Aquatic Production and Carbon Flow in the Colorado River

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Abstract

Dams alter physical and biological processes in rivers in predictable ways, yet we have little understanding of how dams alter carbon fluxes into rivers and secondary production (elaboration of biomass through time) of animals. Production is essential to understand how the size of fish populations might be limited by the amount of available energy. We hypothesize that dams reduce inputs of transported organic matter to downstream river reaches with a subsequent increase in photosynthesis providing the energy base for the food web. We have begun measuring primary and secondary production in the Colorado River below Glen Canyon Dam. Primary production, i.e., the rate of photosynthesis, increases with declining suspended sediment concentrations and can equal rates from small, well-lit streams suggesting primary production is an important carbon source for the river food web. Aquatic invertebrates derive a large portion of their diet from algae when rates of primary productivity are high. Secondary production, i.e., the rate of invertebrate biomass accumulation, ranged from high below Glen Canyon Dam to low downstream near Diamond Creek; this variance likely is driven in part by the availability of carbon from photosynthesis. Knowledge of carbon flow within a managed tailwater like the Colorado River will assist in predicting outcomes of management decisions that alter energetics of food webs.

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Introduction

The Colorado River drains a large fraction of the arid Intermountain West and is a primary water supply for users in seven States. The river holds a unique assemblage of fish species; of the 36 fish species that are native to the Colorado River system, 64 percent are found nowhere else (Carlson and Muth, 1989). The Colorado River has been extensively altered by dams to facilitate water storage and power generation. These dams alter the physical habitat and temperature regime in predictable ways (Ward and Stanford, 1983) and decrease biotic integrity, causing fish and invertebrate species to become locally extirpated. For example, the Green River in Utah below Flaming Gorge Dam lost more than 90 percent of its mayfly species following dam construction (Vinson, 2001) and now supports a productive, but nonnative, trout fishery. Four species of native fish are no longer found in the Grand Canyon reach of the Colorado River (Gloss and Coggins, 2005); one of the remaining species—humpback chub (*Gila cypha*)—is listed as endangered under the Endangered Species Act.

An important part of maintaining biological integrity at higher trophic levels is ensuring that there is a sufficient food supply to support the population. This need has been translated into policy as part of the strategic plan of the Glen Canyon Dam Adaptive Management Program, whose first goal is “Protect or improve the aquatic food base so that it will support viable populations of desired species at higher trophic levels.” But prior to managing the river for maintenance of an adequate food base it is necessary to measure carbon inputs to the ecosystem and determine how these are transferred up the food web to fish populations.

Declines in native fish populations and other undesirable changes in ecosystem function are, in part, a problem of energetics. Food limitation can be one of several aspects (e.g., predation, spawning habitat, migration) that can limit fish recruitment and production. For example, in the Colorado River tailwater of Glen Canyon Dam, artificially low water temperatures during most of the year limit rates of fish and invertebrate growth; high light penetration because of clear-water leads to increased rates of primary production; nonnative New Zealand mud snails (*Potamopyrgus antipodarum*)

may represent a dead end for carbon flow in the food web because their thick shells protect them from fish predation; and nonnative trout, an important sportfish in the tailwater reach, may compete with and prey upon native fish in downstream reaches. Measuring organic matter flow into a river reach and through the food web in a common currency (g organic matter·m^{-2}·y^{-1}) provides a powerful framework for evaluating the effect of management actions on animal populations in the river. In addition, lower trophic levels will respond more quickly to changing dam operations than will slower-growing fish. The goals of this paper are to (1) describe why measurements of rates and sources of organic matter input into the river and associated production of animals can help us understand ecological function in heavily altered sections of the Colorado River, and (2) demonstrate the utility of these approaches from data we are collecting in the Grand Canyon reach of the Colorado River.

Carbon Inputs to the Base of River Food Webs

Animal production in any ecosystem, including rivers, is ultimately limited by the amount and quality of food resources entering the bottom of the food web. Physical conditions (e.g., habitat quality, temperature) certainly regulate the total animal production of an ecosystem, but the ultimate limits are set by the availability of carbon resources. Rivers with high rates of primary production or terrestrial inputs of carbon (i.e., leaf litter from streamside trees) can have higher rates of secondary productivity, assuming the physical conditions are also conducive to high production. For example, removing leaf litter inputs dramatically reduced secondary production of invertebrates in a mountain stream (Wallace and others, 1997). Secondary production of New Zealand mud snails in warm springs of the Yellowstone region are some of the highest ever measured for animal populations, but this is only possible because primary production of these springs is also extremely high (Hall and others, 2003). In turbid desert rivers, fish abundance can be higher in streams with higher rates of primary production (Fellows and others, 2009), suggesting that primary production is an ultimate control. In addition to the quantity of food resources, the quality of that food resource can also determine production. For example, adding nutrients to a heavily forested stream increased the nutritional quality, but not the quantity, of leaf litter that forms the base of the food web, thereby increasing invertebrate production (Cross and others, 2006).

We can categorize two main sources of carbon to rivers. Allochthonous carbon sources originate from outside the channel, such as leaves from streamside trees or organic matter that has been transported from a small headwater stream downstream to a large river. In contrast, autochthonous carbon is fixed by photosynthesis within the river channel by organisms such as algae or aquatic plants. Allochthonous inputs can dominate the carbon budget of many streams (Fisher and Likens, 1973) and rivers (Meyer and Edwards, 1990) and can be a dominant carbon source to consumers in food webs (Hall and others, 2000). Most streams and rivers are net heterotrophic, meaning that consumption of organic matter exceeds production of new organic matter, because allochthonous inputs allow ecosystem respiration to exceed primary production (Howarth and others, 1996; Webster and Meyer, 1997). Autochthonous production can exceed ecosystem respiration when the ecosystem is highly productive (e.g., small desert streams with warm water that receive abundant sunshine) and (or) when allochthonous inputs are minimal (e.g., spring streams that are for the most part isolated from the surrounding landscape) (Minshall, 1978). More often than not, the relative amounts of allochthonous versus autochthonous inputs vary through time; e.g., autochthonous algal production may dominate at certain times of the year when conditions promote high rates of photosynthesis (Roberts and others, 2007). For example, Roberts and others (2007) found that in a small Tennessee stream, autochthonous production dominated for roughly a 1-month period in the spring before leaf-out. Later in the spring and summer, shading by overstory trees limited algae growth, and in fall and winter leaf litter inputs supported elevated rates of ecosystem respiration, and autochthonous production was low.

Measuring the relative inputs of allochthonous versus autochthonous organic matter is an important step in a food web study because these resources represent the base of the food web, but relative differences in the quantity of these resources may not control which resource is actually providing the carbon source for animal consumers in a river. Algae, such as diatoms, are often a high-quality food source relative to more refractory allochthonous organic matter, so even a relatively small amount of primary production in a highly heterotrophic ecosystem may provide the primary energy source for food webs. In small streams, invertebrates derive their carbon from autochthonous sources at higher rates than predicted by relative differences in autochthonous and allochthonous inputs (McCutchan and Lewis, 2002). Evidence from large rivers suggests that algal production supports much of the animal secondary production, even in turbid rivers that carry large quantities of terrestrial organic matter where algal production is minimal, (Thorp and Delong, 2002). The Riverine Productivity Model (Thorp and Delong, 2002) posits that, despite large quantities of terrestrial inputs either from flood plains or from inefficient processing by upstream reaches, locally produced algal carbon should provide the base for riverine food webs. Evidence supports this model. Carbon isotope data from turbid, desert rivers show that primary production within the river channel supplies nearly all of the carbon to animals, despite high terrestrial inputs (Bunn and others, 2003). Primary production was locally high in these rivers even though they were turbid, and the combination of locally high production with high nutritional quality of algae relative to terrestrial inputs likely contributed to the importance of algae to the food web (Bunn and others,

2003). Hamilton and others (1992), also reported that in grass-dominated flood-plain lakes, animals received nearly all of their carbon from attached microalgae and not from the grass itself.

Production in the Colorado River Below Glen Canyon Dam

Primary Production and Consumption by Invertebrates

"Open-channel" methods are being used to measure primary production on the Colorado River (Odum, 1956; Hall and others, 2007). This procedure measures the change in oxygen (O_2) concentrations in the river as a surrogate for carbon because photosynthesis releases O_2 at approximately the same molar ratio as carbon fixation. Seasonally, we measure O_2 concentration throughout 2 nights and 1 day at five locations in Grand Canyon ranging from Marble Canyon to Diamond Creek. To calculate gross primary production (GPP; i.e., the rate of photosynthesis not including algal respiration), we use a model fitting procedure following Van de Bogert and others (2007), where we fit the following model to the O_2 data:

$$C_t = C_{t-1} + \frac{GPP}{z_t} \times \frac{PAR_t}{\sum PAR} + \frac{CR\Delta t}{z_t} + K(C_s - C_{t-1})\Delta t$$

C_t and C_{t-1} are O_2 concentrations across a 5-minute time step (Δt); C_s is the calculated saturation concentration of oxygen at a given temperature and barometric pressure. K is the rate of oxygen exchange at the air-water interface (1/d) and is calculated on the basis of measured oxygen exchange in the first 20 kilometers (km) of river (R.O. Hall and others, unpub. data, 2009); z_t is water depth (meters, m) at time t; PAR_t is the instantaneous amount of light hitting the river (µE m^{-2} s^{-1}) over a reach length equal to 80 percent of the O_2 travel distance; and ΣPAR is the total light summed for the day. Modeling oxygen concentrations and solving for GPP and ER (ecosystem respiration) is superior to standard calculations (Hall and others, 2007) because it allows calculating uncertainty in any one metabolism estimate. We calculated light as a function of river topography by following Yard and others (2005). The two variables that were solved for were GPP (g O_2 m^{-2} d^{-1}) and community respiration (g O_2 m^{-2} d^{-1}, CR). Because the river was consistently supersaturated with O_2, it was not possible to accurately estimate respiration using this technique, so we solved for CR, but the values were not reported. CR is not robust because it is not known what the O_2 concentration would be in the absence of biological activity. The common assumption is that streams would be at air-saturation if there were no CR and that CR lowers O_2 from this air saturation. Because the river was supersaturated, we have no reference point for which to measure respiration. GPP estimates, on the other hand, are robust because we are modeling the amplitude of the diel excursion and not the absolute concentration. We were able to measure rates of GPP despite extremely high rates of reaeration driven by rapids. Diel changes in oxygen concentrations were about 0.1 to 0.4 milligrams of oxygen per liter (mg O_2/L), which is small but easily modeled (fig. 1). We solved the model by minimizing the negative log-likelihood function between the model and the data. Because we measure invertebrate production by using g ash-free dry mass (AFDM, equivalent to organic matter), we converted these oxygen fluxes to organic matter assuming molar ratios between organic matter and O_2 = 1.

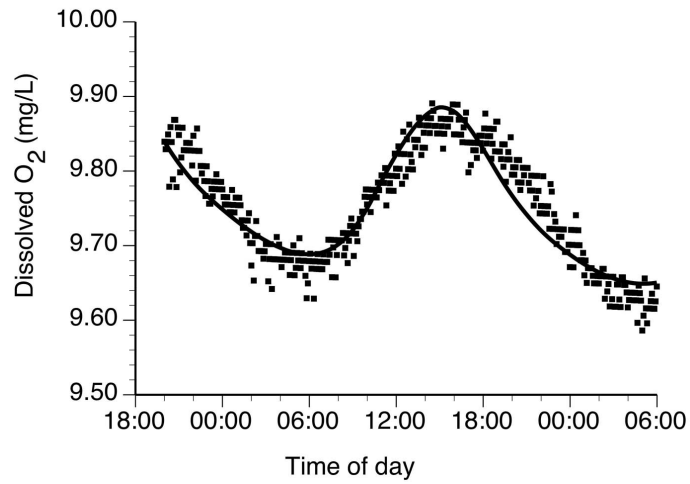

Figure 1. Example of oxygen data (points) versus model (line) for one metabolism calculation near National Canyon, AZ, from July 2008. Gross primary production was 2.6 g O_2 m^{-2} d^{-1}.

Gross primary production was strongly a function of suspended sediment concentrations (fig. 2); high sediment concentrations block light, thus reducing primary production. Because sediment concentration increases downstream, production tends to decline downstream when considering all seasons. The rates of primary production were similar to those in small streams across the United States (Mulholland and others, 2001), including those from high-light areas, which ranged from 0.2 to 24 g organic matter m^{-2} d^{-1} (Hall and Tank, 2003). Rates of primary production were greater than 10-fold higher than for water-column-based rates in tropical rivers (Lewis, 1988). The role of benthic algae in contributing to production in these tropical rivers was unknown but considered small (Lewis, 1988). Most production in the Colorado River is likely from river-bottom algae, though planktonic algae likely contribute to primary production because of a moderate amount of chlorophyll in the water column (0–2 micrograms chlorophyll *a* per liter (µg Chl *a* /L)). Because rates of GPP in the Colorado River can be as high as rates from small streams, the flux of carbon to this river from autochthonous primary production may be high enough to be important for

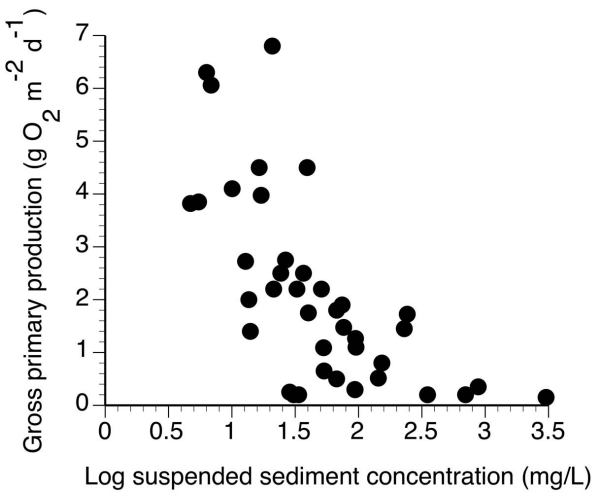

Figure 2. Daily rates of gross primary production decline as a function of $\log_{10}$ suspended sediment concentrations.

consumers, even though rates essentially are zero during times of year of low water clarity.

We also are attempting to make open-channel measurements of GPP in the Glen Canyon tailwater. However, because dam operations contribute to daily changes in O_2, in addition to the primary production of interest, open-channel measurements of GPP will require a different approach that is still being developed. Rates of GPP estimated from chambers that contained individual algae-covered rocks were very high: 15 g organic matter m^{-2} d^{-1} (Brock and others, 1999). This rate is up to 10 times higher than average rates for Grand Canyon. However, comparisons between chamber estimates and open-channel estimates must be made with caution, because high spatial heterogeneity in the distribution of river-bottom algae makes scaling rates measured on individual rocks up to the entire reach difficult. Nonetheless, these limited chamber data suggest that rates of production in the Glen Canyon reach are likely to be very high.

The rates of GPP in Grand Canyon are high enough for algae to represent a significant food resource for animal consumers. We have been measuring the diets of animals from all locations and across all seasons to calculate flows of carbon from basal resources into animal populations. These data show that algae (in this case, mostly microscopic algae known as diatoms) can constitute a large fraction of invertebrate gut contents (fig. 3); diets for the two taxa shown in figure 3 (*Simulium arcticum*, a filter-feeding blackfly, and *Gammarus lacustris*, a small crustacean) can contain up to 60 percent diatoms. Further, the proportion of diatoms consumed is positively related to the rate of primary production at the time and place the invertebrates were collected. These preliminary data suggest that below Glen Canyon Dam, primary productivity supports the growth and production of animal consumers. This finding is consistent with what is known about other desert rivers (Bunn and others, 2003) and theories of carbon flow in big-river food webs (Thorp and Delong, 2002).

Secondary Production of Invertebrates

The effect of large dams on diversity and assemblage structure of invertebrates in downstream ecosystems is well known. Many species of invertebrates have lifecycles that are cued in some way to temperature (Elliott, 1978). Because of relatively cold and constant temperatures downstream from high-head dams, many invertebrates are unable to complete their lifecycle and therefore become locally extirpated (Sweeney and Vannote, 1978). Consequently, the

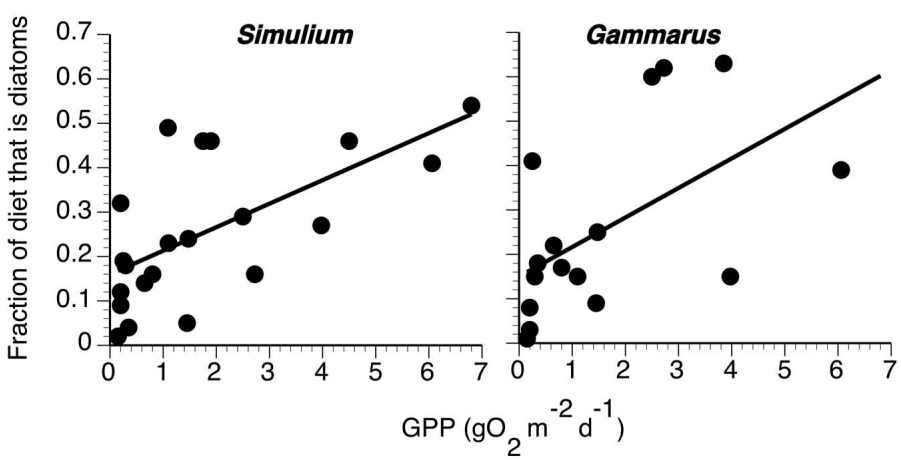

Figure 3. The fraction of invertebrate diet derived from diatoms increases with increasing rates of gross primary production (GPP). Lines are statistically significant least squares regressions, r^2 for *Simulium* = 0.41 and for *Gammarus* = 0.31.

number of invertebrate species often is lower below large dams than in free-flowing rivers. Before construction of Flaming Gorge Dam, the Green River contained more than 30 species of mayflies. After the closure of Flaming Gorge, the number of mayfly species declined to one common and two rare species (Vinson, 2001). Less data are available for the Colorado River below Glen Canyon Dam. Upstream from Lake Powell in Cataract Canyon, Haden and others (2003) found 49 invertebrate taxa of which 9 were mayflies. The Colorado River downstream from Glen Canyon Dam contains about 10 common taxa, none of which are mayflies (Stevens and others, 1997; W.F. Cross and others, unpub. data, 2009). The most common species in this reach are nonnative (i.e., *Oligochaetes*, *Gammarus lacustris*, and *Potamopyrgus antipodarum,* the New Zealand mud snail), suggesting that the Colorado River downstream from Glen Canyon Dam is best suited for stenothermic, cosmopolitan taxa.

To examine the degree to which the amount of invertebrates available for consumption by fish potentially limits the abundance of fish populations, it is necessary to estimate invertebrate production. Invertebrate production represents the amount of invertebrate biomass produced per area (square meters) per time (month, year). In other words, invertebrate production measures the flow of carbon per time through invertebrate assemblages. Although the exact procedures for determining invertebrate production are complicated, production is essentially the product of invertebrate biomass and invertebrate growth rates (Benke, 1984). Invertebrate biomass in tailwater sections immediately below dams is often high (Vinson, 2001), but it is not possible to estimate secondary production based solely on biomass because growth rates are strongly and positively related to temperature and taxonomic identity (Benke, 1984; Huryn and Wallace, 2000).

In contrast to what is known about benthic invertebrate assemblage structure, little is known about how dams alter invertebrate production. We have begun measuring assemblage-level secondary production from six sites in the Colorado River. The upstream site is in the tailwater and runs from Glen Canyon Dam to Lees Ferry. The downstream site is 240 river miles from the dam, at Diamond Creek, and four sites, more or less evenly spaced, are in between. To measure secondary production, we measure taxon-specific (a taxon is grouping of organisms, for example, mayflies) abundance and biomass monthly (Glen Canyon and Diamond Creek) or seasonally (four sites in Grand Canyon). We collect 18 to 20 samples per site each sampling period from a variety of habitats, sort, identify, and measure the length of invertebrates to the nearest 0.1 mm to estimate biomass using length-mass regressions for each taxon. We multiply these estimated biomasses by empirically measured, size-specific growth rates to calculate production as a flux (g organic matter m^{-2} y^{-1}). Secondary production is habitat weighted to reflect the fraction of different habitat types (e.g., cobble bars, cliff faces, sand, etc.) that are present within that particular reach of river. Currently we have data analyzed for 1 year at Glen Canyon and Diamond Creek.

Invertebrate secondary production was about 50 times higher at Glen Canyon than Diamond Creek (fig. 4). At Glen Canyon, production was dominated by New Zealand mud snails, scuds, and freshwater worms (subclass Oligochaeta). Annual invertebrate production in this reach is high relative to many streams and rivers and is in the upper 25 percent of values sampled from the literature (R.O. Hall, unpub. data, 2009). In contrast, annual secondary production in the Colorado River near Diamond Creek is in the bottom 10 percent of values from other streams and rivers and is in the range of "low production" values from Huryn and Wallace (2000). This difference in productivity between the two reaches is likely caused by higher primary production and more abundant hard surfaces in Glen Canyon; the sandy and unstable surfaces that are common along downstream reaches support lower invertebrate biomass and secondary production. It should be noted that the invertebrates that formally were present in this river may have had higher biomass and production in sandy sediments than those currently found.

Which of these two rates of secondary production is likely closest to that for pre-dam conditions? We do not know at this time because there are no secondary production estimates for river reaches in the Colorado River Basin, but we can examine invertebrate biomass at other sites as a first approximation. For example, average biomass on cobble habitats in the relatively unimpacted Cataract Canyon reach was 0.4 $g \cdot m^{-2}$ (Haden and others, 2003), which is comparable to our preliminary estimate of 0.55 $g \cdot m^{-2}$ for cobble habitats at Diamond Creek. For comparison, invertebrate biomass in the Glen Canyon tailwater reach is 7 $g \cdot m^{-2}$, or 17-fold higher than Haden and others' (2003) value for Cataract Canyon. Despite

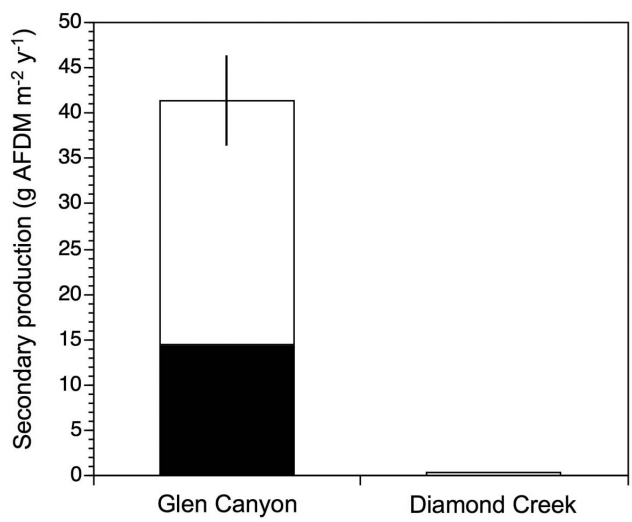

Figure 4. Secondary production in Glen Canyon reach is much higher than that for Diamond Creek reach of the Colorado River, AZ. The dark section of the bar for Glen Canyon is secondary production of New Zealand mud snails (*Potamopyrgus antipodarum*). Error bar is 95 percent bootstrapped confidence interval.

that biomass is similar between these two sites, we cannot speculate that production is the same because the thermal regime and assemblage structure are so different between the two sites that it is likely that assemblage-level biomass turnover and, therefore, secondary production will strongly differ also. Thus it may be that the high secondary production found immediately below a dam may be anomalously high relative to unregulated reaches or reaches where sediment inputs constrain primary and secondary production.

Prospectus

Despite a large body of research examining primary production (Mulholland and others, 2001; Roberts and others, 2007) and secondary production (Huryn and Wallace, 2000) in small streams, knowledge of primary and secondary production in nontidal rivers lags far behind. Measurements of phytoplankton and benthic production for many rivers using chamber approaches (e.g., Lewis, 1988; Cotner and others, 2006; Fellows and others, 2009) show that primary productivity can range from very low to high. In the Colorado River, rates of primary production essentially are unknown outside of rates for reservoirs (e.g., Gloss and others, 1980), and we are only beginning to measure rates of secondary production for animals. A limitation of our research in Grand Canyon is that we have no such data from before the construction of the dam, so we do not have a firm understanding of ecosystem function in the absence of a large dam. Currently, the only way to approximate pre-dam conditions is to perform similar measurements is parts of the Colorado River less altered by dams and other human activities, e.g., Cataract Canyon, Westwater Canyon, and the Yampa River. The huge reductions in downstream carbon transport and insect biodiversity (Vinson, 2001) and changes to habitat suggest that sections of the Colorado River less altered by dams will function much differently.

We argue that knowing rates of organic matter flow in the food web is critical for evaluating how management actions affect animal populations and ecosystem processes; evaluating the effect of management actions on resources is a critical step in the adaptive management process. For example, temperature strongly controls growth rates of invertebrates (Cross and others, in press; Huryn and Wallace, 2000). If a selective withdrawal structure is installed on Glen Canyon Dam to raise the temperature of releases, as was done for Flaming Gorge Dam, how will temperature-mediated increases to invertebrate growth rates alter secondary production and thus food availability for fish? If sediment inputs to the Colorado River increase because of sediment augmentation, how will reductions in water clarity alter riverine primary production and also secondary production of animals? Answers to these questions require detailed knowledge of food web energetics.

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