Macroinvertebrate diets reflect tributary inputs and turbidity-driven changes in food availability in the Colorado River downstream of Glen Canyon Dam

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Macroinvertebrate diets reflect tributary inputs and turbidity-driven changes in food availability in the Colorado River downstream of Glen Canyon Dam

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Abstract. Physical changes to rivers associated with large dams (e.g., water temperature) directly alter macroinvertebrate assemblages. Large dams also may indirectly alter these assemblages by changing the food resources available to support macroinvertebrate production. We examined the diets of the 4 most common macroinvertebrate taxa in the Colorado River through Glen and Grand Canyons, seasonally, at 6 sites for 2.5 y. We compared macroinvertebrate diet composition to the composition of epilithon (rock and cliff faces) communities and suspended organic seston to evaluate the degree to which macroinvertebrate diets tracked downstream changes in resource availability. Diets contained greater proportions of algal resources in the tailwater of Glen Canyon Dam and more terrestrial-based resources at sites downstream of the 1st major tributary. As predicted, macroinvertebrate diets tracked turbidity-driven changes in resource availability, and river turbidity partially explained variability in macroinvertebrate diets. The relative proportions of resources assimilated by macroinvertebrates ranged from dominance by algae to terrestrial-based resources, despite greater assimilation efficiencies for algal than terrestrial C. Terrestrial resources were most important during high turbidity conditions, which occurred during the late-summer monsoon season (July–October) when tributaries contributed large amounts of organic matter to the mainstem and suspended sediments reduced algal production. Macroinvertebrate diets were influenced by seasonal changes in tributary inputs and turbidity, a result suggesting macroinvertebrate diets in regulated rivers may be temporally dynamic and driven by tributary inputs.

Key words: macroinvertebrate diets, regulated rivers, food webs, algal and terrestrial organic matter, resource composition.

Large dams alter the physical template of rivers by changing flow, temperature, and sediment regimes, leading to the degradation of freshwater ecosystems worldwide (Ward and Stanford 1979, Poff et al. 1997, Olden and Naiman 2010). These physical changes alter riverine food webs (Power et al. 1996), reduce biodiversity of algae, macroinvertebrates, and fishes (Allan and Flecker 1993), and often lead to extirpation of native species and facilitation of invasion by nonnative species (Blinn and Cole 1991, Bunn and Arthington 2002). Specifically, large dams directly alter biological assemblages via physical changes (Vannote and Sweeney 1980, Stevens et al. 1997, Vinson 2001), but whether dams alter assemblages indirectly by changing food resources for aquatic food webs is not known.

Changes in the abundance and distribution of macroinvertebrate assemblages below dams are well documented (Blinn and Cole 1991, Stevens et al. 1997,

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Vinson 2001, Robinson et al. 2003) and are often attributed to shifts in temperature and flow regimes (Hauer and Stanford 1982, Olden and Naiman 2010). However, studies of the trophic ecology of macroinvertebrates in large regulated rivers are scarce (Rader and Ward 1989, Stevens et al. 1997, Delong et al. 2001, Hoeinghaus et al. 2007), and the effects of spatial and temporal changes in organic-matter availability on the use of basal resources in aquatic food webs are less well known. Understanding the trophic ecology of macroinvertebrates will help to elucidate the dynamics of macroinvertebrate diversity and production in regulated rivers.

Resources that support riverine macroinvertebrate food webs vary with watershed size (Vannote et al. 1980, Minshall et al. 1983). Large-river food webs may be supported by a combination of autochthonous and allochthonous resources (Benke and Wallace 1997, Rosi-Marshall and Wallace 2002, Zeug and Winemiller 2008) that are derived from local, upstream, or tributary sources. However, large dams drastically reduce downstream transport of organic and inorganic material (Serial Discontinuity Concept [SDC]; Ward and Stanford 1983). Therefore, dams may create discontinuities in the forms of basal food resources available to macroinvertebrates. For example, the tailwaters below dams are typically clear, and algae are a more readily available food resource for higher trophic levels than in undammed rivers of comparable size (Stevens et al. 1997). The SDC further predicts that tributaries may ameliorate the effects of the dam. Therefore, macroinvertebrate assemblages in reaches downstream of large tributaries may rely on different food resources than those residing in the tailwater. In addition, tributary inputs are temporally pulsed because of the seasonal dynamics of flooding, and dam-induced discontinuities in macroinvertebrate food resource use probably vary throughout the year. The influence of dams on macroinvertebrate food webs is poorly understood, especially with respect to spatial and temporal dynamics of food resource use associated with tributaries.

The Colorado River in Grand Canyon provides a model ecosystem in which to explore the influence of a large dam and tributaries on macroinvertebrate diets. Since its completion in 1963, Glen Canyon Dam has altered organic and inorganic matter transport and availability in the Colorado River in Grand Canyon. This large dam has reduced sediment loads by ~94% (Topping et al. 2000) and increased light penetration in the Colorado River (Yard 2003). As a consequence, algal production is high during much of the year in both the tailwater and further downstream of Glen Canyon Dam (Stevens et al. 1997, Hall et al. 2010). However, as distance from the dam increases, tributaries deliver inorganic material that increases turbidity, reduces light levels, and decreases algal production, especially during the late summer/early autumn monsoon season when tributaries flood (Yard 2003, Hall et al. 2010). In the Colorado River, the spatial and seasonal patterns of algal availability may influence macroinvertebrate reliance on algae as a food resource. Tributary floods also are a source of terrestrial organic material, and during times of high turbidity, macroinvertebrates may rely on this alternate food resource. Because dams reduce organic matter inputs from the upstream watershed, we hypothesized that algal (i.e., autochthonous) resources support macroinvertebrate assemblages in the tailwater and tributary-supplied terrestrial (i.e., allochthonous) resources support macroinvertebrates downstream. Shifting resource use has been documented in river networks (Tavares-Cromar and Williams 1996, Rosi-Marshall and Wallace 2002, Whiting et al. 2011), but it has not been examined in response to a large dam.

Here we present a 2.5-y seasonal analysis of macroinvertebrate diets at 6 sites below Glen Canyon Dam. Our primary objective was to quantify the extent to which algal and terrestrial resources support macroinvertebrates in the Colorado River below Glen Canyon Dam. In addition, we examined the extent to which macroinvertebrate diets reflect turbidity-driven changes in the availability of food resources. In particular, we compared food resource composition of the habitats in which macroinvertebrates feed (e.g., seston and epilithon) to macroinvertebrate diet composition.

Methods

Study sites

We sampled 6 sites over a 387-km reach downstream of Glen Canyon Dam in Grand Canyon, Arizona (Fig. 1). River thalweg depth and width averaged ~6 m and 89 m, respectively, at a discharge of 226 m^3/s. Sites encompassed the longitudinal profile of the Colorado River from Glen Canyon Dam through Grand Canyon, and included the broad spectrum of sediment and temperature conditions and major geomorphic reach types (Schmidt and Graf 1990). Site names reference the distance of each site downstream (in km) from the Lees Ferry boat ramp at RKM 0. The most upstream site, RKM 0 (Glen Canyon) encompassed a 25-km reach extending from the downstream end of the Glen Canyon Dam to Lees Ferry. This tailwater reach was above the confluence of permanently flowing major tributaries and, therefore, had consistently clear water (Stevens et al. 1997). The 5

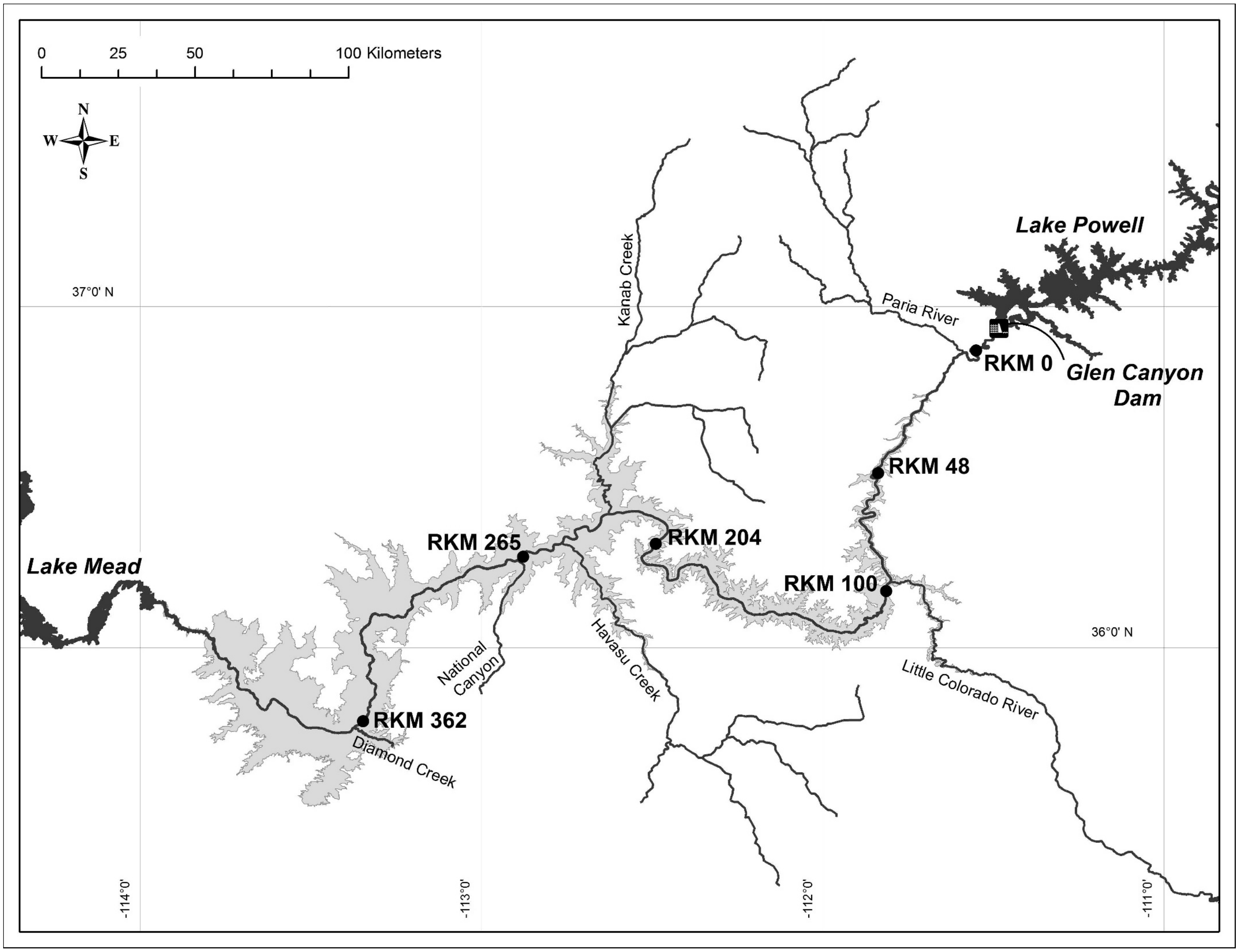

FIG. 1. Map of the Colorado River, Grand Canyon, showing the 6 study sites: River kilometer (RKM) 0 (Glen Canyon), RKM 48 (near South Canyon), RKM 100 (below the confluence of the Little Colorado River), RKM 204 (in the Middle Granite Gorge near Randy's Rock), RKM 265 (above National Canyon), RKM 362 (above Diamond Creek).

downstream sites were in Grand Canyon, from Marble Canyon to Diamond Creek. RKM 48 (near South Canyon), was ~46-km downstream of the Paria River, the 1st major tributary below the dam with a watershed area of 3652 km^2. RKM 100 was below the Little Colorado River, the largest tributary in Grand Canyon with a watershed area of 69,857 km^2. RKM 204 (in the Middle Granite Gorge near Randy's Rock) was below several smaller tributaries including Bright Angel Creek and Shinumo Creek. RKM 265 (above National Canyon) was below Tapeats, Kanab, and Havasu Creeks. The most downstream site, RKM 362, was just upstream of the confluence of Diamond Creek. Cumulatively, tributaries of the Colorado River in Glen and Grand Canyon increase the watershed area of the river by 30%, from 289,561 km^2 at RKM 0 to 374,668 km^2 at RKM 362.

Resource and macroinvertebrate collection

We collected organic matter and macroinvertebrates at each site during June, September, January, and April to encompass the range of turbidity conditions that occur in the river. Low turbidity conditions occurred only at RKM 0, whereas moderate and high turbidity occurred at the downstream sites during June, January, April, and September, respectively. We collected organic matter samples for 1 y, June 2006 to April 2007, and macroinvertebrates for 2.5 y, June 2006 to January 2009. During the year of organic matter characterization, we collected suspended fine particulate matter (seston) samples (2–3/site and date) from the thalweg by pouring ~10 to 15 L of river water through a 250-µm sieve and filtering ~40 to 300 mL onto a 0.45-μm gridded Metricel® membrane filter (Pall Corp., Ann Arbor, Michigan). We scraped epilithic biofilms from 2 to 3 rocks collected from the riverbed and from 2 to 3 cliff faces. We selected rocks of similar size (cobbles) that had moderately stable surfaces to ensure that biofilms were well colonized. We used a scraping/suction device to sample cliff faces below the varial zone to ensure that we sampled permanently wetted biofilms. In the field, we preserved a 30- to 40-mL subsample of biofilm slurry from individual rocks and cliffs with Lugol's solution (Prescott 1978). We sonicated 0.1- to 5.0-mL subsamples from each biofilm sample and filtered them onto gridded Metricel® membrane filters (25 mm diameter, 0.45 μm pore size). We dried seston and epilithon filters and mounted them on slides for preservation using Type B immersion oil and nail polish sealant. We analyzed 2 to 3 seston and epilithon slides for each site and season. We haphazardly collected macroinvertebrates from dominant habitats throughout each of the 6 reaches, preserved them in Kahle's solution (Stehr 1987) in the field, and brought them to the laboratory for gut-content analysis.

We examined diets of taxa from 4 functional feeding groups (Cummins and Klug 1979): collector-filterers (*Simulium arcticum* [Insecta:Diptera:Simuliidae]), shredders (*Gammarus lacustris* [Crustacea:Amphipoda:Gammaridae]), collector-gatherers (chironomids [Insecta:Diptera:Chironomidae]), and scrapers (*Potamopyrgus antipodarum* [New Zealand mud snails; Gastropoda:Neotaenioglossa:Hydrobiidae]). These taxa dominated production of the macroinvertebrate assemblage or contributed substantially to fish production (Cross et al. 2011). Twenty-four species of chironomids live in this segment of river (Stevens et al. 1998), and we consistently collected 4 genera (*Cricotopus*, *Orthocladius*, *Eukiefferiella*, and *Tvetenia*; subfamily Orthocladiinae) for gut-content analysis. For the purposes of this study, dietary compositions of chironomids of all 4 genera were averaged at each site for each season, and we did not examine spatial and seasonal trends among taxa.

We assessed macroinvertebrate diets with standard gut-content analyses (Benke and Wallace 1980, Rosi-Marshall and Wallace 2002). We suspended dissected gut contents in water, sonicated and filtered them onto gridded Metricel® membrane filters (25 mm diameter, 0.45 μm pore size), and mounted them on slides for preservation using Type B immersion oil and nail polish sealant. Macroinvertebrates varied in size and gut fullness. Therefore, we filtered the gut contents of 1 to 4 macroinvertebrates onto each slide to ensure that a sufficient number of particles were present. We analyzed 2 to 4 slides for each taxon at each site and season.

Microscopy

We measured the fractional area of organic particles to calculate the proportion of each particle type in the seston, epilithic biofilms, and diets. We identified and measured the area of ≥50 individual particles on each slide along random transects with image analysis software (ImagePro Plus®, Media Cybernetics Inc., Bethesda, Maryland) attached to a compound microscope at 100× magnification (Rosi-Marshall and Wallace 2002). We identified and categorized particles as: diatoms, filamentous algae, terrestrial leaf material, fungi, aquatic macrophyte, animal material, cyanobacteria, and amorphous detritus.

Relative proportion of food resources assimilated (RPA)

We used food-specific assimilation efficiencies (percentage of a food type that a macroinvertebrate is able to assimilate) to estimate the relative proportion of algal and terrestrial resources assimilated by macroinvertebrates (Benke 2011). Applying assimilation efficiencies allowed us to weight diet proportions by the quality of each resource (Benke and Wallace 1980, Benke 2011). We used literature-derived assimilation efficiencies for macroinvertebrates (see Benke and Wallace 1980): 30% for diatoms and filamentous algae; 10% for amorphous detritus, macrophytes, leaf material, and cyanobacteria; and 70% for animal material and fungi (Bärlocher and Kendrick 1975, Benke and Wallace 1980, 1997). For each food type, we calculated relative proportion assimilated (RPA) as:

$$\mathrm{RPA} = \frac{G_i \times AE_i}{\sum_{i=1}^{n} G_i \times AE_i} \qquad [1]$$

where G_i = proportion of food type i in the gut and AE_i = assimilation efficiency of food type i.

Amorphous detritus can be algal or terrestrially derived because it may be composed of bacteria; flocculated or assimilated dissolved organic matter; exopolymeric secretions from bacteria, algae, and fungi; sediment particles; and small detrital fragments (Mann 1988, Carlough 1994). In the tailwater segment of the Colorado River, algal production is high and inputs of terrestrial C from ephemeral tributaries or the riparian zone are negligible (Kennedy and Ralston 2010). However, tributary-derived terrestrial C inputs increase greatly downstream of the Paria River because of seasonal floods from large tributaries. Therefore, any amorphous detritus present in the tailwater is likely to be algal, whereas amorphous detritus in downstream reaches is a combination of algal and terrestrial material. Diatoms are the most common and widely distributed type of algae in this river, and we found them at all sites throughout the year. Based on the reasoning above, we assumed that all amorphous detritus in the tailwater reach was derived solely from algae (specifically diatoms), and we used the seasonal ratio (RA) of amorphous detritus (AD) to diatoms (DIA) in tailwater epilithic biofilms

$$RA = \frac{\%\ \text{AD in tailwater biofilm}}{\%\ \text{DIA in tailwater biofilm}} \qquad [2]$$

to calculate the algal fraction (AF) from diatoms of amorphous detritus in downstream macroinvertebrate diets. We multiplied RAs by the % diatoms in each macroinvertebrate diet at each downstream site (%DIA DIET). AF was calculated as:

$$AF = RA \times \%\text{DIA DIET}. \qquad [3]$$

For example, during June, % AD in tailwater biofilm was 9 and % DIA in tailwater biofilm was 65, so RA was 0.14. Applying this RA to an *S. arcticum* collected at RKM 48, where the diet contained 54% diatoms and 44% amorphous detritus, AF of the amorphous detritus would be 8%. Therefore, % algal resources consumed by *S. arcticum* at RKM 48 increased from 54% to 62%.

We applied apportioned amorphous detritus to estimate the relative proportion of algal (diatoms + filamentous algae + algae-derived amorphous detritus) vs terrestrial (leaf material + terrestrial-derived amorphous detritus) resources assimilated by each macroinvertebrate taxon. We averaged seasonal estimates for all years for each taxon to estimate the relative proportion of algal and terrestrial resources assimilated over the 2.5-y time period. For the 5 downstream sites, we averaged the assimilation estimates for each taxon for comparison with the tailwater site.

Statistical analyses

We averaged data from each season over 2.5 y (10 seasons) to calculate the proportion of particle types in the diet of each taxon. We qualitatively examined longitudinal differences in macroinvertebrate diets by estimating the mean proportion of algal resources (diatoms + filamentous algae) consumed among the 6 sites. We used bootstrap analysis to estimate medians and 95% confidence intervals (CIs) for the proportion of algal resources consumed at each site by each macroinvertebrate taxon and the entire assemblage. For each taxon, we resampled the proportion of algal resources consumed data with replacement 1000 times and calculated the median and 2.5% and 97.5% quantiles from the bootstrapped distribution. We used the same approach to develop means and CIs for the assemblage.

We assessed differences in diets among taxa by comparing the proportion of algal resources consumed by each taxon in the tailwater and downstream. The proportion of algal resources consumed in the tailwater represented the mean of all seasons. The proportion of algal resources consumed downstream represented the mean of all downstream sites during all seasons. We used 1-way analysis of variance (ANOVA) and Tukey's Honestly Significant Difference (HSD) test for this comparison. We $\arcsin\sqrt{(x)}$-transformed proportional data before analysis to meet the normality assumption for ANOVA.

Variability in macroinvertebrate diets

Turbidity varied among seasons and sites. This variability enabled us to explore the connection between turbidity and macroinvertebrate diets. We compared the proportions of the dominant food resources consumed in low-, moderate-, and high-turbidity conditions. Seasonal suspended-sediment data (in mg/L) were generated by a Laser Acoustic Monitoring System that recorded suspended sediment concentrations at 15-min intervals at 5 US Geological Survey (USGS) stations: Colorado River at river-km 48, Colorado River above Little Colorado River near Desert View, Arizona (09383100), Colorado River near Grand Canyon, Arizona (09402500), Colorado River above National Canyon near Supai, Arizona (09404120), and Colorado River above Diamond Creek near Peach Springs, Arizona (09404200). Primary production rates in the Colorado River in the Grand Canyon approach 0 when suspended silt/clay concentrations are >316 mg/L (Hall et al. 2010). Therefore, we classified water conditions as low turbidity if mean suspended sediment concentrations were <5 mg/L, moderate turbidity if suspended sediment concentrations were 5 to 316 mg/L, and high turbidity if suspended sediment concentrations were >316 mg/L. The tailwaters of Glen Canyon Dam were consistently clear (average 5 mg/L suspended sediment). Therefore, we used this concentration (5 mg/L) as the upper limit for low turbidity (LT) conditions. We grouped macroinvertebrate diet data by turbidity. The low-turbidity diets were collected at RKM 0, moderate-turbidity diets were collected at downstream sites during summer, winter, and spring, and high-turbidity diets were collected at downstream sites during the late-summer monsoons. We compared proportions of dominant food resources in macroinvertebrate diets (diatoms, filamentous algae, amorphous detritus, and leaf material) among turbidity conditions using 1-way ANOVA and Tukey's HSD test. We $\arcsin\sqrt{(x)}$-transformed proportional data before analysis.

We used quantile regression to evaluate the relationship between suspended sediment concentration and the proportion of algal resources in macroinvertebrate diets. We used the continuous suspended sediment concentration data that were available for each site (http://www.gcmrc.gov/products/other_data/gcmrc.aspx) to develop a metric of turbidity (MT) that represented the number of observations in the 30 d prior to macroinvertebrate collections when silt/clay concentrations were >316 mg/L. The range of MT was 0 (no observations of silt/clay concentrations >316 mg/L) to 2880 (all observations >316 mg/L) (4 measurements/h × 24 h/d × 30 d). We used linear quantile regression to examine changes in % algal resources consumed by each macroinvertebrate taxon (at the 5th, 25th, 50th, 75th, and 95th quantiles) as a function of MT for each site and season over 2.5 y. We tested the hypothesis that the slope of each regression was 0 (no relationship between % algal resources consumed and MT) (Koenker 2005) by estimating 95% CIs for each slope by inverting a quantile-rank score test for each quantile. We used the *quantreg* package in R (Koenker 2010) to run the quantile regression analyses.

We used correlation analysis to assess the degree of correspondence between macroinvertebrate diets and the availability of food resources in the river during the 1st y of sampling. For each of the dominant particle types (diatoms, filamentous algae, amorphous detritus, and leaf material), we examined the relationship between % composition of the particle type in a particular feeding habitat (seston for filter-feeding black flies and epilithic biofilms for the 3 collecting/scraping taxa) and percentages of the particle type in the diets of each taxon at each site and season. For example, we compared % diatoms in the seston at each site during each season to % diatoms in the gut contents of *S. arcticum* collected concurrently. We used Pearson's product–moment correlation coefficient (r) to measure the strength of the linear association between the 2 variables.

We ran statistical analyses with the software package Systat® (version 10.0; SSI San Jose, California) or R (version 2.12.2; R Development Core Team, Vienna, Austria), and Microsoft Excel (Microsoft Corporation, Redmond, Washington).

Results

In the Colorado River downstream of Glen Canyon Dam, macroinvertebrate diets mainly consisted of diatoms, filamentous algae, leaf material, and amorphous detritus. Fungi, macrophyte, animal material, cyanobacteria, and red algae were present in diets, but in low proportions. Overall, location along the river (i.e., in the tailwater reach vs below major tributaries), macroinvertebrate identity, and turbidity influenced diet composition.

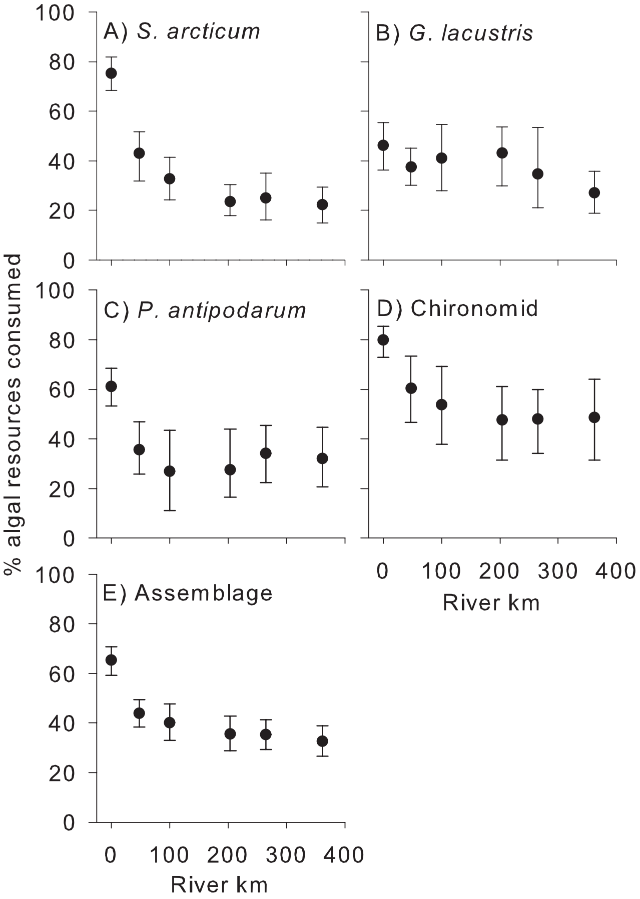

FIG. 2. Mean (± 95% bootstrap CI) % algal resources consumed at each site by *Simulium arcticum* (A), *Gammarus lacustris* (B), *Potamopyrgus antipodarum* (C), chironomids (D), and all taxa (E). The mean % algal resources consumed by each taxon and by the combined assemblage was lower at downstream sites (RKM 48–362) than in the tailwater (RKM 0), but did not differ among downstream sites. Means were calculated over 2.5 y.

Longitudinal trends in macroinvertebrate diets composition

Consumption of algal resources (diatoms + filamentous algae) was higher in the tailwater reach than at sites downstream of tributaries, but the magnitude of difference depended on taxon. *Simulium arcticum* and *P. antipodarum* consumed significantly lower % algal resources at all downstream sites (RKM 48–362) than in the tailwater (RKM 0) (Fig. 2A, C). In contrast, *G.*

lacustris consumed similar % algal resources in the tailwater and at all downstream sites (Fig. 2B). Chironomids consumed lower % algal resources at all downstream sites (RKM 48–362) than in the tailwater (Fig. 2D). However, % algal resources in chironomid diets did not decline significantly until RKM 100 (nonoverlapping CIs, Fig. 2D). As a result of taxon-specific differences, % algal resources in macroinvertebrate diets decreased as distance from RKM 0 increased (Fig. 2E). Specifically, at RKM 0, algal resources made up 65% of macroinvertebrate diets, whereas at downstream sites, algal resources made up 33 (RKM 362) to 44% (RKM 48) of macroinvertebrate diets. Consumption of algal resources did not differ among downstream sites (Fig. 2E). Therefore, we aggregated all downstream sites in subsequent analyses.

Diet comparison among taxa

Percent algal resources consumed differed among taxa in the tailwater ($F_{3,39} = 13.145$, $p < 0.001$) and at downstream sites ($F_{3,194} = 11.177$, $p < 0.001$). Chironomids consumed higher % algal resources than the other taxa. In the tailwater, chironomids consumed significantly higher % algal resources than *G. lacustris* and *P. antipodarum* (Tukey's HSD, $p < 0.001$ and $p = 0.015$, respectively), and *S. arcticum* consumed significantly higher % algal resources than *G. lacustris* (Tukey's HSD, $p < 0.001$). At downstream sites, chironomids consumed significantly higher % algal resources than *S. arcticum*, *G. lacustris*, and *P. antipodarum* (Tukey's HSD, $p < 0.001$, $p = 0.006$, $p < 0.001$, respectively), but % algal resources consumed did not differ among the other taxa (Tukey's HSD, $p > 0.199$).

Influence of turbidity on diet

The extent to which macroinvertebrate diets differed among turbidity conditions depended on macroinvertebrate identity. In general, diets contained more amorphous detritus and leaf material and fewer diatoms under turbid conditions. *Simulium arcticum*, *P. antipodarum*, and chironomid diets contained higher % amorphous detritus ($F_{2,62} = 39.9$, $p < 0.001$, $F_{2,51} = 10.8$, $p \leq 0.001$; $F_{2,60} = 10.0$, $p \leq 0.001$, respectively) and leaf material (*S. arcticum*: $F_{2,62} = 7.6$, $p < 0.024$; *P. antipodarum*: $F_{2,51} = 4.3$, $p = 0.014$) and lower % diatoms ($F_{2,62} = 37.8$, $p < 0.001$; $F_{2,51} = 10.7$, $p \leq 0.001$; $F_{2,60} = 4.8$, $p < 0.039$, respectively) during either moderate- or high-turbidity conditions than low-turbidity conditions (Fig. 3A, C, D). *Simulium arcticum* was the only taxon whose diet differed between moderate- and high-turbidity conditions, and their diets contained significantly more amorphous detritus during high-turbidity conditions than during moderate-turbidity conditions ($F_{2,62} = 39.9$, $p = 0.011$; Fig. 3A). In contrast to the other taxa, *G. lacustris* diets differed significantly only between low- and high-turbidity conditions. Their diets contained significantly higher % diatoms during low- than during high-turbidity conditions ($F_{2,56} = 4.2$, $p = 0.027$; Fig. 3B).

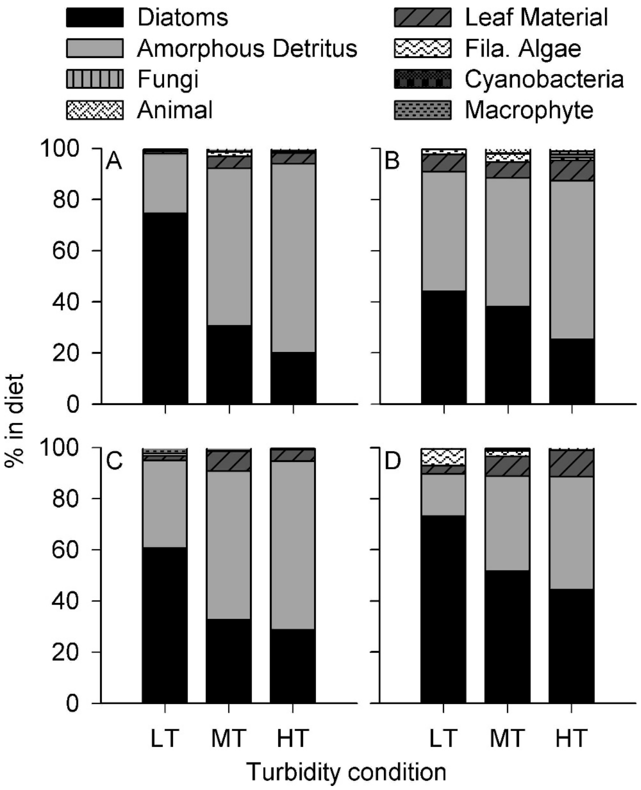

FIG. 3. Percentages of particle types in diets of *Simulium arcticum* (A), *Gammarus lacustris* (B), *Potamopyrgus antipodarum* (C), and chironomids (D) during low-turbidity (LT), moderate-turbidity (MT), and high-turbidity conditions (HT). Macroinvertebrate diets consisted of higher proportions of algal resources during LT conditions than during MT and HT conditions. Fila. = filamentous.

Drivers of patterns in diet composition

Macroinvertebrates consumed lower % algal resources during seasons and years with higher MT values (Fig. 4A). Percent algal resources in diets decreased with increasing MT for quantiles 0.05 to 0.95, and rates of decrease were greater for higher quantiles (Fig. 4A, B). The slopes of quantiles >0.35 were steeper (−0.02 to −0.01) than the slopes for quantiles 0.05 to 0.25, which approached 0 (−0.008 to −0.003) (Fig. 4B). The variations in slope as a function of quantile showed that factors other than turbidity controlled macroinvertebrate algal consumption in

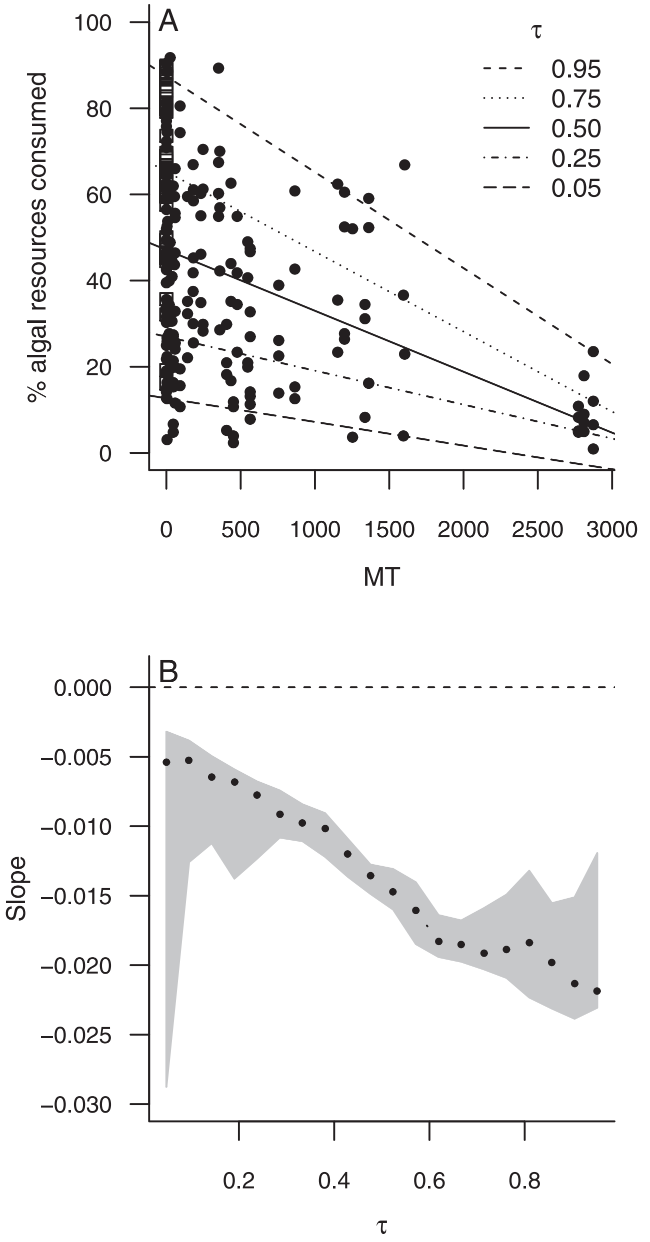

FIG. 4. A.—Quantile regression of % algal resources consumed as a function of turbidity. Percent algal resources in macroinvertebrate diets was negatively related to the metric of turbidity (MT) for quantiles 0.05 to 0.95. MT is the number of observations in the 30 d prior to sampling when silt/clay concentrations were >316 mg/L and when gross primary production was ~0. Samples were collected seasonally at 6 sites over 2.5 y (n = 241). Solid and dashed lines correspond to 0.95, 0.75, 0.5, 0.25, and 0.05 linear regression quantile (τ) estimates. Open squares represent RKM 0. Solid circles represent downstream sites. B.—Slope of quantile regression as a function of quantiles (τ = 0.05–0.95). Shaded area represents 95% confidence intervals of the slopes testing the H_O:slope = 0. The dashed line shows slope = 0.

low-turbidity conditions. However, at high turbidity levels, macroinvertebrates ate little algal material (Fig. 4A, B).

Diets relative to resource availability

Macroinvertebrate diet proportions generally followed patterns of food resource availability across space and time. For example, the percentages of diatoms and amorphous detritus in the seston were positively related to the percentages of diatoms and amorphous detritus in the diets of the filtering *S. arcticum* (Fig. 5A, B). However, percentages of other components of the seston, such as leaf material and filamentous algae, were not related to percentages in *S. arcticum* diets (Table 1). Percentages of diatoms and amorphous detritus in *G. lacustris, P. antipodarum*, and chironomid diets were positively related to the percentages of these resources in the epilithon (Fig. 5C–H). In addition, the percentage of leaf material in *P. antipodarum* diets was positively related to the percentage in the epilithon (Table 1).

RPA

Seasonal and longitudinal patterns of resources assimilated by macroinvertebrates were similar to patterns for diets. Algae-based food resources (algae-derived amorphous detritus + diatoms + filamentous algae) dominated trophic support of macroinvertebrates throughout the year in the tailwater, whereas both algal and terrestrial (terrestrially derived amorphous detritus + leaf material) resources were assimilated by macroinvertebrates at downstream sites. Specifically, in the tailwater, 97 to 99% of resources assimilated by *S. arcticum*, *G. lacustris*, *P. antipodarum*, and chironomids were algae-based (Fig. 6A). In contrast, at downstream sites, 52 to 72% of resources assimilated by macroinvertebrates were algal and 24 to 43% were terrestrial (Fig. 6B).

Discussion

Macroinvertebrate diets tracked downstream changes in resource availability in the Colorado River. Diets contained greater percentages of algal resources in the tailwaters of Glen Canyon Dam and more terrestrial resources downstream. Diet percentages and RPAs of terrestrial resources by macroinvertebrates were highest during late-summer monsoons when tributaries flooded. By examining macroinvertebrate diets in a large regulated river that undergoes dynamic changes in organic matter availability, we were able to identify spatial and temporal patterns that may influence their production. The response of

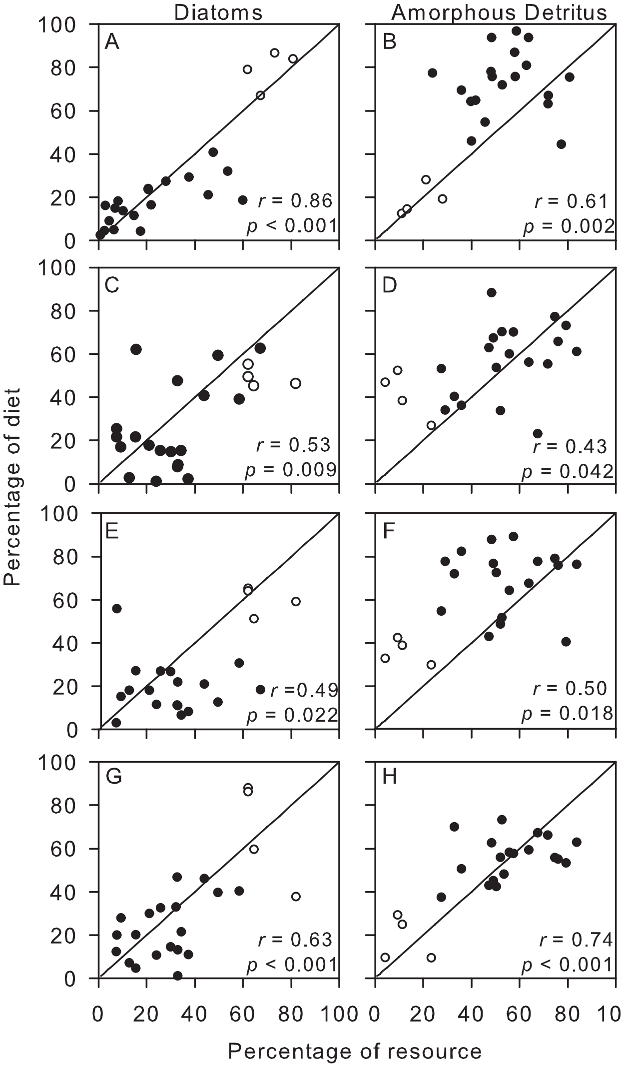

FIG. 5. Mean percentages of particle types—diatoms (A, C, E, G) and amorphous detritus (B, D, F, H)—composing an available food resource (seston or epilithon) vs the mean percentage of the particle type in the diets of *Simulium arcticum* (seston) (A, B), *Gammarus lacustris* (epilithon) (C, D), *Potamopyrgus antipodarum* (epilithon) (E, F), and chironomids (epilithon) (G, H) at each site during each season. Percentages in the diet tracked the availability of resources in the seston and epilithon at RKM 0 (open circles) and downstream sites (solid circles). Pearson product–moment correlation coefficients (r) and associated p-values are given. Line represents the line of equity (one-to-one relationship).

riverine food webs to large dams and the extent of serial discontinuity associated with these dams may be temporally dynamic, especially in regions with variable precipitation regimes (e.g., monsoonal rains). Our results support the Serial Discontinuity Concept and illustrate the spatial responses originally predicted by Ward and Stanford (1983). In addition, our findings demonstrate that the spatial pattern in diets were consistent throughout the year despite temporal changes in diets at these sites because of seasonal flooding.

Our results agree with those of foodweb studies in the Colorado River in which diet or stable-isotope analyses were used to characterize trophic relations. Pinney (1991) found that diatoms made up >93% of the diet for *G. lacustris*, but his study was restricted to the tailwater reach. Stevens et al. (1997) found that % diatoms in the diets of Chironomidae larvae decreased with distance from the dam—from a high of 61% in the tailwater to a low of 8% at a site 386 km downstream of the dam—but their study spanned only a single season. Angradi (1994) used stable-isotope analyses to study trophic relations among aquatic macroinvertebrates and found that algal resources supported macroinvertebrates in the Glen Canyon tailwater, whereas terrestrial resources supported macroinvertebrates in downstream tributaries. We used gut-content analysis from multiple seasons and years to show that macroinvertebrates relied on a combination of algae and tributary-derived resources and that tributary inputs drove patterns of resources consumed along the river.

Macroinvertebrate diet patterns in the Colorado River probably were a result of differences in food acquisition and relative availability of resources. Diets of the filtering *S. arcticum* were positively correlated with seston composition, as has been found by other investigators (Erman and Chouteau 1979, Hart and Latta 1986, Hart 1987). In addition, the composition of *S. arcticum* diets suggested they consumed tributary-derived resources, and as such, these filtering organisms may benefit from increased seston concentrations. However, seston quality can vary considerably in large rivers (Rosi-Marshall and Meyer 2004), and further research on the relative influence of seston quantity vs quality on macroinvertebrate growth is warranted. Moreover, seston from reservoirs may make up a large proportion of the food resources for filter feeders downstream of dams (Richardson and Mackay 1991, Voelz and Ward 1996, Doi et al. 2008). The diets of *S. arcticum* collected in the tailwater reach contained a large percentage (~60%) of a reservoir-derived planktonic diatom, *Fragilaria crotonensis* (Wellard Kelly 2010). However, the percentage of *F. crotonensis* among diatoms in the diets of *S. arcticum* collected at downstream sites was <16% (Wellard Kelly 2010).

Gammarus lacustris diets tracked available resources in epilithic biofilms, and they consistently ate diatoms regardless of site and season, except during high-turbidity conditions when the % diatoms in their diet decreased. *Gammarus* species are omnivorous

TABLE 1. Results of correlation analyses examining the relationship between the % composition of a particle type in the seston or epilithon and the % of each particle in the diets of each taxon. DIA = diatoms, AD = amorphous detritus, LM = leaf material, FA = filamentous algae. *r* = Pearson product–moment correlation coefficient and associated *p*-value.

			Particle type			
Food resource	Taxon	Statistic	DIA	AD	LM	FA
Seston	*Simulium arcticum*	*r*	0.861	0.607	0.074	0.023
		p	<0.001	0.002	0.737	0.918
Epilithon	*Gammarus lacustris*	*r*	0.531	0.428	−0.199	−0.163
		p	0.009	0.042	0.362	0.456
Epilithon	*Potamopyrgus antipodarum*	*r*	0.487	0.500	0.789	0.405
		p	0.022	0.018	<0.001	0.062
Epilithon	Chironomid	*r*	0.632	0.742	0.310	0.214
		p	<0.001	<0.001	0.149	0.326

(MacNeil et al. 1997), and because they can move upstream by swimming and crawling along substrates (Hughes 1970), they are not constrained to feeding in one habitat. *Cladophora glomerata* dominates the epilithon of the tailwater of Glen Canyon Dam and is the preferred habitat of *G. lacustris* (Shannon et al. 1994) possibly because epiphytic diatoms are a preferred food resource (Pinney 1991, Shannon et al. 1994, Wellard Kelly 2010). Downstream, *G. lacustris* inhabits cliff faces, root wads associated with undercut banks, macrophytes and bryophytes, reeds and sedges, such as *Phragmites australis* and *Carex aquatilis*, and rarely cobble bars (HAWK, unpublished data). *Gammarus lacustris* can use a variety of habitats to feed selectively on preferred resources (Bärlocher 1985, Arsuffi and Suberkropp 1989, Friberg and Jacobsen 1994), which may explain the higher percentage of algal resources in their diets downstream during moderate-turbidity conditions.

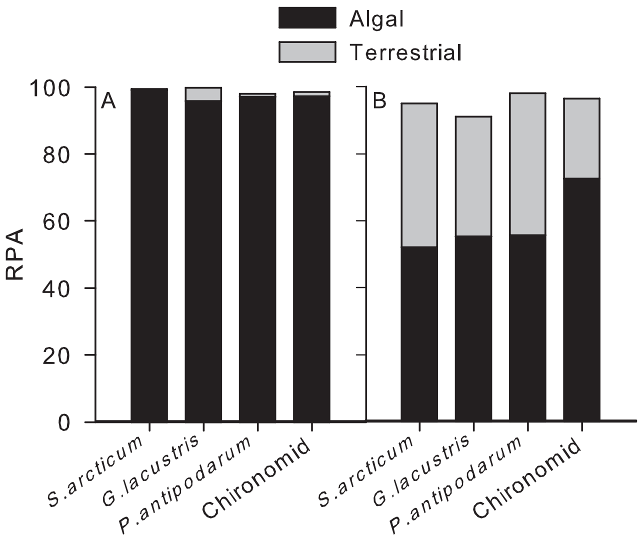

FIG. 6. Mean % of algal (diatoms + filamentous algae + autochthonously derived amorphous detritus) and terrestrial (leaf material + allochthonously derived amorphous detritus) resources assimilated (RPA) by *Simulium arcticum*, *Gammarus lacustris*, *Potamopyrgus antipodarum*, and chironomids in tailwater (A) and at downstream sites (B). Mostly algal resources were assimilated by macroinvertebrates in the tailwater, and both terrestrial and algal resources were assimilated by macroinvertebrates at downstream sites. Means were calculated over 2.5 y for all 4 seasons.

In the Colorado River, *P. antipodarum* diets tracked changes in epilithon resource availability. For example, in the low-turbidity tailwater, algae made up a high percentage of their diets. In contrast, at downstream sites, the % algae in their diets was related to the availability of algae in the epilithon and was reduced by higher-turbidity conditions. The low availability of algae downstream may explain the low abundance and production of *P. antipodarum* at downstream sites (HAWK, unpublished data, WFC, CVB, EJRM, ROH, TAK, K. C. Donner [Little Traverse Bay Bands of Odawa Indians], S. E. Z. Seegert [Loyola University], HAWK, and K. E. Behn [US Geological Survey], unpublished data). *Potamopyrgus antipodarum* are facultative scrapers that feed on epilithic biofilms and eat a variety of resources including diatoms, green algae, and plant and animal detritus (Haynes and Taylor 1984). This snail thrives in autochthonous-based ecosystems (Hall et al. 2006) because algae are a higher-quality food resource than terrestrial material (Fuller and Mackay 1981).

Chironomid diets tracked the composition of epilithic biofilms, and chironomids consistently consumed the highest proportions of algal resources compared to other taxa although terrestrial resources increased in their diets downstream. Chironomids are most commonly classified as collector-gatherers, but they are opportunistic omnivores that use multiple feeding modes and typically rely on a variety of resources (Berg 1995, Henriques-Oliveira et al. 2003, Ferrington et al. 2008). The ability of chironomids to find and eat algal resources may explain their higher biomass and production at downstream sites relative to *P. antipodarum* and *G. lacustris* (Stevens et al. 1997, WFC, CVB, EJRM, ROH, TAK, K. C. Donner, S. E. Z. Seegert, HAWK, and K. E. Behn, unpublished data). We did not examine ontogenetic and species-specific variation in diets, which may also affect the biomass and production of chironomids in the river.

The extent of turbidity in the Colorado River, as measured by MT, explained some of the variability in macroinvertebrate diets. MT and macroinvertebrate algal consumption were negatively related. At low MT, consumption of algal resources was highly variable, possibly because of the greater variability of algal resources during low-turbidity conditions. The concentration of suspended sediments and turbidity in the river reduces water clarity, light levels, and gross primary production (Yard 2003, Hall et al. 2010). Therefore, during periods with lower MT values and higher rates of primary production, algal resources probably will support a large proportion of macroinvertebrate production. Our findings demonstrate that river-wide changes in turbidity influenced macroinvertebrate diets, which may in turn affect macroinvertebrate secondary production. This relationship may have substantial foodweb consequences because macroinvertebrates are the dominant food resource supporting fish production (WFC, CVB, EJRM, ROH, TAK, K. C. Donner, S. E. Z. Seegert, HAWK, and K. E. Behn, unpublished data).

The types of food resources available in rivers vary longitudinally (Vannote et al. 1980), and these downstream changes can be pronounced below large dams (Stanford and Ward 2001). Therefore, longitudinal changes in the quality of food resources available to and consumed by macroinvertebrates may influence their growth and production (Bird and Kaushik 1984, Rosi-Marshall and Wallace 2002). Algal material is more easily assimilated than terrestrial detritus (Bärlocher and Kendrick 1975, McCullough et al. 1979). Thus, shifts in resource availability may alter macroinvertebrate production. In addition to changes in the relative amounts of terrestrial vs algal resources, the quality of terrestrial resources can vary seasonally and longitudinally. For example, microbial colonization of terrestrial resources in the tributaries may increase quality by adding microbes as a food resource or decrease quality by processing the resource, resulting in more recalcitrant material (Short and Smith 1989, Abelho 2001, Graça and Canhoto 2006). Last, a common food resource for macroinvertebrates in many rivers, including the Colorado, is amorphous detritus (Benke and Wallace 1997, Rosi-Marshall and Wallace 2002). The source (i.e., algal vs terrestrial) of this material may affect its quality and digestibility (Rosi-Marshall and Meyer 2004). The high availability of amorphous detritus and the large amounts found in diets may compensate for its variable nutritional quality.

Recovery of rivers below dams has been assessed by examining how properties such as temperature, flow, and species distributions change as distance from the dam increases (Ward and Stanford 1983). Dam size, operation, and location along a river continuum combined with the size, number, and discharge of unregulated tributaries may influence river recovery from dams (Ward and Stanford 1995, Stanford and Ward 2001). However, some rivers downstream of dams may never recover (Stevens et al. 1997, Stanford and Ward 2001). For example, in Grand Canyon, temperature, discharge, and macroinvertebrate species richness does not recover before the river encounters the next reservoir (~400 km downstream) (Stevens et al. 1997, Stanford and Ward 2001). However, if we expand the definition of recovery to include turbidity and reliance on tributary resources, our conclusions may differ. During certain times of year, the Colorado River downstream of the major tributaries has similar turbidity to the predam river and macroinvertebrates eat terrestrial resources that may be more akin to resources that supported predam macroinvertebrates than the resources that support them now. However, the combination of the macroinvertebrates now present in the postdam river, limited algal availability at downstream sites, and physical factors (e.g., water temperature and discharge) probably limits overall recovery of macroinvertebrates in the Colorado River below Glen Canyon Dam (Stevens et al. 1997, WFC, CVB, EJRM, ROH, TAK, K. C. Donner, S. E. Z. Seegert, HAWK, and K. E. Behn, unpublished data). As a consequence, dam management actions that alter temperature, sediment, habitat, and the availability of high-quality food resources (e.g., sediment augmentation and a selective withdrawal device for temperature mitigation) have the potential to influence macroinvertebrate production in the Colorado River.

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