and the organic matter may accumulate in backwaters and support detrital food webs. Indeed, the trend towards lower P:R during steady discharge relative to fluctuating discharge (steady, 0.7; fluctuating, 3) indicates heterotrophic processes dominated during the turbid conditions of September 2008 while autotrophic processes dominated during the clearer water conditions that occurred during other sampling.

The data presented here have advanced the effort to answer the question of whether backwaters are disproportionately valuable to small-bodied fish in Grand Canyon. However, the unfortunate confounding of flow with tributary inputs limits our ability to provide managers with conclusions about flow regime. Additional data collected during clear-water steady flows, along with the results of projects focusing on other aspects of fish, temperature, and backwaters, will help greatly in answering this question.

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