Ecological Monographs, 83(3), 2013, pp. 311–337
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Food-web dynamics in a large river discontinuum

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Abstract. Nearly all ecosystems have been altered by human activities, and most communities are now composed of interacting species that have not co-evolved. These changes may modify species interactions, energy and material flows, and food-web stability. Although structural changes to ecosystems have been widely reported, few studies have linked such changes to dynamic food-web attributes and patterns of energy flow. Moreover, there have been few tests of food-web stability theory in highly disturbed and intensely managed freshwater ecosystems. Such synthetic approaches are needed for predicting the future trajectory of ecosystems, including how they may respond to natural or anthropogenic perturbations.

We constructed flow food webs at six locations along a 386-km segment of the Colorado River in Grand Canyon (Arizona, USA) for three years. We characterized food-web structure and production, trophic basis of production, energy efficiencies, and interaction-strength distributions across a spatial gradient of perturbation (i.e., distance from Glen Canyon Dam), as well as before and after an experimental flood. We found strong longitudinal patterns in food-web characteristics that strongly correlated with the spatial position of large tributaries. Above tributaries, food webs were dominated by nonnative New Zealand mudsnails (62% of production) and nonnative rainbow trout (100% of fish production). The simple structure of these food webs led to few dominant energy pathways (diatoms to few invertebrate taxa to rainbow trout), large energy inefficiencies (i.e., <20% of invertebrate production consumed by fishes), and right-skewed interaction-strength distributions, consistent with theoretical instability.

Below large tributaries, invertebrate production declined ~18-fold, while fish production remained similar to upstream sites and comprised predominately native taxa (80–100% of production). Sites below large tributaries had increasingly reticulate and detritus-based food webs with a higher prevalence of omnivory, as well as interaction strength distributions more typical of theoretically stable food webs (i.e., nearly twofold higher proportion of weak interactions). Consistent with theory, downstream food webs were less responsive to the experimental flood than sites closest to the dam. We show how human-induced shifts to food-web structure can affect energy flow and interaction strengths, and we show that these changes have consequences for food-web function and response to perturbations.

Key words: ecotrophic efficiencies; energetics; food-web stability; Glen Canyon Dam, Colorado River; interaction strengths; organic-matter flows; regulated river; secondary production; species interactions; trophic basis of production.

Introduction

There are virtually no ecosystems free from human alteration (Vitousek et al. 1997*a*, Vörösmarty et al. 2010). Widespread agriculture, forestry, and urbanization have led to strong demands on our water, energy, and mineral resources. These demands have resulted in novel landscapes that now harbor only a subset of historic flora and fauna, and support increasing numbers of invasive species (Vitousek et al. 1997*b*, Poff et al. 2007, Strayer 2010, Cardinale et al. 2012).

Manuscript received 6 October 2012; revised 9 February 2013; accepted 28 February 2013. Corresponding Editor: K. O. Winemiller.

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Large human-induced changes to the structure of ecological communities can modify how energy and materials flow in ecosystems (Jones and Lawton 1995, Chapin et al. 2000). These modifications occur because species interactions and ecological efficiencies at the consumer–resource interface fundamentally control how energy and materials flow, and can limit consumer growth and productivity, as well as patterns of species dominance and food-web stability (McCann 2000, Sterner and Elser 2002). In human-dominated ecosystems where species deletions and additions have occurred, assemblages may comprise interacting species that have not co-evolved (Hobbs et al. 2006), and missing or new links in the food web may lead to large energy inefficiencies, changes in energy pathways that support top predators, and destabilizing food-web characteristics (Vander Zanden et al. 1999, Pauly et al. 2002, Sherwood et al. 2002). Predicting how these novel assemblages will respond to perturbations will benefit from a food-web perspective that quantifies the identities, magnitudes, and strengths of trophic interactions across space and time (Polis and Strong 1996, Vander Zanden et al. 2006).

Dams and flow regulation affect most rivers globally (Nilsson et al. 2005, Sabo et al. 2010, Vörösmarty et al. 2010). Ever-increasing use and redistribution of water resources have altered river flow, temperature, and sediment regimes (Ward and Stanford 1983, Syvitski et al. 2005, Poff et al. 2007, Schmidt and Wilcock 2008, Olden and Naiman 2010). As a consequence, river assemblages and ecosystem processes have been greatly modified (Power et al. 1996, Bunn and Arthington 2002, Dudgeon et al. 2006), and many aquatic species are currently imperiled (Ricciardi and Rasmussen 1999, Strayer and Dudgeon 2010). River assemblages below dams commonly shift towards dominance by taxa that can tolerate the new physical regime and local extinction of those that cannot (Minckley 1991, Lytle and Poff 2004, Olden et al. 2006). In many cases, nonnative taxa that fill vacant niches or lack effective predators thrive and may dominate biomass and production (e.g., Marchetti and Moyle 2001, Olden et al. 2006, Cross et al. 2010). Changes to the physical regime may also fundamentally alter the river's energetic basis, with a trend towards algal production as the dominant fuel for food webs (e.g., Ward and Stanford 1983, Stevens et al. 1997, Davis et al. 2011), particularly in river segments directly below large dams (i.e., tailwaters).

Despite a long history of research describing the effects of flow regulation on river ecology (e.g., Ward and Stanford 1979, Lillehammer and Saltveit 1984), little progress has been made in examining how changes to ecological structure affect the function and dynamics of river food webs. In particular, few studies have quantified the effects of river discontinuities on integrative ecological measures such as the trophic basis of secondary production or the sources and dominant pathways of energy flow in food webs (e.g., Cross et al. 2011). Moreover, relatively few attempts have been made to test predictions based on food-web theory with detailed empirical research in human-altered ecosystems. However, it is precisely this reconciliation between theory and empirical research that will be necessary for understanding and managing human-altered ecosystems into the future (Power et al. 1996, Thompson et al. 2012).

We constructed organic-matter flow food webs at six sites along a 386-km segment of the Colorado River in Glen and Grand Canyon for three years. This effort allowed us to produce a detailed empirical assessment of food-web structure and function at increasing distances from Glen Canyon Dam, the location of greatest human modification. We had two overarching objectives in this study. First, we sought to quantify longitudinal patterns in animal production, trophic basis of production, and the identities, patterns, and magnitudes of species interactions, particularly between fishes and their invertebrate prey. Because our sites were located above and below major tributaries that input large amounts of sediment and organic matter, we predicted that food webs would shift towards higher reliance on detritus-based pathways, higher dominance of native fish taxa, and more efficient use and transfer of energy from invertebrates to fishes at sites below large tributaries. In essence, we predicted that food webs downstream of tributaries would begin to exhibit characteristics more typical of large unregulated river ecosystems in the region.

Our second main objective was to confront theoretical predictions about food-web "stability" with a large empirical data set. A rich body of theory has demonstrated that certain characteristics of food webs may confer long-term stability, defined here as a continuous metric that measures the long-term persistence of interacting species (see McCann 2000, Rooney and McCann 2012). For example, theoretical studies have shown that persistence is associated with a larger proportion of weak trophic interactions (e.g., McCann et al. 1998), a moderate level of omnivory (e.g., Emmerson and Yearsley 2004, Gellner and McCann 2012), and incorporation of detritus or the coupling of "fast" and "slow" energy channels (e.g., DeAngelis et al. 1989, Polis and Strong 1996, Rooney et al. 2006). We predicted that our empirical food webs would exhibit characteristics of low stability near Glen Canyon Dam, with increasing evidence of stability downstream, below large tributaries. We also had the opportunity to assess food-web stability in response to an experimental flood released from Glen Canyon Dam in March 2008. Based on the longitudinal food-web patterns, we predicted that assemblages closest to the dam would be least resistant to perturbations and would show the largest relative change in secondary production in response to the flood.

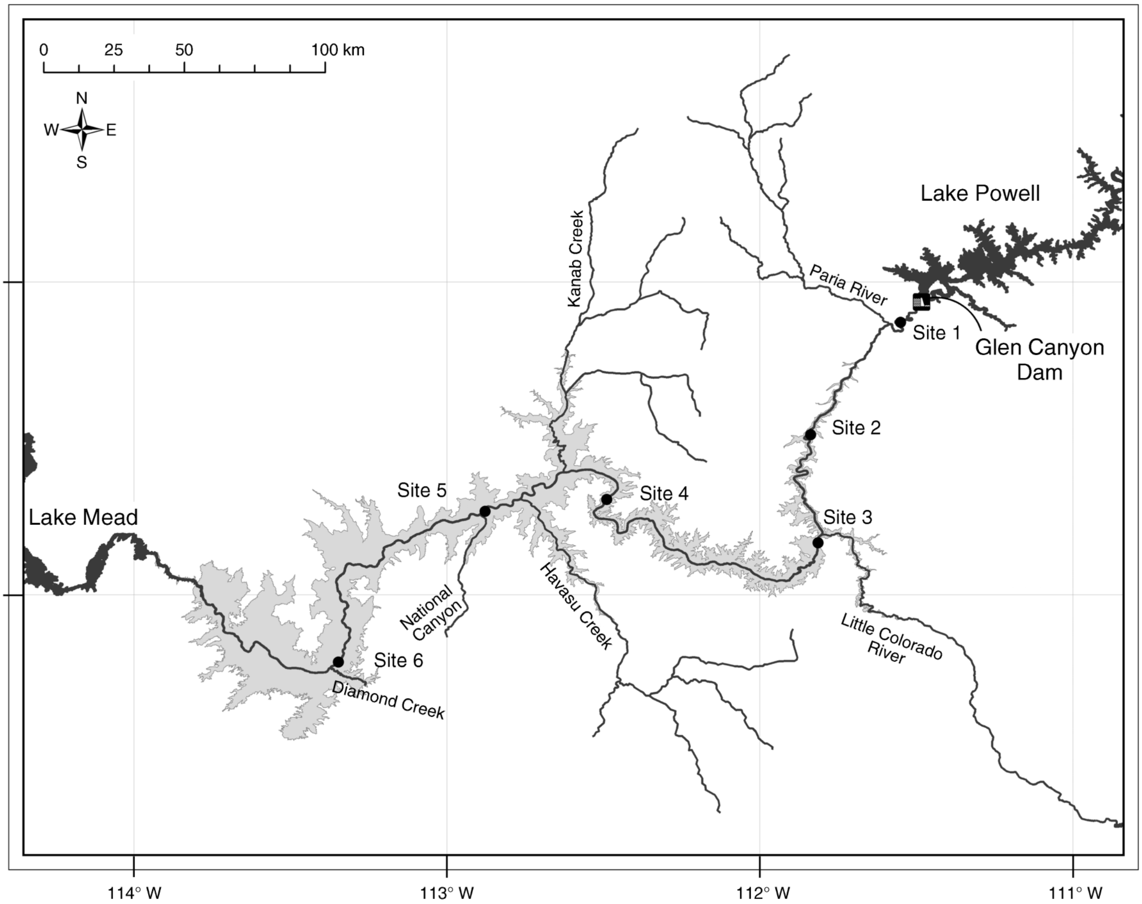

FIG. 1. Map of the Colorado River in Arizona, USA, showing Glen Canyon Dam, sampling locations (sites 1–6), and dominant tributaries.

SITE DESCRIPTION

The Colorado River watershed drains a large area (~629 000 km^2) of the western United States on its path toward the Gulf of California. Six major dams regulate flow in the lower Colorado River basin (i.e., downstream of Lake Powell), and the timing and magnitude of discharge is now largely determined by fluctuating demand for irrigation water and electric power (Topping et al. 2003). Glen Canyon Dam, completed in 1963, has severely altered flow, temperature, and sediment delivery (Stevens et al. 1997, Howard and Dolan 1981, Gloss et al. 2005), changing the river ecosystem and allowing establishment and proliferation of many nonnative taxa (e.g., Blinn and Cole 1991, Stevens et al. 1997, Cross et al. 2010). Below Glen Canyon Dam, the Colorado River travels 472 km through Glen Canyon and Grand Canyon before entering the next major reservoir, Lake Mead. Although more than 750 ephemeral and perennial tributaries enter the mainstem along this path (Webb et al. 2000), two of them—the Paria River and the Little Colorado River (LCR)—contribute over 90% of the annual fine-sediment load to the mainstem (Topping et al. 2000). However, the present-day fine-sediment inputs to Grand Canyon represent only 16% (~3.6 million metric tons [Mg]) of pre-dam inputs (~23 million Mg/yr; Topping et al. 2000).

Study location

We studied six sites between Glen Canyon Dam and Lake Mead (Fig. 1; see Plate 1) that we chose to capture key geomorphic and biotic characteristics that broadly represent this stretch of river. Sites were also located in segments that contained long-term physical (i.e., discharge and sediment transport; data *available online*)[10] and biological (i.e., fish population estimates) data. Site 1 was our upstream tailwater site that spanned the 25-km river segment in Glen Canyon directly below the dam. This site had relatively cold temperatures, minimal variability in temperature, and low concentrations of suspended silt and clay. Average flow during the study period at site 1 was 370 m^3/s. Site 2 was located 73 km below the dam and downstream of the Paria River tributary. This site was also relatively cold and variably

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[10] http://www.gcmrc.gov/discharge_qw_sediment/

turbid as a result of sediment inputs during Paria River floods. Site 3 was located 125 km below the dam, just below the confluence of the LCR. This site was usually turbid as a result of material inputs from upstream tributaries; suspended silt and clay concentrations were generally higher at site 3 than site 2. Sites 4, 5, and 6 were located at 229 km, 290 km, and 387 km downstream of the dam, respectively. While temperature increased with distance downstream (site 1 maximum, 13.6°C and site 6 maximum, 18.7°C; Appendix A), suspended silt and clay concentrations were generally similar at sites 3 through 6, reflecting a minimal increase in cumulative watershed area downstream of the LCR. The length of the study reach at each site varied (range, 7 to 21 km), but multiple units of the dominant habitat types were sampled. Additional site description can be found in Stevens et al. (1995, 1997) and Gloss et al. (2005).

In March 2008, during our study, the Department of Interior released a controlled flood from Glen Canyon Dam (Melis et al. 2010, Cross et al. 2011). Water flowed through bypass tubes in Glen Canyon Dam for 60 hours to elevate discharge to $\sim$1200 m^3/s. This flood produced discharge that was roughly 4 times background, but the magnitude was only $\sim$50% of the average annual predam flood (Topping et al. 2003).

METHODS

Physical characteristics

We monitored water temperature at 15-minute intervals at each site using either HOBO temperature loggers or YSI water quality sondes (Voichick and Wright 2007). Total suspended silt and clay was also monitored at 15-minute intervals at a subset of sites (sites 1, 2, and 6) using sideways-looking acoustic-Doppler profilers (Topping et al. 2007). Suspended silt and clay estimates for site 3 were derived from a sediment monitoring station located 42 km downstream of this site, a river segment with no major tributary inputs. Thus, this station represents a reasonable proxy for site 3. Water temperature, river discharge, and suspended solids data can be downloaded (see footnote 10).

Invertebrate abundance, biomass, and secondary production

We quantitatively sampled invertebrates at each site between July 2006 and June 2009. We sampled sites 1 and 6 monthly because these sites were accessible by road and they bracketed the range of longitudinal conditions. For the remaining sites, 2 through 5, we conducted quarterly sampling because they were only accessible by launching two-week-long river trips that traveled through Grand Canyon. At each site we sampled the three predominant habitat types, which included cobble/gravel bars, talus/cliff faces, and sandy depositional zones (hereafter referred to as cobble–gravel, talus–cliff, and depositional). The number of samples collected from each habitat on each date was roughly proportional to their areal contribution based on our habitat area estimations (see *Habitat area estimation,* below). From each site on each date we collected a total of 18 to 20 benthic samples. Dam operations generate daily "tides" that produce a varial zone (the near-shore area that is wet and dry over a 24-h period in response to hydropower flows from the dam) on the river shoreline that is dry for large portions of the day and represents habitat that is not fully colonized by benthic macroinvertebrates (Stevens et al. 1997). Therefore, we collected benthic samples during minimum daily discharge to ensure that samples were collected from the permanently wetted zone (Blinn et al. 1995).

We used two different methods to sample cobble–gravel habitat because of large increases in cobble embeddedness and size with distance downstream. At site 1 we used a Hess sampler (0.085 m^2, 250-μm mesh size) to collect benthic material to a depth of $\sim$10 cm. At all other sites, we removed individual cobbles by hand, scrubbed the surfaces with a brush into a bucket with water, and poured the bucket contents onto a 250-μm sieve. This method was effective because the fauna from this habitat were largely sessile and not easily disturbed by this approach. To test this assumption, at the beginning of the study we held a drift net below cobble that were removed and found that the number of invertebrates dislodged was negligible relative to the total. We photographed each cobble next to laminated graph paper to estimate planar surface area with digital image analysis (ImagePro Plus; Media Cybernetics, Bethesda, Maryland, USA). We sampled talus–cliff habitat with a custom suction device that consisted of a battery-powered submersible bilge pump connected to a pool hose, a Nitex mesh bag (250-μm mesh), and a meshed retaining cup. Each suction sample comprised 30 pooled sequential intakes totaling a sample area of 0.066 m^2. Depositional habitat was sampled with a standard Ponar dredge sampler (0.052 m^2) deployed from a motorboat.

We preserved benthic samples in the field using 95% ethanol and brought them to the laboratory for subsequent processing. We rinsed each sample onto nested sieves (pore sizes 1 mm and 250 μm) and elutriated retained sample to separate organic from inorganic material. All invertebrates were removed from the large fraction (>1 mm) at 10× magnification, counted, and total body length measured (nearest 1 mm) of the first 30 individuals encountered of each taxon. Prohibitively large samples were subsampled using a device modeled after the Folsom Plankton Splitter (Wildco, Buffalo, New York, USA). Organic material in the smaller fraction (i.e., <1 mm and >250 μm) was placed into a known volume of water, suspended in a modified Imhoff cone (Wards Natural Science, Rochester, New York, USA) with forced air, and subsampled (by volume) with a 60-mL plastic syringe. Invertebrates in subsamples were removed at

15× magnification, counted, and measured to the nearest 1 mm (first 30 encountered of each taxon). Individuals counted but not measured were assumed to have the same size distribution as those that were directly measured on that date. Biomass of each taxon was calculated using either length–mass relationships developed for Glen Canyon or previously established literature-based relationships (Benke et al. 1999, Cross et al. 2010; U.S. Geological Survey Grand Canyon Monitoring and Research Center, Flagstaff, Arizona, USA, *unpublished data*).

We estimated annual secondary production (g AFDM [ash-free dry mass]$\cdot$m$^{-2}\cdot$yr^{-1}) of invertebrate taxa using methods most appropriate for each taxon (Benke 1993, Benke and Huryn 2006). We used the instantaneous growth method to quantify production of New Zealand mudsnails (*Potamopyrgus antipodarum*) and amphipods (*Gammarus lacustris*) by applying empirically derived size-specific growth rates from site 1 (*Potamopyrgus* growth (d^{-1}) = $-0.006 \times$ shell length (mm) + 0.029; *Gammarus* growth (d^{-1}) = $-0.016 \times \ln$(body length [mm]) + 0.042; Cross et al. 2010). We also used the instantaneous growth method to estimate production of dominant Oligochaeta taxa using either literature-based size-specific growth rates (Lumbricidae; Barne and Striganova 2005) or application of a constant daily growth rate (0.0095 d^{-1}) derived from Poddubnaya (1980; initial and final body size [3 and 23 mm] and a maturation time of 7.5 months; Tubificidae; estimate based on moderate density and temperature). We corrected predicted growth rates for downstream changes in temperature by using a Q_{10} value of 2. ("Q_{10}" is a unitless factor that describes the rate of change in a biological or chemical system in response to a temperature increase of 10°C.) For Chironomidae, we used the size- and temperature-specific equation of Huryn (1990). This equation, based on a different geographic region, may have led to error in our production estimates. However, large variability in biomass across samples and dates (>1000-fold) far exceeded the variation in individual growth rates for Chironomidae reported in the literature. For other dominant taxa with overlapping and/or indistinguishable cohorts, we used the size–frequency method corrected with our best estimate of cohort production interval (CPI) based on size frequency data (Hamilton 1969, Benke 1979, Benke and Huryn 2006). For these taxa, downstream CPI values were corrected using the temperature-correction factor derived from the Q_{10} approach. For remaining taxa, we multiplied mean annual biomass values by appropriate production : biomass (P:B) ratios. Error in our production estimates based on the size frequency method or P:B ratios would have a relatively small influence on our results as these taxa composed a small proportion of total assemblage biomass (generally <10%, except site 3 where *Hydroptila arctia* made up 10–20%; Supplement 1).

We used bootstrap and Monte Carlo methods to generate medians and 95% confidence intervals for annual invertebrate abundance, biomass, and production (Manly 1997, Benke and Huryn 2006). Briefly, we resampled with replacement (1000 times) size-specific abundance data from replicate samples in each habitat type on each date to generate vectors of mean size-specific abundance and biomass. For those taxa in which we applied the instantaneous growth method, each of the biomass estimates was multiplied by size-specific growth rates and the time interval between sampling dates to generate 1000 estimates of interval production. These estimates were summed across sampling intervals to generate a vector of annual production. For production estimates that used the size–frequency method, two sources of variation were included in bootstrapped estimates: (1) resampled abundance data and (2) randomly selected CPIs within a restricted range based on size frequency data (e.g., between 335 and 365 days; selected from a normal distribution; temperature-corrected at downstream sites). We first generated vectors of annual abundance, biomass, and production for each taxon in each separate habitat. Habitat-weighted vectors were then produced by multiplying values in each habitat-specific vector by the relative proportion of that habitat per average square meter (see *Habitat area estimation*). Finally, we summed these values across habitats to generate total habitat-weighted vectors. Medians and the 2.5% and 97.5% quantiles were calculated from habitat-weighted vectors to estimate bootstrap 95% confidence intervals. All production computation was carried out in R (R Development Core Team 2010; specific code developed by Benjamin J. Koch: Supplement 2).

Habitat area estimation

We quantified the contribution of each habitat type to total benthic area at each site. At site 1, where visibility was high, we used a motorboat and an underwater video sled to quantify habitat coverage at 48 linear transects between 9.7 and 24 km below Glen Canyon Dam (see Cross et al. [2010] for details). At downstream sites, where visibility did not permit use of the video approach, we used a combination of multi-beam and single-beam bathymetry to estimate the relative proportion of habitat types (M. Polino, P. E. Grams, and T. A. Kennedy, *unpublished manuscript*). The varial zone that was subject to daily inundation and drying was not included in our habitat area estimates.

Fish production

Fish production was quantified on an annual basis during 2007–2008 and 2008–2009, corresponding to the second and third year of invertebrate production data. Intensive sampling of fish size structure and abundance took place at all six sites on 3–4 dates per year. Adults and juveniles of large-bodied species (>150 mm adult length) were sampled in near-shore habitats using methods of the long-term fish monitoring program in Grand Canyon (Makinster et al. 2010). Briefly, fishes were collected after dusk using single-pass electrofishing in 0.16-km-long channel units at each site (15–45 units per site). Abundance was estimated by dividing the number of fish caught in a monitoring segment by species-specific mean capture efficiencies (flannelmouth sucker [*Catostomus latipinnis*] and bluehead sucker [*C. discobolus*], 0.021; rainbow trout [*Oncorhynchus mykiss*], 0.095; brown trout [*Salmo trutta*], 0.09; common carp [*Cyprinus carpio*], 0.06). Species-specific capture efficiencies were derived from prior mark-recapture (R.S. Rogers [Arizona Game and Fish Department], *unpublished data*) and depletion studies (Speas et al. 2004, Coggins et al. 2011) conducted in Glen and Grand Canyons as part of a long-term monitoring program (Gloss et al. 2005). Because capture efficiency for single-pass electrofishing was a large source of error in our estimates of fish abundance, we used a method of resampling data within the 2.5% and 97.5% quantiles of capture efficiency reported by Speas et al. (2004) to generate realistic variation in our estimates of abundance. For most small-bodied fishes (e.g., speckled dace [*Rhinichthys osculus*], fathead minnow [*Pimephales promelas*], red shiner [*Cyprinella lutrensis*], plains killifish [*Fundulus zebrinus*], juvenile trout, and suckers), abundance was calculated by dividing catch estimates by species-specific capture efficiencies (capture efficiencies for most species: 0.09–0.11). For endangered juvenile and adult humpback chub (*Gila cypha*), we used reported status and trend data (1989–2008) estimated from a stock assessment model (Coggins et al. 2006, Coggins and Walters 2009) that corresponded to our study years.

Biomass of individual fish was estimated by applying species-specific length–wet mass regressions and converting to percentage ash-free dry mass (AFDM; R. S. Rogers, [Arizona Game and Fish Department], *unpublished data*; K. C. Donner, *unpublished data*). Mean biomass (g AFDM/m^2) on a given sampling date was calculated using size structure and abundance estimates, as well as riverbed area. Annual secondary production for most species was quantified with the instantaneous-growth method using size-specific instantaneous-growth rates (Busacker et al. 1990) based on size-at-age curves developed for the Colorado River (R.S. Rogers, *unpublished data*). We were not able to develop size-at-age curves for common carp or small-bodied fishes. Production of carp was estimated by applying a relatively conservative net production efficiency of 0.1 to consumption rates, which in this case were estimated based on a gastric evacuation method (rate $= 0.027$ h^{-1}; Kevern 1966, Donner 2011) rather than production (as described in *Food-web analysis*). We used literature-based growth rates to estimate production of small-bodied fishes (Minckley and Klaassen 1969, Robinson and Childs 2001). Due to extremely low captures of channel catfish (*Ictalurus punctatus*) and black bullhead (*Ameiurus melas*), these species were excluded from our analyses.

Food-web analysis

At each site we constructed organic-matter flow food webs that provided annual estimates of energy flow (i.e., consumption), trophic basis of production (i.e., relative and absolute resource assimilation by animals), and interaction strengths. This effort required data on invertebrate and fish secondary production, diet composition, and ecological assimilation and production efficiencies.

Invertebrate diet composition was quantified at each site seasonally from June 2006 to January 2009 ($n = 9$ seasons) using standard gut-contents analysis (Benke and Wallace 1980, Hall et al. 2000; Wellard Kelly et al. 2013). On each sampling occasion at each site, dominant invertebrate taxa were collected haphazardly from multiple habitats and immediately preserved in Kahle's solution (Stehr 1987). The four taxa that were consistently abundant at all sites (*Simulium arcticum*, *Gammarus*, *Potamopyrgus*, and non-Tanypodinae chironomids) were the primary focus of our gut-contents analysis. Other taxa (Lumbricidae, Tubificida, *Hydroptila*) were collected inconsistently across sites and dates, so we applied averaged gut-content proportions (i.e., not site or date specific) to these taxa when and where they were present. Together, the taxa for which we had quantitative gut-contents information represented between 85% and 96% of annual habitat-weighted invertebrate production.

Dissected invertebrate gut contents were sonicated, filtered onto gridded Metricel membrane filters (25-mm diameter, 0.45-μm pore size; Pall Corporation, Ann Arbor, Michigan, USA), and mounted on slides using Type-B immersion oil and nail polish sealant. For the preparation of each slide, we used gut contents of one to four individuals of each taxon. For each sampling date two to four slides of each taxon were analyzed. Approximately 50 food particles from each slide were identified along random transects, and their area was measured using image analysis software (ImagePro Plus; Media Cybernetics, Rockwell, Maryland, USA) and a phase-contrast compound microscope (100×; 400× to confirm difficult identifications) equipped with a digital camera. Particles were categorized as diatoms, filamentous algae, amorphous detritus, leaf material, fungi, macrophytes, or animal material. We calculated the proportion of each food item in the gut by dividing the area of each category by the total area of the 50 particles measured. We also estimated the proportions of amorphous detritus derived from autochthonous (i.e., algal) vs. allochthonous (i.e., terrestrial detritus) sources following Wellard Kelly et al. (2013). Our trophic bases of production calculations, described below, were based on average values from multiple slides.

We quantified diet composition of fishes on six dates between April 2007 and January 2009 (total $n = 1855$).

In general, 10–15 individuals of each of the dominant species were collected at each site during each season. Sample sizes were sometimes smaller for uncommon species ($n = 1$–10; e.g., plains killifish, red shiner). Fishes were collected in parallel with nighttime electrofishing; however, some uncommon species were collected by daytime seining in shallow-water habitats. The entire gut tract of each fish was removed within hours of collection and immediately preserved in 95% ethanol. When possible, gut contents were collected across a range of body sizes to account for possible ontogenetic shifts in diet. To quantify gut contents of endangered humpback chub, we collected individuals using hoopnets set for 2 h, and a non-lethal gastric lavage technique (Stone 2004). This method limited our humpback chub diet samples to individuals >150 mm.

Fish foregut contents were removed in the laboratory and manually separated into categories (i.e., filamentous algae, amorphous detritus/diatom mixture, terrestrial plant material, fish prey, human food, terrestrial invertebrates, and aquatic invertebrates) under a dissecting microscope at 7× to 30× magnification. We further separated aquatic invertebrates into groups that corresponded to the same level of taxonomic resolution as benthic invertebrate samples. Subsequently, invertebrate prey items that were rare in diets were grouped together as "other invertebrate primary consumers" or "other invertebrate predators" for the purpose of constructing flow food webs. Diet categories of each individual were oven-dried at 60°C for 24 h and weighed (g dry mass). Final dietary proportions were based on the relative contributions of each food item to total dry mass.

Gut contents of small-bodied fish (<150 mm) were quantified in a similar manner to invertebrates using digital analysis of images taken at 100–400× magnification (ImagePro Plus and Leica Application Suite [Leica Microsystems, Heerbrugg, Switzerland]). This method yielded composition estimates that were statistically indistinguishable from the gravimetric method (Seegert 2010). Mean annual dietary composition was calculated for each species by averaging across seasons in a given year.

The "amorphous detritus/diatom" category represented a large proportion of some fish diets and was therefore further analyzed to separate algal from detrital material on a subset of individuals and taxa (flannelmouth suckers, $n = 33$; bluehead suckers, $n = 8$; common carp, $n = 19$). Briefly, we homogenized, subsampled, and mounted this material on slides in an identical manner to invertebrate gut contents. We identified diatoms, leaf detritus, and amorphous detritus, which was further divided into algal- vs. terrestrially derived amorphous detritus following Wellard Kelly et al. (2013), as above.

We quantified annual organic-matter flows through the food web following Benke and Wallace (1980). This method estimates (a) the relative and absolute contributions of different food resources to animal production, and (b) the amount of resource consumption required to support production. For each invertebrate or fish taxon, seasonal proportions of food types consumed during a given year were averaged to obtain annual average proportions. The relative fraction of annual production attributed to a given food type (F_i) was calculated as

$$F_i = (G_i \times \mathrm{AE}_i \times \mathrm{NPE}) \tag{1}$$

where G_i is proportion of food type i in a consumer's gut, AE_i is assimilation efficiency of food type i, and NPE is net production efficiency. The actual amount of consumer j's production attributed to each food type (PF_{ij} measured in g AFDM·m^{-2}·yr^{-1}) was calculated as

$$PF_{ij} = \frac{F_i}{\sum_{i=1}^{n} F_i} \times P_j \tag{2}$$

where P_j is annual secondary production (g AFDM·m^{-2}·yr^{-1}) of consumer j. Lastly, annual consumption of each food type i by consumer j (FC_{ij} measured in g AFDM·m^{-2}·yr^{-1}) was calculated as

$$\mathrm{FC}_{ij} = \frac{\mathrm{PF}_{ij}}{\mathrm{AE}_i \times \mathrm{NPE}}. \tag{3}$$

We used the following assimilation efficiencies for invertebrate consumers: diatoms, 0.3; amorphous detritus, 0.1; leaf litter, 0.1; filamentous algae, 0.3; macrophytes, 0.1; fungi, 0.7; and animal material, 0.7 (Bärlocher and Kendrick 1975, Benke and Wallace 1980, 1997). NPE of invertebrates was assumed to be 0.5. We used a wide range of literature-based assimilation efficiencies for fishes depending on species identity and dietary item (Appendix B). In a few cases where assimilation estimates were not available (e.g., assimilation of human food items introduced by river users such as rafters) we applied assimilation efficiencies that matched food types of generally similar nutritional quality (e.g., pork chop = "animal material"). Assimilation efficiencies for a given taxon and food item were kept constant across sites.

There are multiple approaches for estimating consumption by fishes (e.g., bioenergetics models: Kitchell et al. 1977, Hanson et al. 1997). We used the trophic-basis-of-production approach (Benke and Wallace 1980, Huryn 1996) because we had detailed and site-specific information on size-specific growth rates for some taxa (e.g., rainbow trout, flannelmouth suckers, humpback chub). A benefit of this approach is that it avoids uncertainties associated with unknown parameters in bioenergetic models for many species. However, the trophic-basis-of-production method is typically applied to invertebrates and frequently assumes constant NPE. Because allometric differences in NPE can be substantial for fishes, we applied a coarse body size–NPE relationship that was established by comparing consumption estimates based on bioenergetics model output for rainbow trout in Glen Canyon to estimates based on an assumed constant NPE of 0.25 (Hanson et al. 1997, Donner 2011). We used confidence intervals from this relationship to estimate uncertainty at a given body size.

Uncertainty in estimates of organic-matter flows to invertebrates was quantified by resampling secondary production values (randomly selected from a uniform distribution with the upper and lower production limits as the boundaries) to generate 1000 estimates of annual flows and 95% bootstrapped confidence intervals. Uncertainty in flow estimates to fishes was quantified using variation in both secondary production (randomly selected from uniform distribution) and NPE. Although uncertainty in AE was not included in our analysis, error associated with realistic differences in assimilation efficiency is far outweighed by other sources of error that we incorporated in our resampling efforts (e.g., abundance, production). All flow webs were drawn using the network analysis software "Pajek" (*available online*).[11]

We quantified "ecotrophic efficiencies" at all sites by dividing total fish consumption of invertebrates by total invertebrate production (e.g., Christensen and Walters 2004). Here, ecotrophic efficiency represents the percentage of total habitat-weighted invertebrate production consumed by fishes at higher trophic positions. We also quantified the strength of trophic interactions between fish predators and their prey by calculating the proportion of annual production of a specific prey item consumed by a given predator (Woodward et al. 2005*b*, Benke 2011):

$$C/P = \frac{\mathrm{FC}_{ij}}{P_j} \tag{4}$$

where FC_{ij} is the mean annual consumption (g AFDM·m^{-2}·yr^{-1}) of a given prey item by a predator (as defined above) and P_j is the mean annual habitat-weighted production of that prey item (g AFDM·m^{-2}·yr^{-1}). A value of 1 indicates that the predator consumed all of the prey production over that year and consequently represents a very strong interaction (Woodward et al. 2005*b*, Wootton and Emmerson 2005). Values >1 are not theoretically possible unless predators consume subsidies of prey from outside of the direct study area. Values >1 may also indicate underestimates of prey production or overestimates of predator consumption.

We compared bootstrap percentile 95% confidence intervals to assess differences among years in secondary production, trophic basis of production, organic-matter flows, and species interaction strengths. Means with nonoverlapping confidence intervals were interpreted as significantly different.

We examined patterns of trophic position and total autochthonous vs. allochthonous support of fishes at each site in 2007–2008 and 2008–2009 using the matrix approach described by Ulanowicz (1986). Briefly, we constructed matrices for each site–year combination that included consumers as column headings and resources as row headings. Matrix entries were the fraction of a consumer's production derived from a given food resource (i.e., the "**G**" matrix described by Ulanowicz 1986; also see Hall et al. 2000). We calculated an "**A**" matrix as

$$\mathbf{A} = [\mathbf{I} - \mathbf{G}]^{-1} \tag{5}$$

where **I** is an identity matrix consisting of 0's with 1's along the diagonal. Columns in **A** represent the extended diet of each consumer (i.e., both the proximate diet and the diets of consumed animals), and the sum of each column is equal to the average trophic position of a consumer at a given site–year combination. We quantified the proportion of a consumer's extended diet derived from autochthonous (diatoms, filamentous algae, macrophytes, and amorphous detritus of autochthonous origin) and allochthonous material (leaf detritus, amorphous detritus of allochthonous origin, and human food) by summing these components in each column of **A**. We also calculated the extended diet and trophic position of fishes by summing columns of **A** (see Ulanowicz 1986, Hall et al. 2000). Among-site differences in trophic position and proportion of production derived from aquatic invertebrates and allochthonous material were assessed with Pearson's correlation.

We examined the distribution of interaction strengths at each site (limited to invertebrate-fish linkages) by plotting (a) log interaction strengths vs. rank and (b) cumulative probability functions. The former allowed us to view simple patterns in the number and distribution of interaction strengths, while the latter provided a quantitative assessment of the proportion of interactions at each site that exceeded a given strength. The cumulative probability plots are analogous to hydrologic "flow duration curves," but are based on interaction-strength data.

We also examined longitudinal patterns of food-web complexity (average links per species), connectance (links/species^2), and the proportion of "weak" interaction strengths (defined here as interaction strengths <0.1). Correlations between these metrics and distance from the dam were assessed with Pearson's correlations on ln- or logit-transformed data (proportions; Warton and Hui 2011). Some larger taxonomic groups, such as Chironomidae, were treated as "species" in food-web analyses, but such treatment was consistent across sites.

We constructed flow food webs for the second and third years of the study (2007–2008 and 2008–2009) for which we had complete information for all food-web components. To investigate longitudinal (i.e., inter-site), rather than inter-annual, differences, we averaged food webs across these two years. This averaging allowed us to (a) better capture the range of river conditions representative of the Colorado River management regime, and (b) overcome potential idiosyncrasies that

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[11] http://pajek.imfm.si/doku.php?id=pajek

may result from smaller sample sizes associated with individual years. We found that major inter-annual differences in food-web characteristics were largely manifested at site 1, and these results are interpreted and reported in Rosi-Marshall et al. (2010) and Cross et al. (2011). Here, we limit our inter-annual analysis to quantifying effects of the 2008 flood perturbation on "stability" of consumer production. In this case, we define *stability* as a metric of resistance to change in response to the perturbation (e.g., Tilman and Downing 1994). Specifically, we calculated an integrated "flood response variance" at each site as

$$\sum_{i=1}^{n}\left[0-\ln\left(\frac{\text{postflood}_i}{\text{preflood}_i}\right)^2\right] \tag{6}$$

where i is a fish or invertebrate taxon, postflood_i is annual production of taxon i after the flood, and preflood_i is production of taxon i before the flood. We interpret large values of this metric as consistent with low food-web stability and small values with high food-web stability. To avoid unrealistically inflated values from rare taxa that had very low production, we restricted our analysis to taxa with annual production greater than 30 mg $\text{AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. To generate estimates of uncertainty in the mean for each site, we resampled taxon-specific values with replacement prior to summation and repeated this process 1000 times to derive medians and bootstrap percentile 95% confidence intervals.

Results

Temperature, discharge, and suspended silt and clay concentrations

Water temperature varied seasonally at all sites (Appendix A), with warmest temperatures occurring in August–October and coldest temperatures occurring in January–March. The amplitude of seasonal variation was relatively constrained at site 1 (range, 7.6° to 13.6°C) and increased with distance downstream (e.g., range, 7.3° to 18.7°C at site 6). Among-site differences in temperature were much more apparent in the summer (difference of ~5°C between sites 1 and 6) than in the winter (difference of ~1°C among sites). Temperature varied little among years (Appendix A).

River discharge varied strongly on a diel basis (up to 218 m^3/s over a single day), but showed relatively low seasonal variation (Fig. 2a; total range of 232 m^3/s over three years at site 1 outside of the experimental flood). In general, higher discharge was released from Glen Canyon Dam during winter (December–February) and summer (June–August) months due to greater demand for hydroelectric power during these seasons. Differences in discharge between sites 1, 3 (downstream of the LCR tributary), and 6 (387 km downstream of Glen Canyon Dam) were small, reflecting the minor contribution of tributaries to total river discharge in the study area (Fig. 2a). In March 2008 the experimental flood increased river discharge about threefold for 60 hours (Fig. 2a; Melis et al. 2010, Cross et al. 2011).

Total suspended silt and clay concentrations varied dramatically among sites and seasons. Site 1, the Glen Canyon Dam tailwater, had consistently low concentrations (average of 5 mg dry mass/L), with only a small increase during the 2008 experimental flood (Fig. 2b). Sites 2 and 3 had much higher suspended silt and clay concentrations (average of 160 and 540 mg/L, respectively) as a result of seasonal inputs from the Paria and LCR tributaries (Fig. 2c, d). There was little difference in the concentration and timing of silt and clay concentrations between sites 3 and 6, demonstrating the low contribution of the many smaller tributaries between these sites to river turbidity (cf. Fig. 2d, e). The highest suspended silt and clay concentrations generally corresponded with the summer monsoon season (July–September) when large storms occur in the uplands. Total flux of suspended silt and clay at site 3 was highest in 2006 (9.3 million metric tons [Mg]), relatively similar in 2007 and 2008 (7.8 and 7.0 million metric tons), and lowest in 2009 (3.3 million Mg).

Invertebrate and fish assemblage structure and production

Total habitat-weighted invertebrate biomass and secondary production varied significantly across sites and this variation was linked to the position of dominant tributaries. Total invertebrate biomass declined significantly (non-overlapping 95% CIs) from an average of 6.8 g AFDM/m^2 in the tailwater to <0.5 g AFDM/m^2 at the four most downstream sites (Fig. 3a). Annual habitat-weighted secondary production showed a similar pattern, declining from 23.7 g $\text{AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at site 1 to <2 g $\text{AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at the four most downstream sites (Fig. 3b). Both invertebrate biomass and secondary production exhibited stepped declines below the two dominant tributaries (Fig. 3). Interannual variability in total invertebrate production was higher at sites 1 and 2 relative to downstream sites. Most notably, total biomass and secondary production at site 1 declined precipitously (~2.2-fold reductions) in year three following the experimental flood relative to years one and two.

Although most of the dominant invertebrate taxa were present at all study sites (Supplement 1), the contributions of these taxa to total biomass and production varied dramatically across sites (Fig. 3c). *Potamopyrgus*, *Gammarus*, Tubificidae, and Lumbricidae dominated biomass and production at site 1, with the recent invasive *Potamopyrgus* composing 42% and 33% of average biomass and production, respectively. At site 2, below the Paria River, *Simulium* dominated, comprising over 60% of total biomass and production. Assemblages downstream had more taxa present (Supplement 1), but biomass and production were dominated by *Simulium*, non-Tanypodinae Chironomidae, and Tubificidae, with other substantial contri-

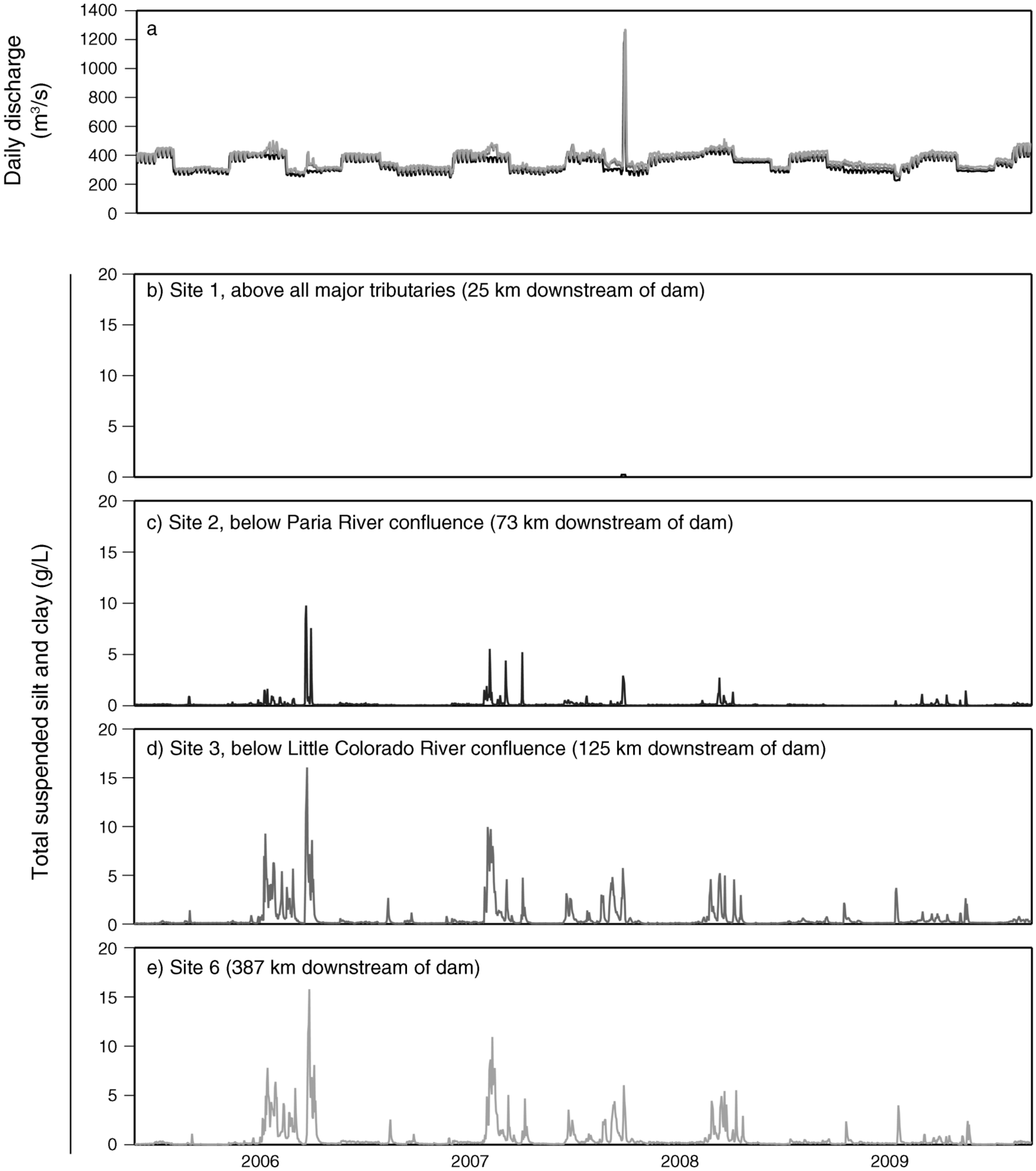

FIG. 2. (a) Mean daily discharge at sites 1 (black), 3 (dark gray), and 6 (light gray) between 2006 and 2009. (b–e) Total suspended silt and clay downstream of Glen Canyon Dam at sites 1 (concentrations extremely low, ~0.005 g/L), 2, 3, and 6.

butions by *Hydroptila*, *Gammarus*, and Lumbricidae. There were a number of consistently rare taxa at all sites and these taxa made up relatively small proportions (<10%) of invertebrate biomass and production (Supplement 1).

Habitat type had little effect on invertebrate production at site 1, but strongly affected production at downstream sites (Fig. 4). Invertebrate production at site 1 was high (average 22.4 g AFDM$\cdot$m$^{-2}\cdot$yr^{-1}) and similar across all habitats (Fig. 4). At sites 2 through 6, cobble–gravel bars had the highest invertebrate production, with values 200–1000 times higher than talus-cliff and depositional habitats. Cobble–gravel habitat was most abundant at site 5 (58%) and comprised between 18% and 43% of the benthos at other sites (Fig. 4). Depositional habitat, the least productive habitat across all sites, was most abundant at site 6 and constituted between 35% and 67% of the river bottom across sites.

In contrast to invertebrate production, fish production did not systematically decline with distance from Glen Canyon Dam (Fig. 5). In fact, total fish production was often as high or higher at downstream sites than

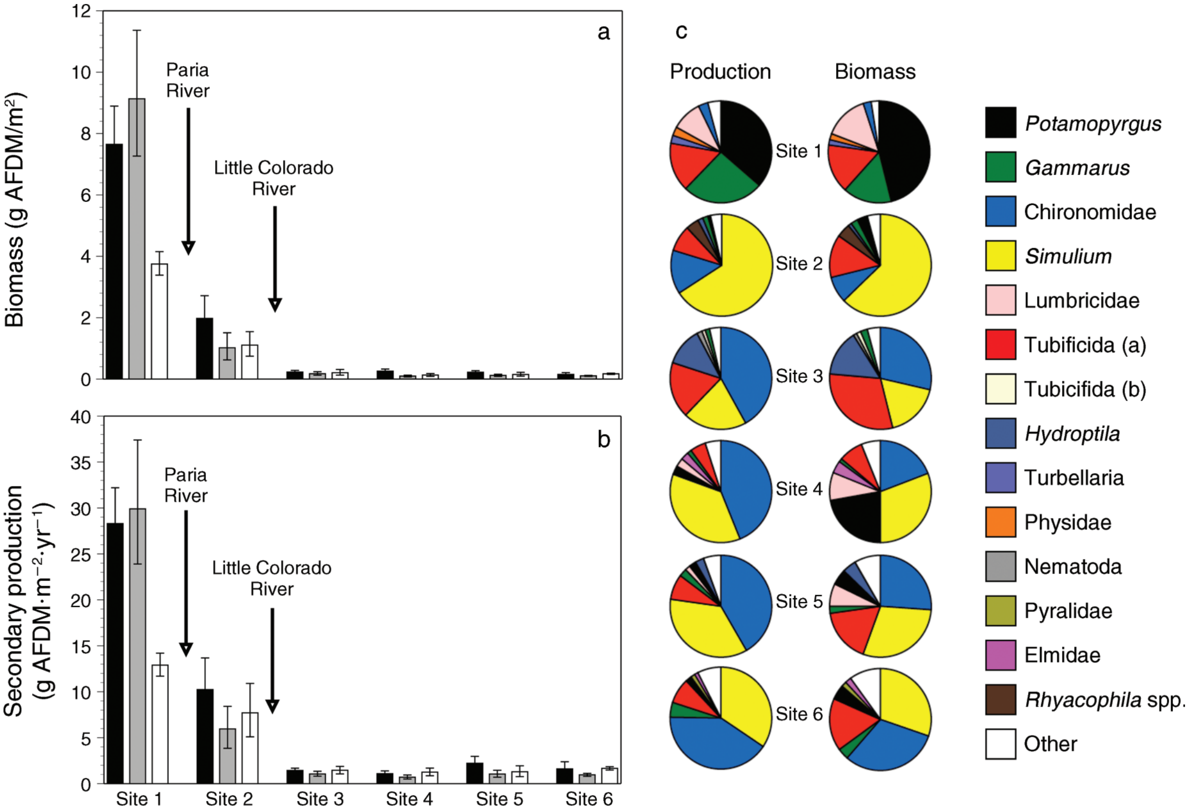

FIG. 3. (a) Annual habitat-weighted invertebrate biomass and (b) secondary production declined with distance from Glen Canyon Dam. Black, gray, and white bars correspond to years one (July 2006–June 2007), two (July 2007–June 2008), and three (July 2008–June 2009) of the study. Data are means and error bars show bootstrapped percentile 95% confidence intervals. (c) Invertebrate assemblage structure shifted from dominance of *Potamopyrgus* and *Gammarus* in the tailwater (site 1) to *Simulium* and Chironomidae at downstream sites. Pie graphs show average proportions of invertebrate taxa contributing to biomass or production across all three years of the study.

upstream sites. In 2007–2008, production was ~2 to 5 times higher at sites 4 and 5 than the other sites, with the lowest production occurring at site 6. In 2008–2009, following the experimental flood, total fish production increased significantly at sites 1 (3.3 times), 2 (2.5 times) and 6 (5.3 times) (Fig. 5). Increased production of nonnative rainbow trout at sites 1 and 2, and a large increase in production of native flannelmouth suckers at the most downstream site drove these interannual differences. Fish assemblage composition shifted longitudinally, with dominance of nonnative taxa (rainbow trout) just below the dam to largely native taxa (flannelmouth sucker) at the most downstream site (Fig. 5). At middle sites (2 through 4), the composition was more species rich, with site 3 containing the greatest number of species, including the endangered humpback chub (Fig. 5).

Ecotrophic efficiencies and the trophic basis of production

The proportion of total invertebrate production consumed by fishes (i.e., ecotrophic efficiency) increased substantially with distance from Glen Canyon Dam, but taxon-specific comparisons showed highly efficient use of some prey items at all sites (Fig. 6). At the whole-assemblage level, fish consumed an average of 16% and 11% of total invertebrate production at sites 1 and 2, respectively, and between 42% and 100% of invertebrate production at downstream sites (Fig. 6; overlapping 95% CIs of invertebrate production and consumption by fish). Nonnative *Potamopyrgus* and *Gammarus* dominated the large surplus of invertebrate prey at upstream sites. Taxon-specific comparisons of the four most productive invertebrate taxa showed that fish consumed nearly all of the available *Simulium*, Chironomidae, *Gammarus*, and *Potamopyrgus* production at most site–year combinations downstream of the LCR (Fig. 6). In a few cases, consumption by fish exceeded invertebrate production estimates, suggesting either error in estimates of demand or supply, or dependence of fishes on prey subsidies from other habitats (i.e., upstream or tributaries).

There were strong links between watershed area, material inputs from tributaries, and the type of food resources supporting fish-assemblage production (Fig. 7). The amount of fish production supported by aquatic

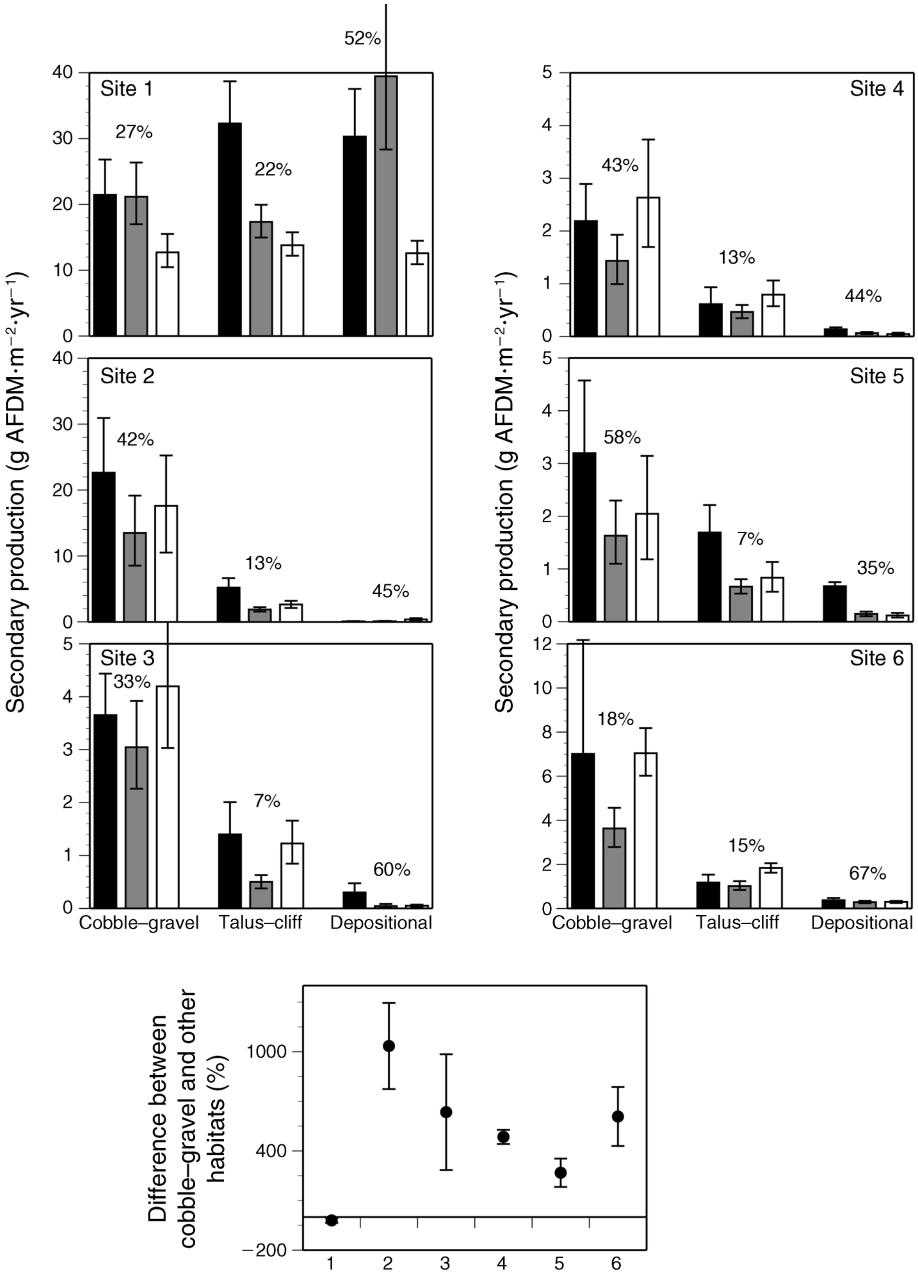

FIG. 4. Annual invertebrate production (mean with 95% CI) was similar among cobble–gravel, talus–cliff, and depositional habitats at site 1 and differed strongly among habitats at downstream sites. Black, gray, and white bars correspond to years one (July 2006–June 2007), two (July 2007–June 2008), and three (July 2008–June 2009) of the study. Panels also show the percentage that each habitat contributes to total benthic area at each site. The bottom panel shows the disproportionately high secondary production (mean ± SD) on cobble–gravel habitats relative to other habitats at sites 2–6.

invertebrates declined significantly with distance from the dam and watershed area (from up to 93% at site 1 to 48% at site 5), but there were only small differences among sites below the LCR (Fig. 7). In contrast, fish production supported by allochthonous detritus increased substantially with watershed area, from less than 10% at site 1 to over 30% at downstream sites (Fig. 7). Again, most of this variation occurred upstream of the LCR, highlighting the role of large tributaries in driving this pattern.

Longitudinal patterns of food-web attributes

Patterns of consumption by invertebrates and fishes showed large differences in magnitude, complexity, and

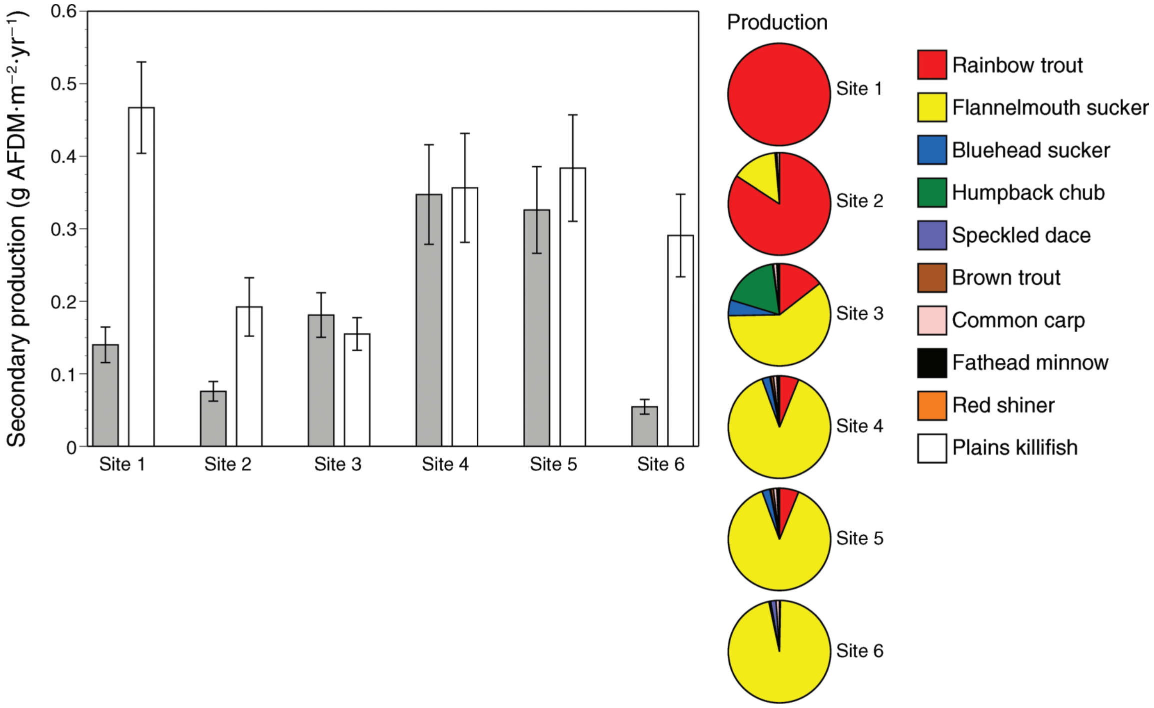

FIG. 5. Annual secondary production (mean with 95% CI) of fishes across study sites in year two (July 2007–June 2008; gray bars) and year three (July 2008–June 2009; white bars) of the study. Pie graphs show average proportions of fish taxa contributing to production across all three years of the study.

degree of dependence on autochthonous vs. allochthonous materials across sites and above and below large tributaries (Fig. 8, left column). Total consumption at site 1 was high (219 g AFDM·m^{-2}·yr^{-1}; invertebrates and fishes), and energy flow was distributed among relatively few pathways. The highest magnitude flows were of algal-based resources (i.e., diatoms, filamentous algae, and autochthonous amorphous detritus) to three productive invertebrate taxa (*Potamopyrgus*, *Gammarus*, and Tubificidae), and invertebrates and filamentous algae to rainbow trout (Fig. 8). At site 2, consumption of algal-based resources by *Simulium* dominated flows (41% of total flows), although terrestrially derived amorphous detritus became a significant dietary component (34% of total flows). Flows to fishes at site 2 included a slightly higher proportion of allochthonous materials (10% of flows to fishes; Fig. 8). At sites 3 through 6, total consumption was distributed among a larger number of taxa and allochthonous materials represented a large fraction of invertebrate and fish diets (average of 42%; Fig. 8). Assimilation webs showed that nearly all assimilated material at site 1 was of autochthonous origin (94%; Fig. 8, middle column), whereas dependence on allochthonous detritus became more prevalent at downstream sites (up to 18% of total assimilation).

Interaction strengths between fishes and their prey varied in number, magnitude, and distribution among sites. The highest magnitude interaction strengths occurred at sites 3, 4, and 5, reflecting low secondary production of diet items coupled with near complete consumption of these items by fishes (Fig. 8, right column). Interaction strengths were consistently high between fishes and their preferred prey, Chironomidae and *Simulium*, which had highest production in cobble habitat. Nearly 6% of all interaction strengths (7 of 124) were greater than 1, suggesting error in estimates of production or consumption, or use of subsidies from outside of the study reaches. However, the 95% confidence intervals of consumption and production overlapped for all but one of these interactions (flannelmouth sucker–*Gammarus* at site 4).

The magnitude of fish–invertebrate interaction strengths plotted against their ranks demonstrated large intersite differences in the distribution of numbers and strengths of interactions (Fig. 9a). Sites downstream of the LCR, excluding site 6, had the greatest number of interactions and the largest magnitude interaction strengths. These food webs had relatively few strong and many weak interactions, consistent with the low surplus of invertebrate production at these sites. Food webs at sites 1 and 2 had few total interactions, a much lower range of interaction strengths, and a smaller proportion of weak interactions (Fig. 9a). The few weak interactions were those that included highly productive taxa that were rarely consumed by fish (e.g., *Potamopyrgus*). Interaction strengths plotted as cumulative probability curves showed that the threshold for "weak"

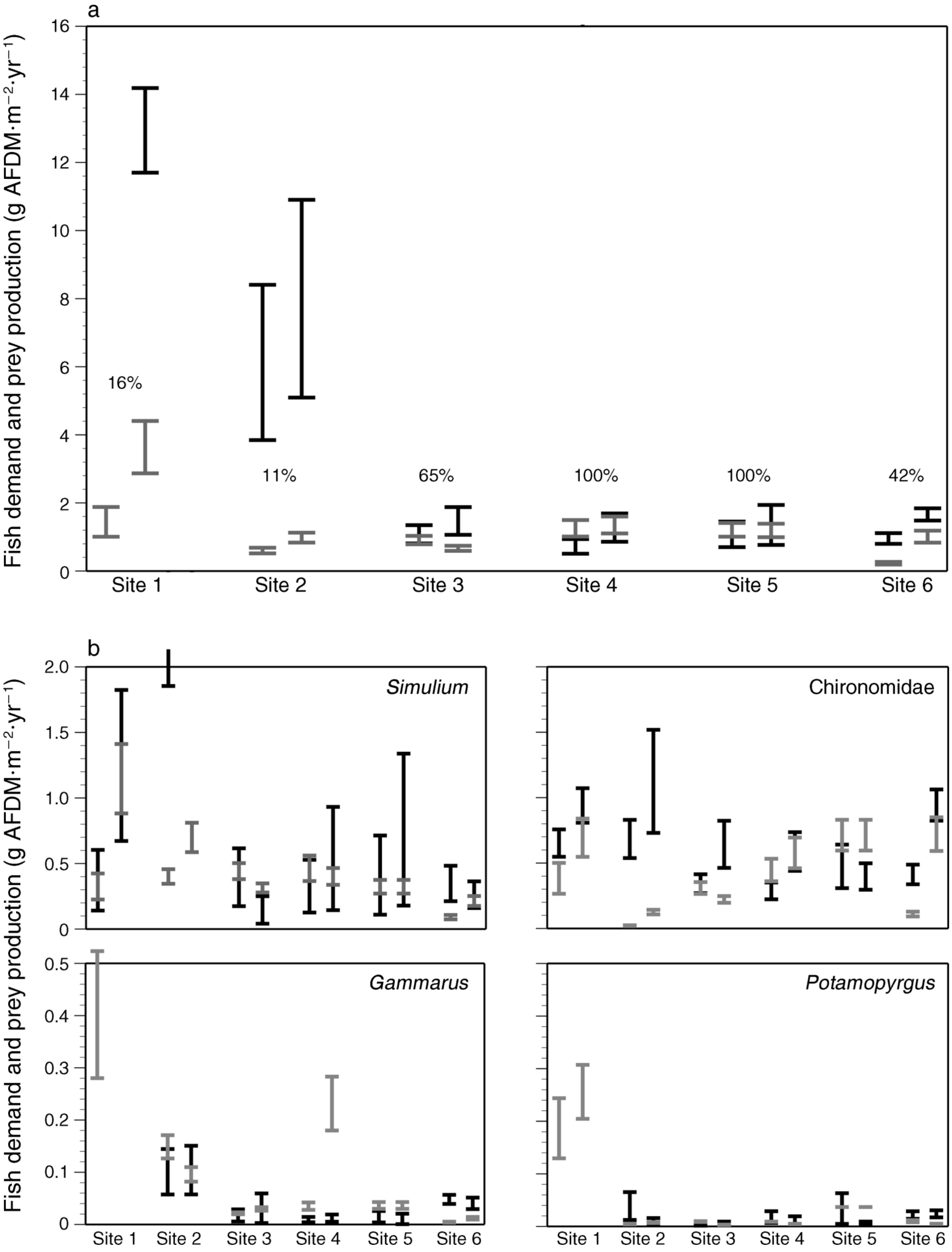

FIG. 6. (a) Total annual fish consumption of invertebrates (95% CI in gray) was lower than invertebrate production (95% CI in black) at sites 1 and 2, and close to, or equal to, invertebrate production at downstream sites. Percentages represent average ecotrophic efficiencies (i.e., percentage of total habitat-weighted invertebrate production consumed by fishes at higher trophic positions) over the two years. When 95% confidence intervals overlapped, ecotrophic efficiencies were assumed to be 100%. (b) Fish demand (95% CI in gray) for some invertebrate prey taxa largely overlapped with prey production (95% CI in black) in most site–year combinations. Years two (July 2007–June 2008) and three (July 2008–June 2009) are shown for each site. For clarity of presentation, data for some years are not shown if they exceed the *y*-axis limit (panel a, site 1, year 2, 95% CI range of production = 23.9–37.3; panel b, *Simuliium*, site 2, year 2, 95% CI range of production = 1.9–6.4; year 3, 95% CI range of production = 2.4–8.1; panel b, *Gammarus*, site 1, year 2, 95% CI range of production = 6.5–11.0, year 3, 95% CI range of production = 2.1–3.4, 95% CI range of demand = 0.8–1.2; panel b, *Potamopyrgus*, site 1, year 2, 95% CI range of production = 6.8–17.0, year 3, 95% CI range of production = 2.0–2.1).

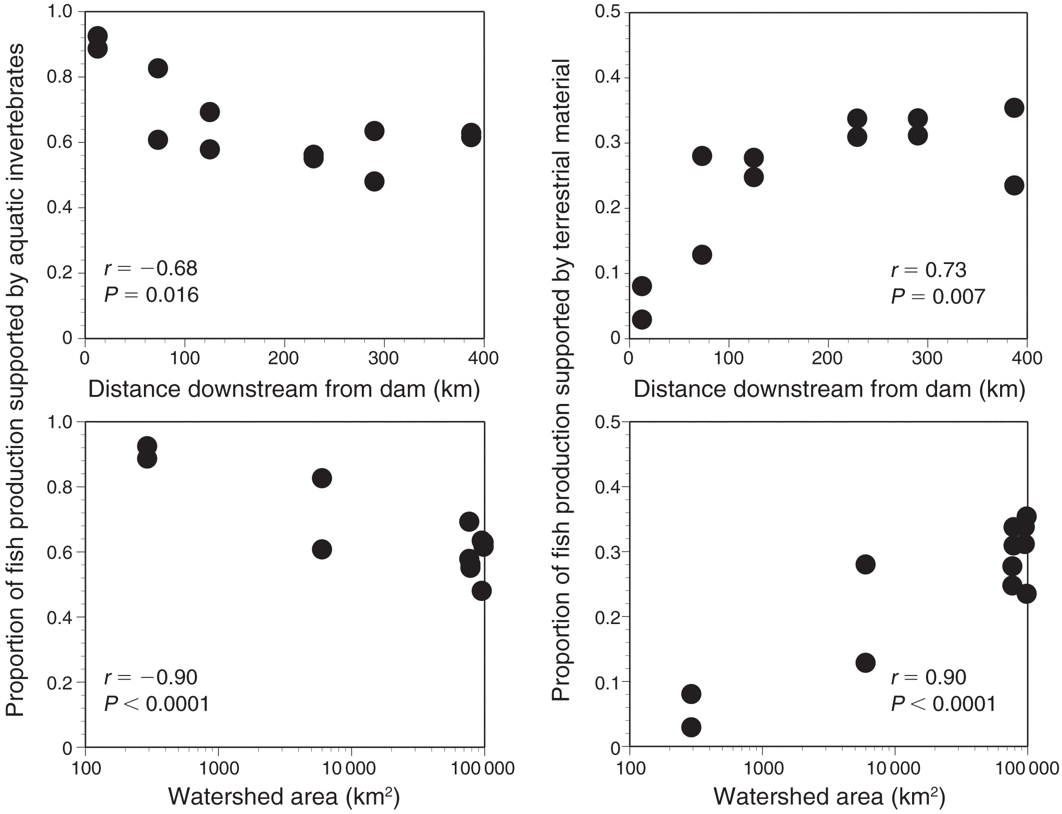

FIG. 7. Pearson's correlations show that the trophic basis of fish production changed with distance from the dam, with a large decline in support by aquatic invertebrates and a large increase in support by terrestrial materials. Most of the longitudinal variation was related to watershed area of contributing tributaries, with little difference among sites below the Little Colorado River. Note the logarithmic scale on the *x*-axis of the bottom two panels.

interaction strengths (i.e., >0.1) was exceeded 68% of the time at site 1, 41% at site 2, 34% at site 3, and between 18% and 26% at sites 4 through 6 (Fig. 9b). Histograms of interaction strengths also showed a general trend toward lower median values with increasing distance from Glen Canyon Dam (Fig. 9c).

Food webs became increasingly naturalized with respect to fish assemblage composition and exhibited patterns consistent with increased food-web stability with distance from Glen Canyon Dam. The proportion of total fish production represented by native fishes increased from nearly zero at site 1 to >90% at site 6 (Fig. 10a). Downstream food webs had a much higher proportion of weak interaction strengths (i.e., <0.1) than upstream food webs (Fig. 10b), and these were strongly associated with the proportion of fish production comprising native species (Fig. 10c). Trophic position of fishes also declined downstream, reflecting an increased prevalence of omnivory (Fig. 10d). Food-web complexity (links/species) was higher at sites below than above the LCR, but a continuous correlation of this trend was not significant (Fig. 10e). Food-web connectance (links/species^2) declined with distance from the dam, but the overall differences were negligible (Fig. 10f).

Food webs at downstream sites were more resistant to the experimental flood perturbation than those at upstream sites (Fig. 11). Mean flood response variance was 10-fold higher at site 1 than site 5 and decreased roughly linearly between these sites. The flood response variance at site 6 was highly influenced by the increased production of flannelmouth suckers at this site in 2008–2009. Exclusion of this taxon resulted in a flood response variance that was comparable to other downstream sites (Fig. 11).

DISCUSSION

Our empirical analysis of food-web dynamics in the Colorado River (Grand Canyon, Arizona, USA) revealed strong longitudinal patterns in food-web structure, energy flow, and species interaction strengths. Food webs close to Glen Canyon Dam were simplified, energy inefficient, and exhibited low resistance to the experimental flood perturbation. In contrast, food webs downstream of major tributaries were more reticulate and complex, had higher ecotrophic efficiencies, and were more resistant to the flood perturbation. Our research demonstrates that large-scale modifications to ecosystems can have far-reaching consequences for how energy enters and flows through food webs. Important-

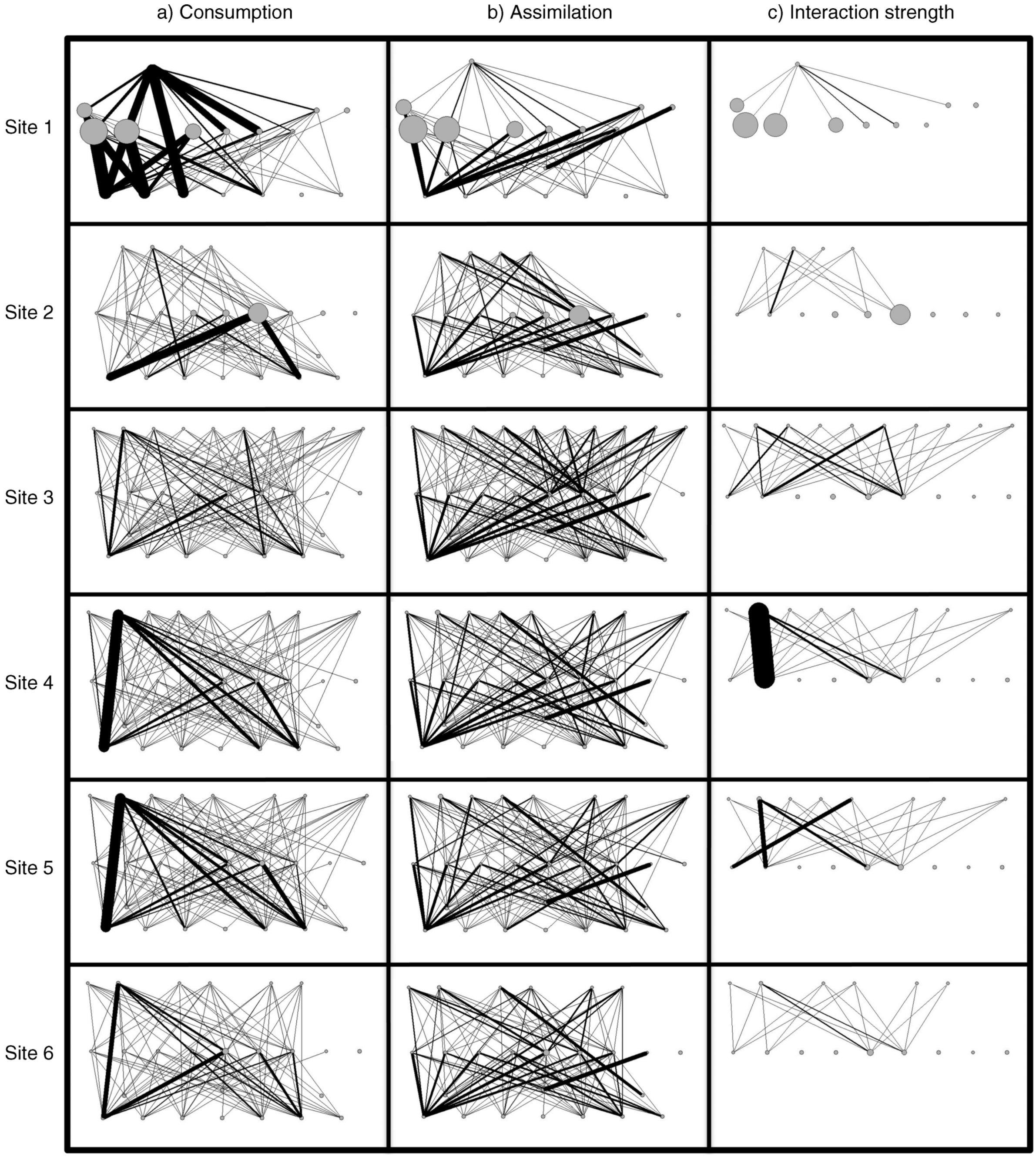

FIG. 8. Averaged-flow food webs for years two (July 2007–June 2008) and three (July 2008–June 2009) at each site depicting (a) the flow of organic matter (g AFDM$\cdot$m$^{-2}\cdot$yr^{-1}) from resources to consumers (Consumption), (b) the trophic basis of consumer production (Assimilation), and (c) the proportion of annual invertebrate production consumed by fishes (Interaction strengths; sensu Woodward et al. 2005*b*). Because consumptive flows to fishes were of much lower magnitude than flows to invertebrates, flows to fishes were multiplied by 50 at site 1 and by 5 at other sites for purposes of visualization. Line widths correspond to the magnitude of flows and interaction strengths (see key in the figure continuation [on next page]). Fishes or invertebrates not collected at a given site do not show up as a node in the panel. In assimilation webs, all lines leading to a given consumer add up to 1. Food-web organization numbers in the key are: 1, diatoms; 2, amorphous algal detritus; 3, filamentous algae; 4, macrophytes; 5, plant detritus; 6, amorphous terrestrial detritus; 7, fungi; 8, terrestrial invertebrates; 9, animal material; 10, fish; 11, *Potamopyrgus*; 12, *Gammarus*; 13, *Hydroptila*; 14, Tubificida; 15, Chironomidae; 16, *Simulium*; 17, other primary consumers; 18, other predatory invertebrates; 19, human food; 20, Lumbricidae; 21, Physidae; 22, Turbellaria; 23, bluehead sucker; 24, flannelmouth sucker; 25, rainbow trout; 26, brown trout; 27, common carp; 28, humpback chub; 29, speckled dace; 30, fathead minnow; 31, red shiner; and 32, plains killifish.

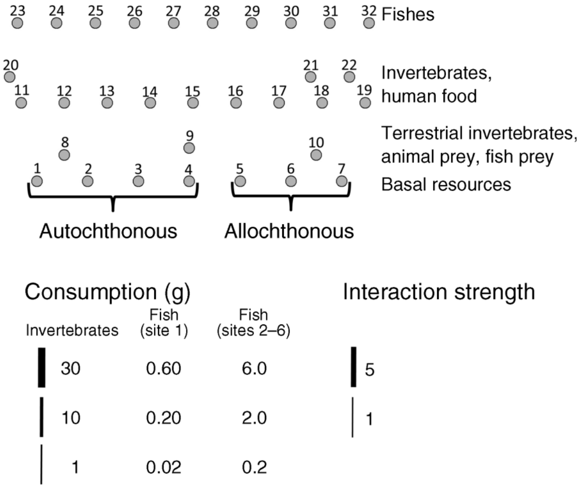

FIG. 8. Continued.

ly, these changes may alter food-web stability, leading to inherently reduced resistance to perturbations in human-dominated ecosystems.

Longitudinal patterns of food-web stability

Much theoretical work has been directed toward understanding relationships between food-web characteristics and stability (McCann 2000, 2012). Several studies have shown that food-web stability may positively relate to both the prevalence of weak interactions and omnivory (e.g., McCann et al. 1998, Emmerson and Yearsley 2004, Gellner and McCann 2012), consistent with detailed empirical observations (e.g., Winemiller 1990). In addition, stability may arise from incorporation of allochthonous detrital subsidies into food webs, and the coupling of "fast" and "slow" energy channels by consumers (DeAngelis 1992, Huxel and McCann 1998, Rooney and McCann 2012). Our study provides empirical evidence that these potentially stabilizing mechanisms tended to increase with distance from Glen Canyon Dam, the location of strongest human intervention. Specifically, we found that downstream food webs had a higher proportion of weak interactions, an increased reliance on detrital subsidies from tributaries, and a more reticulate and complex food-web structure. Downstream webs also contained a higher proportion of native fish taxa and more food-web links per species. Thus, downstream sites exhibited general empirical properties consistent with increased stability and resistance to environmental perturbations.

The experimental flood in March 2008 represented an opportunity to examine the response of Colorado River food webs to a perturbation. This experiment allowed us to examine the degree to which food webs that exhibited patterns consistent with higher stability actually showed greater resistance to the experimental flood. We previously reported a large response to the flood by both invertebrates and fishes at site 1 in Glen Canyon (Cross et al. 2011). Total invertebrate production declined by nearly 60%, while nonnative rainbow trout production increased by ~200%. Interestingly, our estimates of interaction strength and trophic basis of production could have predicted this response; the flood increased production of two prey taxa (i.e., midges, 54% increase from 0.6 to 0.9 g $\mathrm{AFDM \cdot m^{-2} \cdot yr^{-1}}$; blackflies, 490% increase from 0.2 to 1.2 g $\mathrm{AFDM \cdot m^{-2} \cdot yr^{-1}}$) that interacted strongly with, and fueled considerable production of, rainbow trout (Cross et al. 2011). In contrast, community-wide differences between pre-flood and post-flood secondary production at sites downstream of the Little Colorado River (LCR; Fig. 1) were minimal, particularly for invertebrate primary consumers (Figs. 3 and 11; but see Supplement 1 for the few taxa that did show differences among these years). Thus, in this case, theory enabled prediction of which food webs would respond most to the experimental flood (see also Robinson 2012). However, it is important not to lose sight of the mechanism; indeed, life-history or behavioral attributes of the taxa involved can provide significant insight. For example, blackfly larvae constituted a large proportion of secondary production at downstream sites. These invertebrates are generally considered *r*-selected taxa that are resilient to modest flood disturbances (e.g., Hemphill and Cooper 1983, Rosi-Marshall et al. 2010). In contrast, New Zealand mudsnails and *Gammarus*, taxa that are highly susceptible to flood disturbance and showed low resilience (Rosi-Marshall et al. 2010, Cross et al. 2011), contributed relatively small amounts to secondary production at downstream sites. Thus, species identity and life-history characteristics partially determined differential responses to the experimental flood. We suggest that predicting food-web responses to perturbations will benefit strongly from the complementary perspectives of theory and natural history (Polis et al. 1996, Winemiller and Layman 2005).

In addition to the effects of species life history on longitudinal responses to the flood, it is important to consider whether other physical or biological factors may have also varied with distance from the dam. For instance, longitudinal increases in the availability and use of detritus could be driven by increases in detritus supply, as we suggest, or alternatively they could reflect an increase in depositional habitat that retains higher standing stocks of detritus; however, the proportion of depositional zones did not increase along the longitudinal gradient, indicating that increases in detritus supply were responsible for patterns of detritus use in downstream food webs. In addition, geomorphic characteristics such as channel slope and depth, which jointly affect shear stress, could alter disturbance intensity leading to inter-site differences in food web stability that are wrongly attributed to food-web structure and function. In our study reaches, shear stress during the experimental flood did not vary systematically with distance from Glen Canyon Dam (Paul Grams [USGS], *unpublished data*). The above examples highlight the importance of considering a variety of potential confounding factors when examining mechanisms that alter food-web stability along natural gradients.

Among fishes at the top of the food web, responses to the flood perturbation varied across sites. We measured a post-flood increase in rainbow trout production at sites 1 and 2, no production response at sites 3, 4, and 5, and a relatively large increase in native flannelmouth sucker production at site 6 (Fig. 5). Thus, excepting site 6, fishes appeared to be least resistant to changes following the flood at locations closest to the dam. Patterns in long-term abundance of flannelmouth suckers (Walters et al. 2012), as well as closer examination of body size patterns, suggest that the increase in flannelmouth sucker production was most likely due to downstream dispersal of fish from upstream reaches (C.V. Baxter, *personal observation*), rather than a strong new cohort produced at this site. Most flannelmouths at site 6 following the flood were larger than age-0, and one of the upstream sites in National Canyon (site 5) is a nursery for suckers spawned in nearby tributaries. In addition long-term population data show that multiple strong year classes have been produced during the past decade (Walters et al. 2012), and none of these have been associated with flood experiments, unlike rainbow trout in the tailwater (Makinster et al. 2011). We suggest that downstream food webs are more resistant to perturbations, but additional controlled floods coupled with long-term monitoring of food webs will be needed to further evaluate this hypothesis.

Novel food webs and ecosystem efficiencies

Human activities have fundamentally altered ecosystem structure and function (Vitousek et al. 1997*a*) and, on balance, these changes have simplified or homogenized (Olden et al. 2004) assemblages, subjecting them to unstable dynamics. Large regulated rivers, such as the Colorado River, provide classic examples of highly altered ecosystems that exhibit erratic structural and functional behavior (Power et al. 1996, Vinson 2001, Cross et al. 2011). Similar to other human-dominated ecosystems (i.e., agroforestry and monotypic agricultural landscapes), regulated rivers tend to be species poor, highly vulnerable to invasions (Blinn and Cole 1991, Vinson 2001, Marchetti et al. 2004, Cross et al. 2010), and composed of groups of interacting taxa that have not co-evolved (Hobbs et al. 2006). These ecosystems are ideal for studying links between food webs and ecosystem properties because of their novel communities, as well as the research opportunities afforded by large-scale experiments resulting from dam operations (e.g., Ward and Stanford 1984, Vinson 2001, Robinson and Uehlinger 2008, Konrad et al. 2011; Robinson 2012). In addition, these systems provide a useful arena for examining how interactions and ecosystem efficiencies may change over time as species acclimate or adapt to new selective pressures, as well as how patterns of energy flow and efficiencies may depend on presence or absence of taxa with unique behavioral or life-history characteristics.

The Glen Canyon food web (site 1) was dominated by nonnative invertebrate and fish taxa and was generally less species-rich than downstream food webs. These changes to the community led to large energy inefficiencies at multiple trophic positions. For instance, invertebrates in Glen Canyon consumed almost none of the dominant primary producer (i.e., filamentous algae), leading to a large algal surplus and net export of primary production from this segment (Shannon et al. 1996; R. O. Hall, Jr., *unpublished data*). Moreover, rainbow trout consumed little of the most productive invertebrate taxon, nonnative *Potamopyrgus*, resulting in extremely low ecotrophic efficiencies and a large surplus of invertebrate production (i.e., trophic dead end). Thus, the novel food-web composition at sites near Glen Canyon has led to large consumer–resource mismatches, and these changes have strongly influenced the fate of fixed energy at the base of the food web.

In contrast, downstream food webs were more species rich and dominated by native fish taxa. These food webs also showed much higher ecotrophic efficiencies (i.e., fishes consumed most of the invertebrate production), and there was little surplus invertebrate production. This pattern may have resulted from a shift in the identity and feeding behavior of the dominant fish predator (from rainbow trout upstream to flannelmouth suckers downstream), as flannelmouths fed directly on benthic prey, and had high production at downstream sites. Interestingly, flannelmouths also showed a high degree of "multichannel" omnivory (i.e., feeding from both algal and detrital energy pathways; sensu Polis and Strong 1996), and detrital subsidies may have further contributed to their high production and potential top-down influence on benthic prey.

It is important to note that although downstream food webs contained a higher proportion of native fish taxa, these assemblages scarcely resembled historic conditions. Relatively constrained temperatures and close proximity of the next major discontinuity (i.e., Hoover Dam and Lake Mead) limit the species pool that can survive in the mainstem. Indeed, four large-bodied native fish species have been locally extirpated from the Grand Canyon, including a piscivore (Minckley 1991). The dammed nature of the Colorado River also ensures the presence of certain nonnative fish taxa (e.g., common carp), and alters the potential primary and secondary production that may have existed during summer months in the pre-dam era. Indeed, less-regulated sections of the Green, Yampa, and Colorado rivers (all upstream of Lake Powell) contain a diverse invertebrate fauna that contain many taxa that are no longer found in the Colorado River in Grand Canyon (i.e., mayflies, stoneflies; Haden et al. 2003). Thus, although downstream sites were more naturalized and

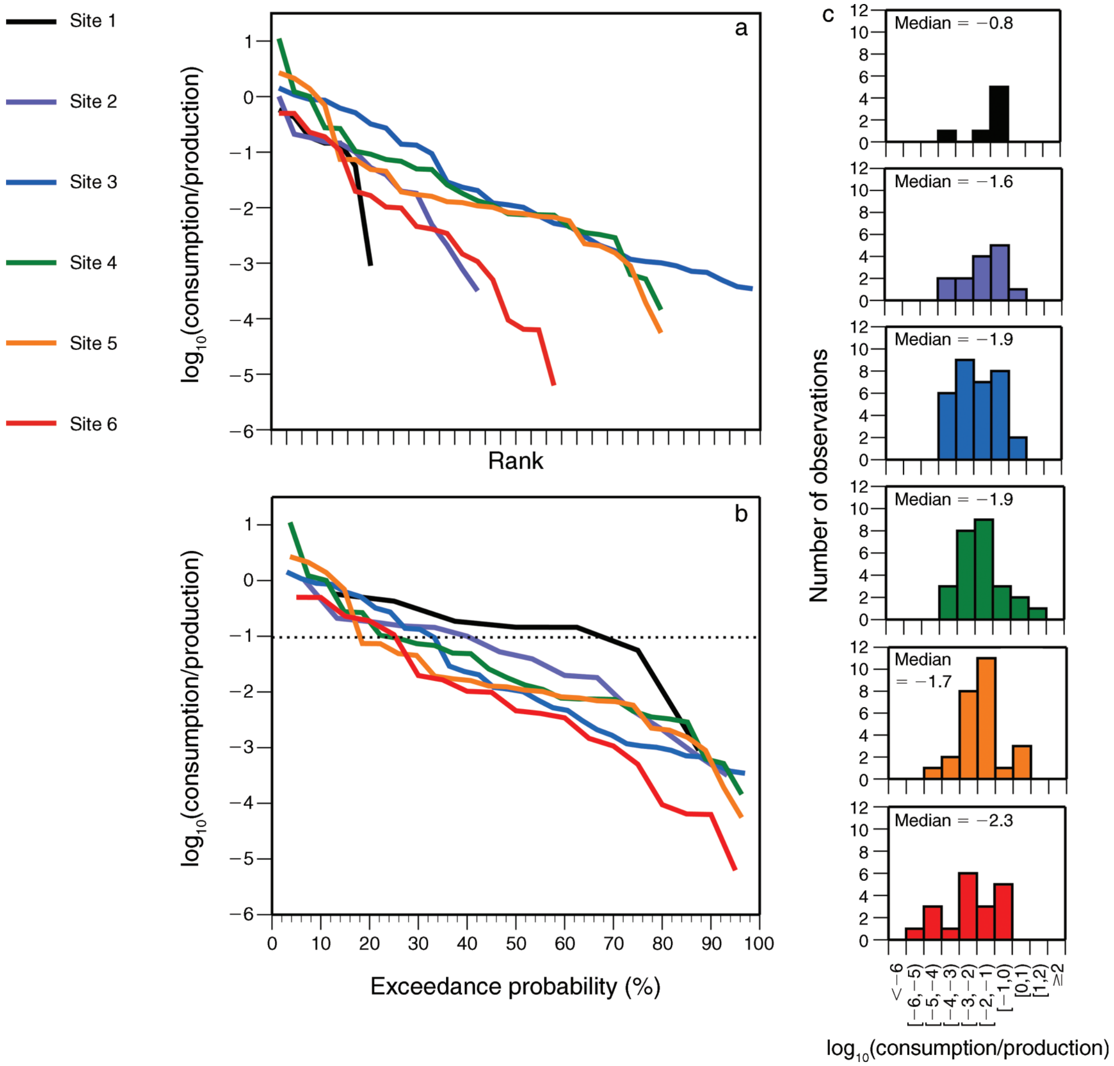

FIG. 9. (a) Ranked interaction strengths [log$_{10}$(consumption/production)] depicting interactions between fishes and their prey at all sites averaged over years two (July 2007–June 2008) and three (July 2008–June 2009). (b) Cumulative probability distributions of the same interactions shown in panel (a), allowing comparisons among sites with different numbers of total interactions. The horizontal dotted line shows the threshold for "weak" interactions (i.e., consumption/production of 0.1, or 10%). (c) Frequency histograms of interaction strengths illustrating the distributions and median interaction strengths at each site.

energy efficient than sites close to the dam, these food webs in no way represented the complexity and species richness of the pre-dam condition.

The key role of tributaries

Tributaries modulated longitudinal patterns of physical and habitat conditions, as well as resource availability and quality (Stevens et al. 1997). From a purely physical standpoint, tributaries deliver gravel, cobble, and boulders during storms that create riffle and rapid habitats at tributary junctions along the river corridor (Howard and Dolan 1981, Rice et al. 2001). Indeed, most of the highly productive cobble habitats in Grand Canyon occur at such junctions. Our study showed that these habitats were extreme hot spots of invertebrate productivity, especially at downstream sites where cobble–gravel production was between two and 10 times higher than other river habitats. This "hotspot" phenomenon is not unique to Grand Canyon; others have identified tributary junctions as hot spots for invertebrate abundance (Kiffney et al. 2006), though comparisons of production are generally lacking. Similarly, wood snags in southeastern blackwater rivers (e.g., Smock et al. 1985, Benke 2001) are hot spots of macroinvertebrate production. However, when disproportionately productive habitats are corrected for total riverbed area, their contribution to total production is generally modest. Benke (2001) showed that while snags were highly productive on a habitat-specific basis, sandy floodplain habitats were much more productive when

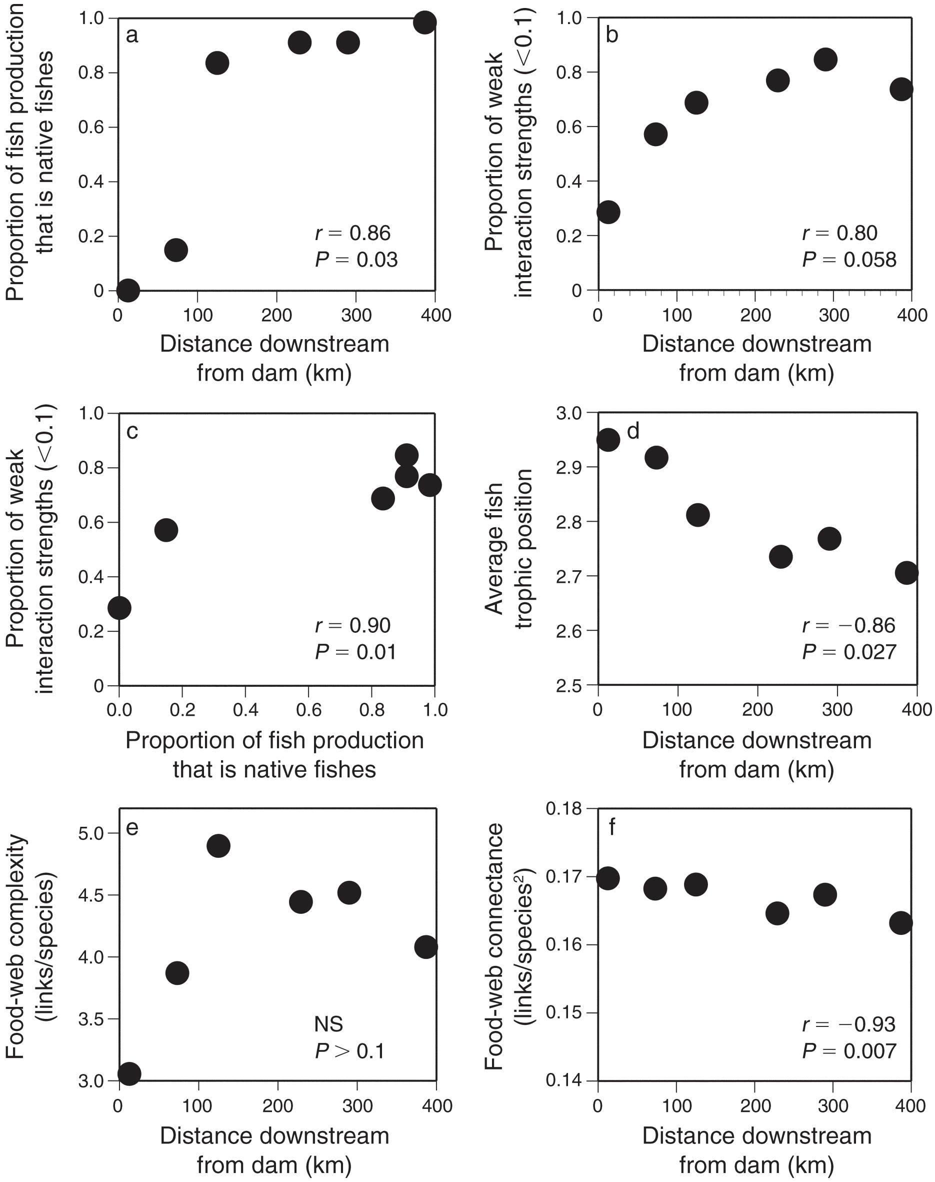

FIG. 10. Food webs showed an increased proportion of (a) native fish production and (b) "weak" interaction strengths with distance downstream from Glen Canyon Dam, and (c) these patterns were correlated. Food webs also showed (d) decreased trophic position of fishes, (e) increased links per species, and (f) decreased connectance, with distance downstream from the dam.

expressed on a total riverbed area basis. Interestingly, similar calculations in Grand Canyon show that cobble–gravel habitat, when expressed on a riverbed-area basis, still produced between 71% and 94% of total invertebrate production at sites 2 through 6. These estimates demonstrate that cobble–gravel habitats, ultimately derived from tributary flooding, produce the vast majority of invertebrates that support fish production. These results are also consistent with research conducted in the upper Colorado River basin, where invertebrate biomass was positively correlated with high-energy habitats relatively free of fine sediments (Osmundson et al. 2002). Exploring relationships between the finer-scale spatial distribution of fish production and the locations of productive cobble–gravel habitat in river networks may shed light on the role of topography and geology in generating food-web hotspots (e.g., Sabo and Hagen 2012).

Tributaries shifted the trophic basis of secondary production. Above major tributaries, invertebrates and fishes showed near-complete reliance on algae. Below the LCR, food webs shifted towards a more balanced reliance on both algae (invertebrates, 50–70%; fishes, 65–85%) and allochthonous detritus (invertebrates, 30–50%; fishes, 15–35%; also see Donner 2011, Wellard-Kelly et al. 2013). These changes are not particularly surprising given the millions of metric tons of fine sediment and organic detritus delivered to the river by tributaries on an annual basis (largely during summer monsoon storms; Andrews 1991; T. A. Kennedy, *unpublished data*). What was more surprising, but nonetheless consistent with conceptual models for large rivers (i.e., Thorp et al. 2006), was that algae constituted a large fraction of the base of the food web, even in river segments that were turbid for large portions of the year (cf. Thorp et al. 2006, but see Zeug and Winemiller 2008). Prior to construction of Glen Canyon Dam, sediment inputs from the upper Colorado River basin led to high levels of turbidity during much of the year (Topping et al. 2000; N. Voichick and D. J. Topping, *unpublished manuscript*) that dwarf turbidity values measured today. For example, average pre-dam turbidity at site 3 was approximately 64 times higher than post-dam values at this site. Questions remain about the relative roles of autochthonous vs. allochthonous resources during the pre-regulation era. Additional food-web research in unregulated reaches that approximate pre-dam conditions (e.g., Cataract Canyon, an unregulated reach upstream of Lake Powell) would be highly informative in this regard.

Tributaries also provide spawning and rearing habitat for native fishes, such as humpback chub, flannelmouth sucker, and bluehead sucker (Childs et al. 1998, Weiss et al. 1998). These habitats may also provide resource subsidies for fishes that remain in tributaries for a substantial portion of their lifespan, or during critical life stages. While much research has focused on patterns of fish movement and use of tributaries (e.g., Kaeding and Zimmerman 1983, Weiss et al. 1998), almost nothing is known about the reliance of Grand Canyon fishes on tributary-derived food resources. Our estimates of annual fish demand exceeded invertebrate production in a few cases, suggesting that we overestimated fish demand, underestimated invertebrate production, or failed to account for resource subsidies coming from outside of our study segments. Indeed, resource subsidies from tributaries or cobble–gravel bars far upstream may have provided the "missing" resource base on some occasions in our study, especially in reaches where cobble made up a small proportion of local habitat. Additional research focused explicitly on tributary food webs and their importance relative to the mainstem would help reduce this knowledge gap.

Strengths and limitations of the flow food-web approach

We used a flow food-web approach (Benke and Wallace 1997, Hall et al. 2000, Benke 2011) to build a detailed "map" of species interactions in the Colorado River. We chose this approach because it provides a robust picture of how energy flows between resources and consumers, and can be used to assess the trophic basis of consumer production (Benke and Wallace 1997, Hall et al. 2000, Cross et al. 2007). In addition, this approach allowed us to estimate dynamic food-web attributes, such as trophic interaction strengths (sensu Wootton 1997, Hall et al. 2000, Woodward et al. 2005*b*), and recent work, including our study, has shown that these observation-based estimates of interaction strength may help predict responses to perturbations (O'Gorman and Emmerson 2009, Novak 2010, Cross et al. 2011, Novak et al. 2011). Although studies that use this labor-intensive approach are few, the effort invested can be extremely useful for providing a baseline understanding of food-web dynamics. In intensively managed ecosystems, such as the Colorado River, this approach can also form the basis for generating hypotheses about responses to changes in dam operations or other agents of change such as shifts in climate or spread of new exotic species.

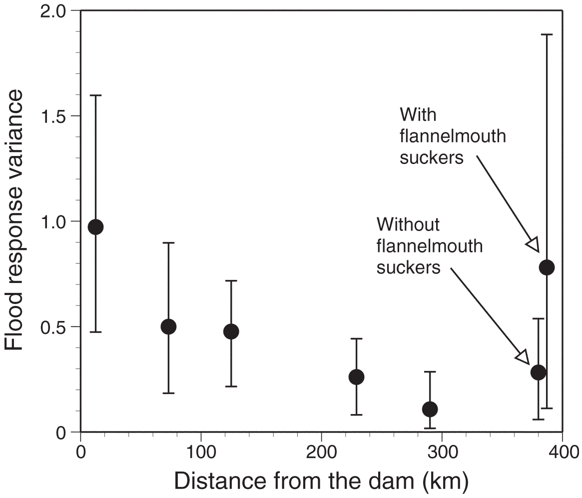

FIG. 11. Invertebrates and fishes at sites close to the Glen Canyon Dam responded much more strongly to the experimental flood (i.e., were less resistant to the perturbation; measured as "flood response ratio") than consumers at sites farther from the dam. The exception to this pattern was flannelmouth sucker production, which increased at site 6 in the year following the flood. The data are means with 95% confidence intervals.

The temporal scale of annualized flow food webs may be seen as both a strength and a limitation of our approach. Sampling throughout an annual cycle incorporates the full suite of conditions experienced by populations, and encompasses factors such as ontogenetic diet shifts, population survivorship, and movement. In the Grand Canyon the annual cycle includes large seasonality in turbidity, light, and temperature—all factors that can affect energy flux, as well as the identity and strength of interactions. Thus, annual estimates of organic-matter flows subsume variation at small scales and provide a generalized picture of food-web dynamics. On the other hand, some may view this generalized picture as much too coarse, potentially missing important interactions or flows that occur at shorter time steps. Others have argued that flow webs

PLATE 1. The opening of Upper Granite Gorge on the Colorado River (USA) immediately upstream of Hance Rapid. Photo credit: R. O. Hall, Jr.

alone are not sufficient to understand community dynamics because energy or material flows are themselves products of species interactions that play out over multiple time scales (DeAngelis 1992, Polis 1994). In addition, flow webs do not explicitly address indirect interactions that can produce counterintuitive responses in both empirical studies and dynamic models (e.g., Yodzis 1988, Menge 1995). Finally, empirical estimates of interaction strengths taken over long time intervals may be difficult to reconcile with theoretical approaches that often deal with instantaneous changes (Berlow et al. 2004, Wootton and Emmerson 2005). Clearly, additional research is needed to understand how time scale, seasonal averaging, and explicit consideration of indirect effects alter interaction strength and organic-matter flow estimates and their predictive capabilities.

The time, effort, and funds devoted to describing an empirical food web of organic-matter flow determines the amount of knowledge gained. Given the labor and cost required to construct reasonably accurate flow webs, many ecologists have turned towards using static attributes, such as body size, as proxies for estimating ecosystem fluxes (e.g., secondary production) or species interaction strengths (e.g., Berlow et al. 2004, Emmerson and Raffaeli 2004, Woodward et al. 2005*a*, Hildrew et al. 2007). There is great promise in these proxies; for example, some studies have shown relatively strong coherence between predicted and measured processes (e.g., Emmerson and Raffaelli 2004, Huryn and Benke 2007). However, continued validation of these proxies will be necessary to justify their use in producing reliable predictions.

The nexus between food-web ecology and river management

The Colorado River ecosystem has been altered to such a degree that its food webs now represent an amalgam of native and nonnative species that have not co-evolved. This situation is not unique to the Colorado River, and may be considered the norm in large regulated rivers and impoundments globally (e.g., Johnson et al. 2008, Arthington et al. 2010). Accordingly, scientists and resource managers must consider how these novel food webs will respond to management actions, such as flow or thermal manipulation. We showed that the Glen Canyon tailwater food web was extremely productive, dominated by nonnative taxa, and sensitive to experimental floods. Nonnative rainbow trout benefitted strongly from both the 1996 and 2008 floods (Cross et al. 2011, Makinster et al. 2011; Korman et al. 2012), and emigration of trout following these floods has led to large population increases at downstream sites (Korman et al. 2012). Thus, managers are now struggling with how to mitigate the potential negative effects of rainbow trout on downstream food webs and species of concern (e.g., predation on endangered humpback chub; USDI Bureau of Reclamation 2011, Yard et al. 2011). At downstream sites we showed that invertebrate production was low, and fishes consumed most of this production. In contrast to the tailwater site, the experimental flood had minimal effect on total invertebrate production at these sites. Thus, an influx of rainbow trout from upstream coupled with a limited resource base suggests that floods may lead to strong competition among fishes at downstream sites (K. C. Donner, *unpublished data*). During the three years of our study, rainbow trout represented a small proportion of fish production at sites 3–6, but recent estimates suggest that this was not the case in 2009–2011 (Korman et al. 2012). Additional research is underway to quantify trout recruitment dynamics and movement among sites. These efforts could lead to future physical removal of trout from Grand Canyon (USDI Bureau of Reclamation 2011), and our food-web research has helped inform this effort.

One of the benefits of building detailed food webs is that key species interactions and pathways of energy flow can be identified. Managers can then use this information in attempts to alter the food web to produce desired outcomes. We found that Chironomidae and *Simulium* were consistently important diet items of fish at all sites and years, and fish consumed most of their secondary production. Thus, management actions that alter the production of these insects could lead to changes in fish production. If increased native-fish production is desired at downstream sites, other management actions could be considered. For example, gross primary production is sensitive to flow management at Glen Canyon Dam (R. O. Hall, Jr., *unpublished data*), and increased primary production at downstream sites may have cascading positive effects on higher trophic levels. Because flow-management experiments represent the core action for learning through adaptive management on the Colorado River, additional experiments coupled with monitoring of both primary and secondary production could be considered in the future (Walters 2002, Melis et al. 2012).

Conclusions

Global change and human transformation of landscapes are leading to widespread restructuring of species assemblages. Many ecosystems now contain a mixture of native and nonnative species that interact in novel ways to affect ecosystem-level properties. It is therefore imperative that we study these ecosystems both as models for understanding linkages between species and ecosystems, and for developing predictions about how perturbations might propagate through these ecosystems to affect the species or services upon which we depend. Our research demonstrated that fragmentation and regulation of the Colorado River by a large dam produced food webs that were energetically inefficient and exhibited characteristics consistent with reduced stability. These food webs also responded to an experimental perturbation in ways that were predicted by food-web theory, suggesting our results and approach may be applied more broadly to other ecosystem types. Although the effects of dams on food webs have a strong spatial component and may slowly dissipate with distance downstream (Ward and Stanford 1983), the degree of fragmentation by dams (Nilsson et al. 2005) is too vast to allow complete recovery in most cases. As such, understanding how these food webs operate, as well as understanding operation of altered food webs in other ecosystem types, should be a top priority in conserving and managing ecosystems worldwide.

ACKNOWLEDGMENTS

We thank the many research technicians who spent countless hours in the field, the laboratory, or on a computer: Adam Copp, Jason Fobair, Amber Adams-Gaul, Carina Hall, Dustin Kincaid, Elizabeth Reese, Tom Sabol, Maria Pacioretty, and Jamina Winston. Iwan Jones and Stephanie Parker assisted with network software used to produce the food-web figures (i.e., "Pajek"). We thank Benjamin J. Koch for developing R code for secondary production analysis. Carol Fritzinger, Brian Dierker, and Humphrey Summit Support, and the entire Grand Canyon Monitoring and Research Center warehouse staff provided excellent logistical support and river knowledge. We thank Ted Melis for continued support and engagement, as well as Josh Korman and Carl Walters for productive discussion about study design and data analysis. Helpful comments on an earlier draft were provided by Scott VanderKooi and members of the Cross lab. Cliff Kraft and two anonymous reviewers also provided excellent suggestions that improved the manuscript. All handling and gastric lavage of endangered humpback chub was done in conformance with applicable laws (U.S. Fish and Wildlife Service permit number TE823156-1). The U.S. Bureau of Reclamation via the U.S. Geological Survey supported this research through cooperative agreements 05WRAG005 to R. O. Hall, Jr., E. J. Rosi-Marshall and C. V. Baxter, and G10AC00141 to W. F. Cross. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Supplemental Material

Appendix A

Mean daily water temperature at all sampling sites between January 2006 and December 2009 (*Ecological Archives* M083-011-A1).

Appendix B

Literature-derived assimilation efficiencies for fish–invertebrate combinations (*Ecological Archives* M083-011-A2).

Supplement 1

Annual mean (± 95% CI) invertebrate abundance, biomass, and secondary production by habitat for each of the six sites (*Ecological Archives* M083-011-S1).

Supplement 2

R scripts defining the set of functions used to calculate secondary production and associated estimates of uncertainty (*Ecological Archives* M083-011-S2).