


Pulsed flows, tributary inputs and food-web structure in a highly regulated river

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Abstract

1. Dams disrupt the river continuum, altering hydrology, biodiversity and energy flow. Although research indicates that tributary inputs have the potential to dilute these effects, knowledge at the food-web level is still scarce.
2. Here, we examined the riverine food-web structure of the Colorado River below Glen Canyon Dam, focusing on organic matter sources, trophic diversity and food chain length. We asked how these components respond to pulsed flows from tributaries following monsoon thunderstorms that seasonally increase streamflow in the American Southwest.
3. Tributaries increased the relative importance of terrestrial organic matter, particularly during the wet season below junctures of key tributaries. This contrasted with the algal-based food-web present immediately below Glen Canyon Dam.
4. Tributary inputs during the monsoon also increased trophic diversity and food chain length: food chain length peaked below the confluence with the largest tributary (by discharge) in Grand Canyon, increasing by >1 trophic level over a 4–5 km reach possibly due to aquatic prey being flushed into the mainstem during heavy rain events.
5. Our results illustrate that large tributaries can create seasonal discontinuities, influencing riverine food-web structure in terms of allochthony, food-web diversity and food chain length.
6. *Synthesis and applications.* Pulsed flows from unregulated tributaries following seasonal monsoon rains increase the importance of terrestrially derived organic matter in large, regulated river food webs, increasing food chain length and trophic diversity downstream of tributary inputs. Protecting unregulated tributaries within hydropower cascades may be important if we are to mitigate food-web structure alteration due to flow regulation by large dams. This is critical in the light of global hydropower development, especially in megadiverse, developing countries where dam placement (including completed and planned structures) is in tributaries.

KEYWORDS

allochthonous inputs, dams, food chain length, hydrologic alteration, maximum trophic position, pulsed flow, serial discontinuity

1 | INTRODUCTION

Dams fragment large river systems across the globe (Nilsson, Reidy, Dynesius, & Revenga, 2005) and are the hallmark of rivers in the western United States (Sabo et al., 2010b). Although the “go-go years” of dam building in the United States (Reisner, 1993) are over, they are just beginning on some of the world’s largest rivers like the Yangtze (Chang, Liu, & Zhou, 2010), Mekong (Grumbine & Xu, 2011), Congo (Kalitsi, 2003) and upper Amazon (da Silva Soito & Freitas, 2011). These dams promise to provide water to grow food and clean energy for growing urban economies. However, they will also impart big changes on downstream ecosystems, most notably on biodiversity and capture fisheries in freshwater and delta ecosystems (Winemiller et al., 2016). Additionally, in the developed world, plans to increase renewable hydropower generation are driving an increase in retrofit projects, often on tributaries (Kosnik, 2010). Overall, the steep increase in dam building and planning across the globe (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015) may bring system-wide consequences on downstream ecosystems.

Dams fragment riparian and riverine habitat alter sediment transport and modify thermal and flow regimes (Bunn & Arthington, 2002; Graf, 2006; Kondolf, 1997; Poff, Olden, Merritt, & Pepin, 2007). Specifically, dams homogenize regional river dynamics by muting peak discharge, enhancing the longevity or timing of low and high flow periods, shifting the seasonality of water delivery, and in the case of hydropower dams, subjecting biota to extreme low and high daily flows (Kennedy et al., 2016; Poff et al., 2007; Sabo, Bestgen, Graf, Sinha, & Wohl, 2012). Accordingly, much research has been devoted to understanding how dams influence downstream biodiversity and food-web interactions (Cross et al., 2011; Ruhí et al., 2016; Sabo et al., 2010a, 2010b; Ward & Stanford, 1983). However, while most big rivers are heavily regulated, their tributaries may not be, and unregulated tributaries can provide a number of important features in riverscapes. Tributaries deliver sediment (Rice, Greenwood, & Joyce, 2001; Sabo et al., 2012) and organic matter and nutrients (Cross et al., 2013; McClain & Naiman, 2008; Wu et al., 2007), resetting the longitudinal profile of the main stem by creating physical discontinuities in terms of discharge, sediment and materials (Benda et al., 2004; Stevens, Shannon, & Blinn, 1997). Tributaries can also provide corridors for recolonization of native fishes and other organisms from upstream catchments (Pracheil, McIntyre, & Lyons, 2013), and in some cases, they provide hotspots of biological activity (Katano et al., 2009; Kiffney, Greene, Hall, & Davies, 2006; Sabo & Hagen, 2012). Tributaries of the regulated Colorado River in the Grand Canyon, for example, are the point source of boulders and coarse sediment (Hanks & Webb, 2006; Webb, Pringle, & Rink,

1989), organic matter (OM) for the aquatic food base (Cross et al., 2013), and breeding and rearing grounds for migratory native fish (Coggins et al., 2006; Douglas & Marsh, 1996; Yackulic, Yard, Korman, & Haverbeke, 2014). Overall, unregulated downstream tributaries may mitigate how dams alter aquatic life downstream (Sabo et al., 2012; Ward & Stanford, 1983, 1995). Given the multitude of planned dams across the globe, we must ponder how best to manage downstream ecosystems in their wake. One potential bright spot is successful protection and management of tributaries—especially large ones.

Here, we focused on the effect of seasonal pulses in OM from large, unregulated tributaries on the carbon basis of production in a highly regulated river system. We explored patterns of resource supply in space and time, dependence of biota on energy from algae vs. terrestrial plants, and the influence of energy flow on two measures of food-web structure: food chain length (FCL) and trophic diversity. A direct way to test whether tributaries restore particular biological functions below dams is to examine the effect of sequential tributaries on variation in food-web structure. We did this in the setting of the highly regulated Colorado River in the Grand Canyon, joined by six major tributaries that collectively increase the drainage area of the basin by 34% compared with that upstream of Glen Canyon dam (Figure S1 in Appendix S1; Table 1). Immediately below the dam, OM budgets of the river are dominated by autochthonous production of algae (Cross et al., 2011, 2013; Stevens et al., 1997). In mid-summer, the region exhibits a change in precipitation patterns associated with the monsoon, which typically spans mid-July to mid-September. We tested whether consumers’ allochthony responded significantly to distance from dam and whether this relationship differed before and after monsoon rains. In addition, we asked whether tributaries modify the seasonal dependence of the Colorado River on algae, and how pulsed flows of terrestrial OM resulting from monsoon thunderstorms influence food-web structure. We hypothesized that large tributaries would create seasonal discontinuities, abruptly increasing the dependence of consumers on terrestrial resources post-monsoon that would manifest as an increase in FCL and trophic diversity.

2 | MATERIALS AND METHODS

2.1 | Study site and sampling design

Our study took place in 2006 along a 388-km reach of the Colorado River below Glen Canyon Dam, Arizona, USA (Figure S1 in Appendix S1). The Colorado River below Glen Canyon Dam is a large river (average daily discharge in 2006 c. 332 m³/s) with highly regulated flows resulting in daily fluctuations in stage of nearly 1 m.

The river is canyon bound, with local geomorphology influenced heavily by tributary junctures that enhance productivity and alter the carbon basis of production and energy flow (Cross et al., 2013), even though average tributary discharge is $<10 \text{ m}^3/\text{s}$. We assessed the role that pulsed flows play in altering food-web structure by collecting data pre-monsoon (clear water) and post-monsoon (turbid water). Our eight sampling reaches were distributed along the Colorado River below Glen Canyon Dam (Figure S1 in Appendix S1, Table 1). The placement of our sites was chosen based on previously available physical (geomorphologic) and biological (fish abundance) data (Cross et al., 2013; Johnstone, Laretta, & Trammell, 2004). Similarly, we chose two sampling periods (June 20–July 16, 2006, *pre-monsoon*; September 14–October 11, 2006, *post-monsoon*) that reflected seasonal patterns in precipitation and turbidity, and thus, for potentially observing changes in the assimilation of different sources of plant-derived energy downstream of Glen Canyon Dam (see Appendix S1, Figure S1 in Appendix S1, and Table 1 for details).

At each site, we collected water samples for $\delta^2\text{H}$ analysis using 60-ml glass vials with no headspace. We also collected samples of the algae *Cladophora glomerata* (hereafter "*Cladophora*"), riparian vegetation (primarily tamarisk *Tamarix ramosissima* and willow *Salix* sp.), coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM). CPOM was collected mid-stream using a nylon net (mesh 25 μm), and FPOM by filtering river water through glass-fibre filters (1 μm) and a hand pump. We collected primary consumers (Simuliidae [black flies], Chironomidae [midges], *Gammarus lacustris* [amphipods] and *Potamopyrgus antipodarum* [New Zealand mud snails]) opportunistically, using kick nets and D-net sweeps and hand collections from cobbles to rocks. These few species represent most of the invertebrate biomass and production downstream

TABLE 1 Sampling reaches defined in terms of river KM from Glen Canyon Dam (RKM) along the Colorado River, Grand Canyon and their corresponding distance from Glen Canyon Dam. Several end members were also collected at RKM 26 (Lees Ferry), near the confluence of the Paria River. This opportunistic sampling was done during the pre- but not post-monsoon season, and we present the results in Figure 1. Invertebrates and fish were not collected at Lees Ferry, and hence, this site is not included in all of our analyses

Site	Reach	RKM range of named site	RKM site (actual sample location)
1	Glen Canyon	0–20	10
2	Fence Fault	73–78	74
3	Above Little Colorado river	121–124	124
4	Below Little Colorado River	126–131	127
5	Below Bright Angel Creek	163–174	168
6	Below Kanab Creek	255–265	258
7	Below Havasu Creek	279–294	287
8	Above Diamond Creek	385–388	388

of the dam (Cross et al., 2013). Finally, we used electrofishing boats and hoopnets (Makinster, Persons, Avery, & Bunch, 2010) to capture rainbow trout (*Oncorhynchus mykiss*), flannelmouth sucker (*Catostomus latipinnis*), humpback chub (*Gila cypha*), channel catfish (*Ictalurus punctatus*), bluehead sucker (*Catostomus discobolus*) and speckled dace (*Rhinichthys osculus*), and then subsampled muscle plugs (except for federally listed *G. cypha*, for which we used fin clips) for stable isotope analysis.

2.2 | Stable isotope methods

All samples were sorted and then air-dried in the field using a passive thermal oven, followed by oven-drying and pulverization in the laboratory. FPOM and CPOM samples were visually inspected for calcium carbonate, and when visible, we fumigated by exposure of the sample to hydrogen chloride vapour for 24 hr in a glass desiccator. For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, samples were weighed into tin capsules and analysed by Dumas combustion in a Costech elemental analyser coupled to a Thermo Electron Delta Plus Advantage mass spectrometer. For $\delta^2\text{H}$ analysis, samples were weighed into silver capsules and analysed by coupled pyrolysis/isotope-ratio mass spectrometry using a thermo-chemical elemental analyser interfaced to a Thermo Electron Delta Plus XL continuous flow gas-isotope ratio mass spectrometer. Water samples from both the mainstem and the tributaries were analysed for $\delta^2\text{H}$ using headspace equilibration on the Gas Bench peripheral which was also interfaced to the Delta Plus XL mass spectrometer. We conducted all isotope analyses at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University (www.isotope.nau.edu).

2.2.1 | Sources of organic matter

We assessed the contribution of autochthonous (aquatic) and allochthonous (terrestrial) energy sources to fish and invertebrate production using a Bayesian mixing model implemented in the "SIAR" R package (Parnell, Inger, Bearhop, & Jackson, 2010) (see Appendix S1). *Cladophora* was defined as the aquatic end member, and FPOM the terrestrial end member due to its similarity in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$ to riparian vegetation (Figure S2 in Appendix S1). CPOM was aquatic in origin in Glen Canyon and became terrestrial downstream (Figure 1), so it was not used as an end member. There were no missing data for the FPOM end member at any site during any season; when *Cladophora* was missing, we estimated the autochthonous end member by using the site immediately upstream during the same season (Appendix S1). We initially included $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$ in SIAR models, but there was significant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ overlap of autochthonous and allochthonous end members in both seasons across reaches. In contrast, deuterium exhibited clear separation between the aquatic and terrestrial end members in both seasons; we, therefore, focus on the models that contained $\delta^2\text{H}$. We did not include trophic enrichment factors, concentration dependence or dietary priors in the deuterium models (Appendix S1). Prior to analysis, all samples were corrected

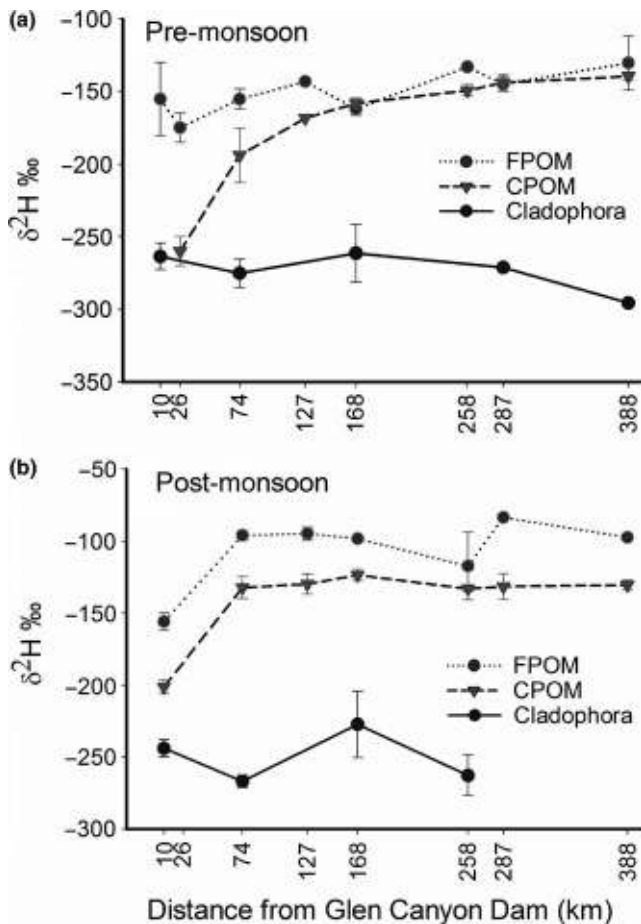


FIGURE 1 Deuterium (per mil) for coarse particulate organic matter (CPOM), *Cladophora*, and fine particulate organic matter (FPOM) in the drift. Key: RKM 10 (Glen Canyon), 26 (below the Paria River), 124 & 127 (above and below confluence of the Little Colorado River), 168 (Bright Angel Creek), 258 (Kanab Creek), 287 (Havasu Creek) and 388 (Diamond Creek), for pre-monsoon (top) and post-monsoon (bottom) data

for exchangeable hydrogen in local water vapour by the 3-point equilibration method (Wassenaar & Hobson, 2003). Fish and invertebrate data were corrected for dietary water per Solomon et al. (2009) and the $\delta^2\text{H}$ value of river water ($\mu = -106.3\text{‰}$ in mainstem; $\mu = -71.5\text{‰}$ in the Little Colorado River) using the following equation (DeKor, King, Back, Whigham, & Walker, 2012):

$$[\text{raw consumer } \delta^2\text{H} - (\text{river water } \delta^2\text{H} * 0.17)]/0.83 \quad (1)$$

2.2.2 | Food chain length

We used $\delta^{15}\text{N}$ to estimate FCL following the Maximum Trophic Position (MTP) convention, as:

$$\text{MTP} = [\text{Max } \delta^{15}\text{N Dev}]/\Delta + 2, \quad (2)$$

where Max $\delta^{15}\text{N Dev}$ is the maximum deviation in $\delta^{15}\text{N}$ between putative baseline groups and top predator species (typically, *O. mykiss*), and Δ is a trophic fractionation factor assumed to be 3.4‰ (Anderson & Cabana, 2007; Post, 2002). Our baseline group consisted of generalist primary consumers, typically black flies

(Simuliidae); hence, we added two to $[\text{Max} \cdot \delta^{15}\text{N Dev}]/\Delta$ to render Max FCL a measure of separation in $\delta^{15}\text{N}$ between basal resources and the apex predator (Appendix S1).

2.2.3 | Trophic diversity

We also quantified trophic diversity at each site as the area of $\delta^{15}\text{N}$ - $\delta^2\text{H}$ space occupied by all consumers, with relatively larger isotopic spaces being occupied reflecting a relatively higher trophic diversity among species (Layman, Arrington, Montaña, & Post, 2007). To do this, we first visualized data using convex hulls and standard ellipse areas (SEA). SEAs are equivalent to bivariate standard deviations and summarize variance in the isotopic space (here $\delta^2\text{H}$ and $\delta^{15}\text{N}$). Here, we used the Bayesian version of SEA (or SEA_b), which allows for a robust comparison among datasets (Jackson, Inger, Parnell, & Bearhop, 2011); in our case, pre- and post-monsoon food webs (Appendix S1). These analyses were made using the SIBER (Stable Isotope Bayesian Ellipses in R) functions of the "SIAR" R package (Parnell et al., 2010).

2.2.4 | Statistical analysis of spatiotemporal patterns

We used General Additive Models (GAM) to fit nonlinear responses and 95% confidence intervals to longitudinal changes in allochthony by consumers (i.e. mode dietary proportion of FPOM, the allochthonous end member). Allochthony for each consumer was the response variable, and distance from dam and season was explanatory variables. To assess longitudinal variation in allochthony, distance from dam was the smoothing term, whereas season was a nominal variable (pre- vs. post-monsoon). We generated two sequential models (i.e. $\text{GAM}_{\text{global}}$, $\text{GAM}_{\text{seasonal}}$) for each consumer taxa, where $\text{GAM}_{\text{global}}$ merged the two seasons and $\text{GAM}_{\text{seasonal}}$ provided a regression spline for each season. For each consumer, we selected the best model ($\text{GAM}_{\text{global}}$ or $\text{GAM}_{\text{seasonal}}$) using Akaike information criterion (AIC). GAMs were fitted using the "mgcv" R package (Wood & Wood, 2016).

2.3 | Quantifying flood-pulse variability in the Grand Canyon

The strength of the monsoon and flood pulse in the Colorado River from Glen Canyon Dam to Lake Mead is variable. To give historical reference for our single-year observations, we quantified seasonal and stochastic variation in daily discharge of key tributaries over the 10-year period preceding our sampling. We quantified stochastic variation using the Discrete Fast Fourier Transform (Sabo & Post, 2008) on US Geological Survey (USGS) daily average discharge data for the Paria River, Little Colorado River and Bright Angel Creek. We also estimated spatial and inter-annual variation in the tributary flood pulse entering the Colorado River mainstem in the Grand Canyon, as the annual sum of daily discharge above normalized annual discharge:

$$\text{extent} = \sum_{t=1}^d (Q_t - 1), \forall Q_t > 1, \quad (3)$$

where Q_t is log₁₀-transformed and demeaned, or normalized daily average discharge at time t (in days), d is duration (days) of high flow ($Q_t > 1$), and normalized annual discharge is unity. This definition of flood-pulse extent is similar to that of Welcomme (1979), but we use normalized annual instead of bankfull discharge because our purpose is not to estimate overbanking, but rather above-average inputs to the mainstem.

3 | RESULTS

3.1 | Aquatic and terrestrial organic matter in the food base

During the pre-monsoon (clear water) period, $\delta^2\text{H}$ signatures for *Cladophora* and FPOM changed very little with distance from GCD. $\delta^2\text{H}$ of FPOM was consistently c. 100 ‰ more enriched than $\delta^2\text{H}$ of *Cladophora* (Figure 1a), reflecting a predominance of terrestrial OM sources in FPOM (see Figure S2 in Appendix S1 for comparison to terrestrial vegetation). $\delta^2\text{H}$ values for CPOM reflect strong dominance by *Cladophora* in Glen Canyon, but $\delta^2\text{H}$ enrichment reveals an increasing contribution of terrestrial OM after the confluence of the Paria River until it reaches a peak (nearly pure terrestrial OM) below the LCR and Bright Angel Creek at approximately river kilometres (RKM) 127 and 168, respectively. During the post-monsoon period, $\delta^2\text{H}$ signatures of *Cladophora* were almost identical to those of the dry season in Glen Canyon (Figure 1a,b). FPOM $\delta^2\text{H}$ values were similar in Glen Canyon between the pre- and post-monsoon periods but became enriched post-monsoon, likely reflecting an input of terrestrial matter from the Paria River (RKM 26). CPOM $\delta^2\text{H}$ was

intermediate during the monsoon, falling between *Cladophora* and FPOM in Glen Canyon, but its signature was enriched reflecting a contribution of more terrestrial sources of OM from the Paria River tributary. Hence, during the dry and wet seasons, the signature of the detrital portion of the resource base of the food web (CPOM) was autochthonous in Glen Canyon, but reverted to allochthonous (terrestrial) within c. 168 km of GCD. In addition, the portion of terrestrially derived detritus in the FPOM fraction increased after monsoon floods.

3.2 | Consumer responses to changes in the food base

The primary consumers examined here (Simuliidae, *G. lacustris* and *P. antipodarum*) represent a broad range of functional feeding groups, including filter feeders, collector-gatherers and grazer-scrapers. All three consumer groups were generalists, feeding on a mixture of autochthonous and allochthonous resources, but two of the three groups showed increased reliance on terrestrial sources of OM post-monsoon (Figure 2a,c,e). Across all sites sampled in the river, an average of 6%–54% of Simuliidae diet by site was derived from terrestrial sources pre-monsoon, which increased to 35%–73% after pulsed flows occurred. Likewise, *P. antipodarum* diet averaged 17%–42% terrestrial in the dry season but increased to 21%–59% terrestrial after monsoon flooding occurred. *G. lacustris* was not as influenced by tributary inputs, as terrestrially derived OM in the diet averaged 39%–62% pre-monsoon and 12%–78% post-monsoon (Figure 2). All three primary consumers showed lower allochthony (proportion terrestrial organic H) in Glen Canyon (RKM 10) than at

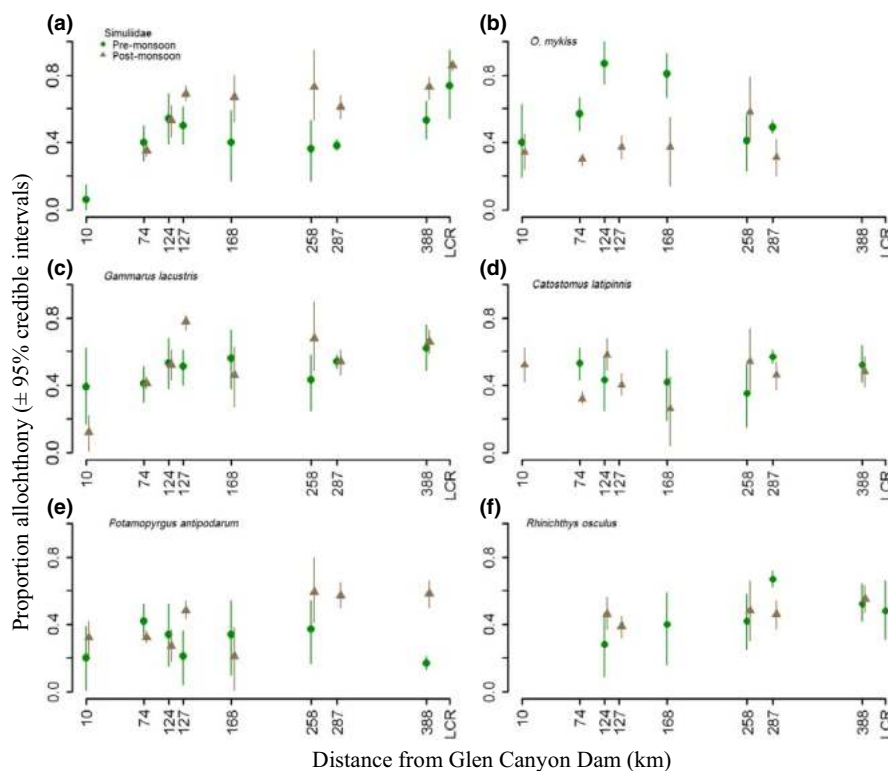


FIGURE 2 Proportion of allochthony (mode \pm 95% credible intervals) for invertebrates [left (a, c and e)] and fish [right (b, d and f)] during the dry season (pre-monsoon, green circles) and wet season (post-monsoon, brown triangles). We also show data when available for the Little Colorado River (LCR) and add these to the right of the Colorado River sites to reflect the independence of the LCR from the Glen Canyon Dam discontinuum in the mainstem

most sites downstream of the first major tributary (Paria River). All three primary consumers also had higher allochthony immediately downstream of the largest tributary (Little Colorado River), but only after post-monsoon floods. Furthermore, this large change in allochthony was measured over a distance of just 3 km (RKM 124-127; Figure 2a,c,e).

Secondary consumers (fish) included non-native, semi-piscivorous *O. mykiss* and two native insectivores, including *C. latipinnis* and *R. osculus*. All fishes showed moderate to high levels of allochthony from GCD to Lake Mead in both seasons (Figure 2b,d,f), with *O. mykiss* deriving 40%–87% of dietary OM from terrestrial sources pre-monsoon and 30%–58% post-monsoon. For *C. latipinnis*, pre-monsoon allochthony was 35%–57% and post-monsoon was 26%–58%. *R. osculus* derived 28%–67% of their diet from terrestrial sources pre-monsoon and 39%–55% post-monsoon (Figure 2). In general, allochthony did not vary between Glen Canyon (RKM 10) and the Grand Canyon (all other sites) for *C. latipinnis*, but was higher in the Grand Canyon for *O. mykiss*. Interestingly, allochthony was highest in mid-reaches of the Grand Canyon (at the LCR and Bright Angel Creek confluences) for *O. mykiss* but during the pre- rather than post-monsoon season. This result is the opposite of that for primary consumers, which exhibited peak allochthony in post-monsoon at mid to lower reaches of Grand Canyon (i.e. Kanab, Havasu and Diamond Creeks). For most secondary consumers, allochthony increased with distance from GCD, either linearly or as a saturating function with maximum allochthony occurring somewhere between the confluence of the LCR and our last sampling site (Diamond Creek, RKM 388; Figure 3). Longitudinal allochthony profiles were significantly different in shape between pre- and post-monsoon seasons for all consumers, except *C. latipinnis*, for which allochthony did not vary in space or time (Figure 3). Generalized additive models for primary consumers showed that longitudinal change (with distance from dam) was stronger post-monsoon than pre-monsoon (Table 2). In the case of secondary consumers, patterns were more variable and smoothers of the selected models were not significant (Table 2). Overall, season-specific profiles were better supported than global profiles, with the only exception of *C. latipinnis*, which had nearly identical allochthony across space and time (Figure 3, Table 2).

3.3 | Longitudinal patterns of food-web structure

Food chain length varied longitudinally, with the pattern of this longitudinal variation being qualitatively different between pre- and post-monsoon seasons (Figure 4). During the pre-monsoon season, MTP was lower overall than during the post-monsoon season and declined linearly with distance from dam. By contrast, MTP was higher overall following the monsoon and peaked in the mid-Grand Canyon, near the LCR confluence. Our opportunistic sampling did not allow us to estimate MTP from the same species in all locations during both seasons. In general, MTP was measured using Simuliidae as the baseline organism and the apex predator was *O. mykiss*, though there were notable exceptions (Table 3). Given the proximity of the two LCR confluence sites (3 km), and highly mobile

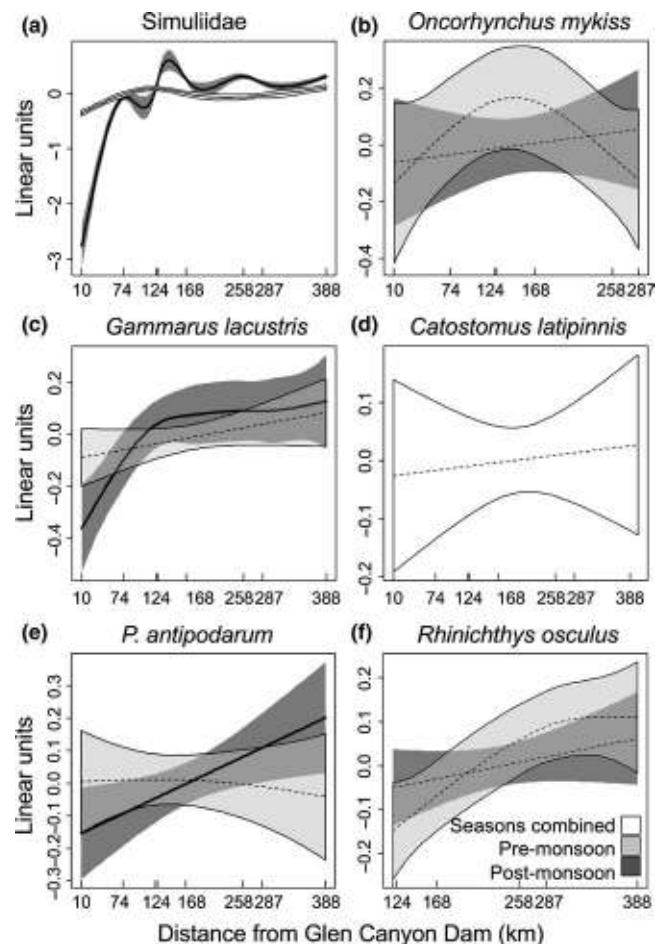


FIGURE 3 Visualization of the general additive models (GAM) testing for longitudinal responses in consumer allochthony (see details in Table 2). Season-specific splines are shown for taxa that supported season-specific responses better than a global response (i.e. all taxa except *Catostomus latipinnis*). *C. latipinnis*' global response is shown in white 95% confidence interval bands, pre-monsoon responses are shown in light grey, and post-monsoon in dark grey. Solid splines represent significant smoother effects, and dashed splines represent non-significant smoother effects. Y-axes represent normalized linear units; lettering corresponds to taxa in Figure 2: (a) Simuliidae, (b) *Oncorhynchus mykiss*, (c) *Gammarus lacustris*, (d) *C. latipinnis*, (e) *Potamopyrgus antipodarum* and (f) *Rhinichthys osculus*

top predators (especially from upstream to downstream) we pooled top predators into a single site (RKM 125) within each season. MTP increased by more than one trophic level at the LCR confluence during the monsoon and remained more than one trophic level longer in post- vs. pre-monsoon samples from the LCR confluence downriver to Diamond Creek during the monsoon (Figure 4, Table 3).

There was a high degree of isotopic overlap in $\delta^{15}\text{N}$ – $\delta^2\text{H}$ space among locations, and greater variation in trophic diversity, in the post- relative to pre-monsoon season (Figure 5a,b). In particular, the standard ellipse area (SEA) in RKM 168 (confluence with Bright Angel Creek) encompassed most of the isotopic space of all other locations in post-monsoon, despite subtle drift in the ellipse centroid among these other locations (Figure 5b). This suggests that the Bright Angel

TABLE 2 Results of the general additive models (GAM) fitted to test for responses in consumer allochthony to distance from dam. Two different model structures were compared: seasons combined (GAM_{global}) vs. seasons separated (GAM_{seasonal}). The model with a relatively better fit (i.e. lower AIC) and the corresponding degrees of freedom and adjusted R^2 (Adj- R^2) are shown in bold. GAM_{global} has a single smoother effect of distance from dam on allochthony; GAM_{seasonal} has season-specific smoother effects (pre- and post-monsoon). The corresponding F and p -values are shown

Organism	GAM model	df	AIC	Adj- R^2	Effect	F	p -value
Simuliidae	Global	4.76	-10.86	.461	Global	3.851	.0372
	Seasonal	13.9	-68.21	.981	Pre-monsoon	45.34	.0211
					Post-monsoon	58.17	.0166
<i>Gammarus lacustris</i>	Global	4.49	-18.21	.462	Global	4.622	.0208
	Seasonal	5.94	-21.47	.586	Pre-monsoon	2.423	.14741
					Post-monsoon	6.064	.00842
<i>Potamopyrgus antipodarum</i>	Global	3.00	-11.28	.0737	Global	2.115	.169
	Seasonal	4.21	-13.48	.249	Pre-monsoon	0.064	.8782
					Post-monsoon	6.287	.0275
<i>Oncorhynchus mykiss</i>	Global	3.56	0.096	.0234	Global	0.505	.609
	Seasonal	4.95	-1.609	.212	Pre-monsoon	1.773	.226
					Post-monsoon	0.348	.571
<i>Catostomus latipinnis</i>	Global	3.08	-18.98	-.0463	Global	0.236	.67
	Seasonal	4.00	-16.95	-.149	Pre-monsoon	0.125	.730
					Post-monsoon	0.182	.678
<i>Rhinichthys osculus</i>	Global	3.00	-15.91	.389	Global	6.721	.0315
	Seasonal	4.78	-17.46	.528	Pre-monsoon	4.700	.0547
					Post-monsoon	1.758	.2311

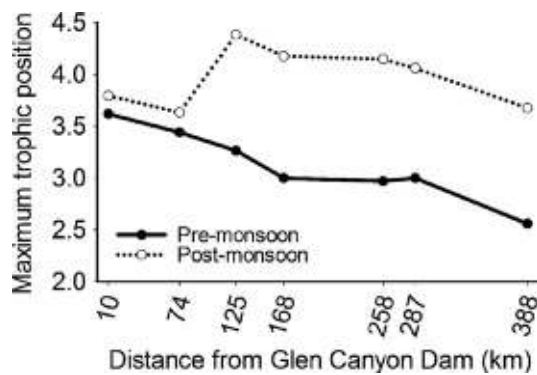


FIGURE 4 Maximum trophic position (sensu Post, 2002) based on $\delta^{15}\text{N}$ for piscivorous fish (mostly *Oncorhynchus mykiss*) during dry season (pre-monsoon, filled circles) and wet season (post-monsoon, open circles). See Table 3 for baseline and apex predator species used in Maximum Trophic Position (MTP) calculations. All data are point estimates for the individual apex predator with the greatest TP (i.e. MTP) at the site, hence no error bars. RKM 125 is MTP of the fish with largest TP captured between RKM 124–127

Creek confluence is representative of all trophic pathways upstream and is the source of new trophic diversity for the basin below this tributary confluence. When computing this metric in a Bayesian framework to take into account uncertainty in the sampled data, we confirmed the relatively higher longitudinal variation in trophic diversity post-monsoon (Figure 5c,d). In both seasons, the median of

the estimate peaked at RKM 168. In addition to RKM 168, trophic diversity was also significantly higher in post- than in pre-monsoon at RKM 10, 124–127 (LCR), 258 (Kanab Creek) and 287 (Havas Creek). These results suggest that tributary inputs significantly altered the resource base and increased the diversity of trophic pathways available to consumers, resetting the river from a system dominated by algae to one in which both algae and terrestrial resources form the base of the food web, particularly following pulsed floods.

3.4 | Spatial and inter-annual variation in discharge and tributary flood-pulse extent

Major tributaries to the Colorado River in the Grand Canyon exhibited flashy hydrographs with undetectable periodicity and hence, no seasonal trends (sensu Sabo & Post, 2008; Sabo et al., 2012). Tributary flood-pulse extent varied over nearly an order of magnitude (Figure 6). Peak discharge tended to be bimodal, with peaks in winter and summer, reflecting frontal storms from the west (January–March) and monsoon precipitation from the south (July–October). Winter precipitation and flooding during our 2006 sampling campaign were negligible compared with discharge patterns of the past decade (Figure 6a,c,e). By contrast, the 2006 monsoon appeared to have been more dominant, and flood-pulse extent was average or below average for 2006 compared with annual totals across the past decade (Figure 6b,d,f). Overall, the flood pulse in the LCR was the strongest in normalized and absolute units. Finally,

TABLE 3 Maximum trophic position (MTP) and baseline and apex predator species used in MTP calculations in Figure 4. Other abbreviations are Pa (*P. antipodarum*), Gl (*G. lacustris*), Sim (Simuliidae), Om (*O. mykiss*), Gc (*G. cypha*), Ip (*I. punctatus*) Cdj (*C. discobolus*). For Figure 4, we pooled fish across RKM 124 and RKM 127 (i.e. RKM 125) and used the highest MTP from the two sites within each season (see Materials and Methods for details)

Season↓	Distance from Glen Canyon Dam (km) →	10	74	125	168	258	287	388	LCR (tributary)
Pre-monsoon	MTP	3.62	3.44	3.26	2.97	2.85	3.00	2.56	4.44
	Baseline	Pa	Gl	Sim	Sim	Sim	Sim	Pa	Sim
	Apex predator	Om	Om	Cdj	Om	Om	Om	Ip	Gc
Post-monsoon	MTP	3.79	3.63	4.38	4.18	4.15	4.06	3.68	NA
	Baseline	Pa	Sim	Sim	Sim	Sim	Sim	Sim	NA
	Apex predator	Om	Om	Om	Om	Om	Om	Cdj	NA

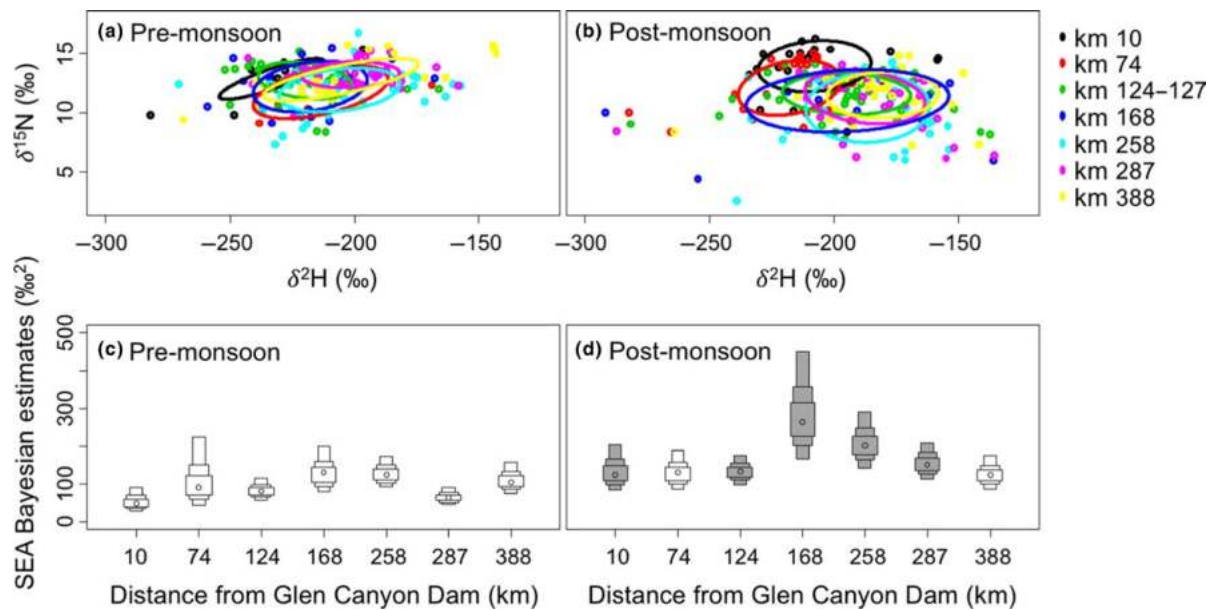


FIGURE 5 Longitudinal variation in trophic diversity in pre- and post-monsoon. By combining stable isotope data ($\delta^{15}\text{N} - \delta^2\text{H}$) of consumers, we obtained the standard ellipses (solid coloured lines) of the food web of each RKM, pre- (a) and post-monsoon (b). The corresponding credible intervals for standard ellipse area (SEA) are shown for each RKM in pre- (c) and post-monsoon (d), with grey shading indicating the RKM where trophic diversity was significantly higher ($p < .05$) in post- than in pre-monsoon (as indicated by the distribution of posterior ellipses)

pulsing was asynchronous across tributaries—localized bursts from monsoon storms and storm paths of Pacific storms caused flooding in a spatially heterogeneous fashion (Figure 6).

4 | DISCUSSION

Dams create serial discontinuity in the river continuum (Ward & Stanford, 1983), and it has been proposed that tributaries—especially those draining a large area—can restore physical and biological properties along a river continuum (Pracheil et al., 2013; Sabo et al., 2012). Here, we showed that the Little Colorado River and other Grand Canyon tributaries reset the discontinuity inherent to the Colorado River downstream of Glen Canyon Dam. The suspended

detrital pool (CPOM) was initially almost entirely algae, and became nearly completely terrestrial following the input of the largest Grand Canyon tributary, the Little Colorado River. The $\delta^2\text{H}$ signature of FPOM did not change (c. -150‰) across all reaches during the dry season. By contrast, the $\delta^2\text{H}$ signature of FPOM became enriched post-monsoon from c. -150‰ downriver of Glen Canyon Dam to c. -100‰ starting below the Paria River confluence. The proportion of allochthonous material in the diet of most consumers increased with distance from the dam, especially for primary consumers. Food chains were longest and food webs had the most diverse set of trophic pathways where the Little Colorado River and Bright Angel Creek join the mainstem river, especially following seasonal pulse flows. Longitudinal profiles for isotope signatures of CPOM, proportional allochthony of consumers, food chain length, and trophic

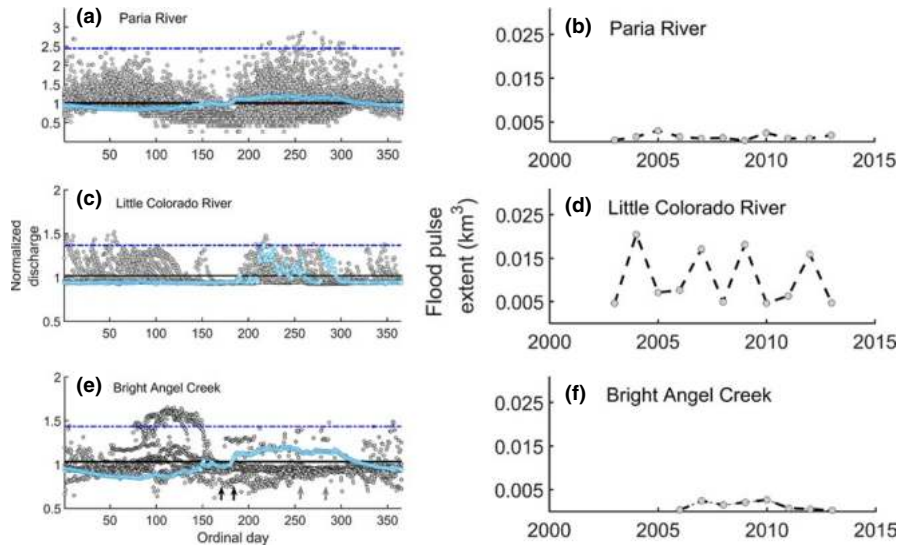


FIGURE 6 Hydrographs (left; a, c, e) and estimated tributary flood-pulse extent (right; b, d, f) for three major Colorado River tributaries in the Grand Canyon (increasing in distance from Glen Canyon Dam from top to bottom). Hydrographs are daily average discharge data (black points), normalized discharge (solid black line), flood magnitude with 2-year recurrence interval (blue dotted line). We highlight with light blue circles the daily average discharge measurements for 2006—the year food-web structure was analysed in this study. Flood-pulse extent (described in more detail in text) is in m^3

diversity varied by season—typically monotonic before the monsoon and unimodal or saturated after the monsoon. These results imply that pulse flows may be able to reset serial discontinuity and food-web structure in heavily regulated rivers.

One of the most immediate ecosystem effects below Glen Canyon Dam is the dominance of the food base by algae (Cross et al., 2011), and subsequent export of this autochthonous resource downstream to the drifting, coarse detrital pool. By contrast, FPOM retains the signature of terrestrial leaves and hence, detritus (Figure S2 in Appendix S1), likely a result of integration of terrestrial resource inputs throughout the watershed above Lake Powell. This terrestrial signature provides a baseline for recovery of the detrital pool to unregulated conditions. Primary production by algae is highest in the clear tailwater and dominates CPOM directly below Glen Canyon Dam, likely because canyon riparian zones and ephemeral tributary drainages contribute <0.1% of the total drainage area, two primary sources of terrestrial CPOM to the Glen Canyon reach (Webb, Griffiths, Melis, & Hartley, 2000). CPOM rapidly shifts to a terrestrial signature downstream of the Paria River, the first perennial tributary, reflecting an increasing contribution of terrestrial portions of the drainage below GCD to the suspended detrital pool. CPOM becomes identical to FPOM at approximately the juncture of the LCR. The decelerating approach of the CPOM $\delta^{2}\text{H}$ signature to that of upstream FPOM suggests that local terrestrial OM, from Grand Canyon riparian vegetation and upland areas, is an important contributor to the aquatic detrital pool. Nevertheless, we observed abrupt increases in the terrestrial signature (enriched $\delta^{2}\text{H}$) of CPOM below the juncture of the Paria River (RKM 26) and LCR (RKM 127) during the monsoon, suggesting that pulse flows from monsoon rains contribute terrestrial CPOM to the mainstem beyond background fluxes from adjacent canyon riparian vegetation.

Primary consumers incorporate an increasing proportion of terrestrial OM and hence allochthony into their diet longitudinally from GCD to Lake Mead. The saturating increase in allochthony with distance from GCD for filter feeders and collector/gatherers closely follows observed changes in $\delta^{2}\text{H}$ of CPOM during the monsoon,

suggesting these consumers may be more dependent on terrestrial resources after the flood pulse. Notably, all three species of primary consumers examined show stronger allochthony after the monsoon, especially downstream of the LCR confluence. Finally, allochthony increases between sites above and below the LCR confluence after the monsoon for all three species, but diet becomes more algal during the clear water season across this same small spatial scale. These data suggest that while local riparian sources of terrestrial OM contribute to primary consumer production between GCD and Lake Powell, the relative influence of terrestrial OM from tributaries is elevated following monsoon rains and floods which likely both flush terrestrial OM into the mainstem Colorado River.

Like primary consumers, allochthony increased with distance downstream for all secondary consumers examined. Native and non-native secondary consumers (*R. osculus* and *O. mykiss*) appear to integrate an increasing proportion of prey derived from terrestrial sources of OM with distance from GCD, but this linear trend is not different before and after the monsoon for *C. latipinnis*. Interestingly, the seasonal differences in longitudinal profiles of allochthony for the introduced species, *O. mykiss*, are reversed when compared with primary consumers. Specifically, pre-monsoon, allochthony peaks near the LCR confluence for *O. mykiss*, in spite of significant primary production upstream in Glen Canyon. We hypothesize that the higher terrestrial signal of these visual-feeding apex predators may reflect higher reliance on subsidies of terrestrial herbivores during clear water conditions, which are more conducive to surface feeding. Moreover, we hypothesize that the importance of these subsidies may peak near the juncture of the LCR where riparian forests are more developed both in the canyon and in proximate reaches of the LCR itself. Pulse flows during the post-monsoon season impair visual feeding in *O. mykiss* downriver of tributary junctions, thereby shifting reliance from terrestrial subsidies to aquatic drift or to stored energy reserves.

Monsoon flooding in the three largest tributaries in the Grand Canyon was highest in the mid-reach (LCR) and was generally high in lower canyon tributaries such as Bright Angel Creek (Figure 6). This

spatial variation in the tributary flood pulse corresponds well to variation in mainstem food webs in space and time. Food chain length and trophic diversity are both higher during the monsoon and peak at the confluence of mid-reach tributaries. The change in FCL over the c. 50 km reach that separates the Fence Fault and LCR sites is on the order of $\frac{3}{4}$ of a trophic level (increase) during the monsoon, and we observe an increase of 1–1 $\frac{1}{4}$ trophic levels at all sites at and below the LCR confluence after the monsoon, with differences diminishing from the LCR downstream. Trophic diversity is highest below the confluence of Bright Angel Creek and encompasses the $\delta^{15}\text{N}$ – $\delta^{2}\text{H}$ bivariate space of consumers at almost all other river locations. Hence, this mid-reach (from LCR to Bright Angel Creek), where tributary inputs are substantial, has the most complex food web.

We hypothesize that peak FCL below the LCR confluence results from increased consumption of aquatic prey flushed into the Grand Canyon mainstem from the LCR during pulse flows following monsoon rains. These tributary resources are likely primary consumers (Simuliidae) that exhibit depleted $\delta^{15}\text{N}$ signatures. Higher MTP for fish in the LCR than the mainstem during the clear water season (Table 3) and 4–5% lower $\delta^{15}\text{N}$ of primary consumers in the LCR compared to average values across the Grand Canyon during the clear water season (Chironomidae, 5.0%; Simuliidae, 4.1%, respectively) support this hypothesis. Note that this hypothesis is mutually consistent with lower allochthony and higher MTP during the monsoon for apex predators at the LCR. Floods displace and kill tributary fauna and provide a seasonally fleeting aquatic resource base for mainstem apex predators. While FCL peaks below the LCR confluence, our results show a clear linear decline in FCL from the LCR to Lake Mead during both seasons. This is likely due to increased consumption of *Cladophora* in the lower reaches of the river by secondary consumers. Diet studies corroborate this, *O. mykiss* consumes significant quantities of *Cladophora*, especially in lower reaches of the river (Cross et al., 2013). Hence, omnivory—here eating lower on the food chain—by apex predators leads to linear declines in FCL in the lower river.

Trophic diversity was highest between the LCR and Bright Angel Creek confluences, and this trend was more pronounced after the monsoon. We hypothesize that maximum diversity mid-canyon occurs due to overlap between the algal-dominated food base characteristic of the upper river and the terrestrial and detrital dominance of the food base in the lower river. In this segment of the canyon, the CPOM becomes nearly completely terrestrial but nonetheless both benthic and suspended algae and terrestrial CPOM from the channel are available. Moreover, tributary inputs of terrestrial CPOM and likely aquatic invertebrates and fish during monsoon floods may contribute further to the higher diversity of resources near Bright Angel Creek. Finally, previous work suggests that tributary food webs—especially Bright Angel Creek—are unique and fundamentally different than simplified mainstem food webs (Whiting, Paukert, Healy, & Spurgeon, 2014) and may, therefore, contribute to enhanced diversity of potential trophic pathways connecting resources to consumers near the Bright Angel Creek confluence. Pulse flows through tributaries during the monsoon reset the food web—increasing FCL and increasing niche width and trophic diversity.

4.1 | Applications of tributary pulse flows

Two of our findings are relevant to management of large rivers with mainstem dams. First, it is important to protect unregulated tributaries even if they do not significantly alter mean annual discharge. Second, hydrographs exhibiting high degrees of seasonal variation or flashy hydrographs in unregulated tributaries can improve trophic diversity and lengthen food chains in mainstems, but these outcomes are observed over seasonal time scales.

Our results derive from a single, emblematic but arguably idiosyncratic system; hence, extrapolation of precise management prescriptions for other rivers should be approached with caution. Nevertheless, we think that the observed results offer an interesting point of departure for developing rules of thumb for the management of river networks, especially those in which buildout of new dams is imminent. First, although the LCR has a large basin area (c. 19% of the total basin area measured at Lees Ferry), the relative discharge is quite low. Specifically, the 10-year mean of daily average discharge for the Little Colorado River is 10.5 m³/s and this tributary input represents <3% of mean annual mainstem discharge at Lees Ferry (354.5 m³/s). Hence, even tributaries in catchments with relatively low discharge levels can be important conservation assets.

Second, although discharge from the Little Colorado River is small relative to the mainstem, day-to-day variation in average daily discharge is exceptional relative to other tributaries in the Colorado River basin. For example, a single month (August) contributed 19% of mean annual flow in 2010, the wettest year within the relatively short 2007–2016 record. Hence, tributaries with seasonal (monsoonal) and/or relatively more stochastic (low relative signal-to-noise ratio, SNR sensu Sabo & Post, 2008) should provide higher conservation value to mainstem rivers with hydropower cascades, especially if tributary flow pulses (and associated sediment, nutrients, detritus and organisms) are asynchronous with mainstem peak discharge.

Finally, we propose that the size of the tributary (in terms of contributing discharge) likely matters more when flow regime seasonality is synchronous with the mainstem and/or highly seasonal rather than stochastic (high SNR, sensu Sabo & Post, 2008). We suspect that this hypothesis and our proposed rules of thumb could be relevant beyond the Grand Canyon. For example, the Yampa River in the upper Colorado River basin (tributary to the Green River and ultimately Lake Mead) is unregulated and resets the thermal regime and discharge variability of the Green River downstream of its confluence (Sabo et al., 2012). Regulation of this river would dampen the restorative effects of unregulated Yampa flows and extend the downstream influence of Flaming Gorge Dam and Reservoir higher up on the mainstem (Green) river.

Beyond the Colorado River, our observation of seasonal (flood pulse) dynamics during the monsoon may allow us to extrapolate to hydropower development in other river basins with monsoons and a flood pulse. Flood-pulse systems world-wide are experiencing rapid impoundment in upland tributary catchments (Figure S3 in Appendix S1) that may block the pipeline of organic matter and source of secondary production from reaching downstream floodplains (Winemiller et al., 2016). For example, some 87%–92% of

dams in place or under construction on the Mekong, Congo and Amazon rivers are on tributaries. More than 70% of those dams proposed for construction on the Amazon and Mekong are similarly slated for tributaries. Our findings suggest that careful planning and protection of unregulated tributaries within the context of larger hydropower cascades could be an important management tool for maintaining ecosystem function and food-web structure in these changing and globally iconic rivers. Specifically, a modest set of reasonably sized tributaries could be used to provide seasonal variation and enhance production of non-migratory or locally migrating fishes vital for food security in rivers where inland fisheries prevail.

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AUTHORS' CONTRIBUTIONS

T.A.K., J.L.S., M.C. and R.D. conceived the ideas and designed methodology; M.C. and R.D. collected the data; M.C., J.L.S., K.L.D. and A.R. analysed the data; J.L.S. and B.A.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the USGS ScienceBase <https://doi.org/10.5066/f7fx78cv> (Dibble, Sabo, Ruhi, & Kennedy, 2018).

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SUPPORTING INFORMATION

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