Annals of Ecology and Environmental Science
Volume 4, Issue 2, 2020, PP 1-16
ISSN 2637-5338

Benthic Discontinuity between an Unregulated Tributary and the Dam-Controlled Colorado River, Grand Canyon, Arizona, USA

Lawrence E. Stevens[1*], Joseph H. Holway[1], and Craig Ellsworth[2]

[1] *Biology Department, Museum of Northern Arizona, 3101 N. Ft. Valley Rd., Flagstaff, USA.*
[2] *Western Area Power Administrations; Salt Lake City, UT*

***Corresponding Author:** Lawrence E. Stevens, Biology Department, Museum of Northern Arizona, 3101 N. Ft. Valley Rd., Flagstaff, USA.*

ABSTRACT

Comparative analysis of factors influencing benthic macro invertebrate (BMI) assemblages in unregulated tributaries can inform management about tributary to mainstream discontinuities (TMDs) with adjacent regulated mainstream rivers. Tapeats Creek is a cool-water tributary of the highly regulated Colorado River ecosystem in Grand Canyon downstream from Glen Canyon Dam, having similar geochemistry, water temperature, and annual relative flow variability compared to the mainstream. The creek supports a diverse BMI assemblage, including Ephemeroptera, Plecoptera, and Trichoptera (EPT) that are absent in the mainstream. We used field measurements and experiments in six microhabitats around the creek mouth to test the impacts of water quality (temperature, geochemistry), flow variability, and substrate embeddedness impacts on BMI distribution, particularly during stepped hydropower-related mainstream stage shifts. The Tapeats Creek TMD was not attributable to temperature, geochemistry, or contemporary low-level hydropower flow fluctuations, but rather to natural embeddedness in mainstream substrata. Tap eats Creek is floored with gravel and cobble, with much interstitial space, whereas the mainstream benthos was composed of cobble/boulders embedded in fine sand, with marginal to suboptimal EPT habitat. The TMD was likely more pronounced in pre-dam time and from 1964-1990 due to larger seasonal and daily flow fluctuations and more prolonged confluence inundation, respectively. The Colorado River in Grand Canyon is adaptively managed to balance hydropower production, fine sediment mass balance for recreational camping and shoreline habitat, as well as native and recreational fisheries. However, strategies to promote both fine sediment storage and an optimal mainstream food base for fish are not be mutually compatible. Thus, not all desired river ecosystem conditions may be simultaneously achieved.

***Keywords:** Benthic macro invertebrate ecology, discontinuity, Colorado River, embeddedness, EPT, Glen Canyon Dam, Grand Canyon, tributary*

INTRODUCTION

Tributaries modify fluvial ecosystems by structuring geomorphology, creating abrupt reach breaks and discontinuities, increasing suspended sediment load, altering water quality (temperature, geochemistry), and by influencing both downstream and upstream ecological contributions and processes (Bruns et al. 1984; Stevens et al. 1997;Rice et al. 2001; Kiffney et al. 2006; Meyer et al. 2007; Wilson & Mc Tammany 2014; Connolly &Pearson 2018). Benthic macroinvertebrate (BMI) assemblages are indicators of fluvial ecosystem and fisheries foodbase integrity, and often are altered by flow regulation, fine sediment deposition, and other anthropogenic activities (Campbell et al. 1982; De Jalon et al. 1994; Sennatt et al. 2006;Katano et al. 2009; Cross et al. 2013; Wharton et al. 2017). Among BMI, Ephemeroptera, Plecoptera, and Trichoptera (EPT) often are regarded as key indicators of stream ecological integrity. BMI discontinuities (sensu Stanford &Ward 1983) naturally exist between tributaries and mainstream rivers, a phenomenon we refer to here as a tributary-to-mainstream discontinuity (TMD). TMDs arise from differences in Strahler stream order, hydrogeology, anthropogenic use, and other factors, and can be exacerbated by flow regulation, but the frequency and causality of such discontinuities are insufficiently studied. Tributaries can serve as refugia and can mitigate dam-generated physical &biotic discontinuities. Comparative measurements and field experiments on BMI assemblages inregulated mainstream rivers and selected unregulated tributaries can reveal the factors influencing TMDs, and improve understanding of fluvial ecosystem ecology, habitat structure, food base, and fisheries stewardship options (Campbell et al. 1982; Ward &Stanford 1983; Bruns et al. 1984, Vincent 2001; Connolly &Pearson 2018).

TMDs are ubiquitous among the BMI assemblages in Grand Canyon perennial tributaries of the Colorado River (Hofknecht 1981;Oberlin etal. 1999), but the array of factors precluding successful mainstream colonization by BMI are debated. Colorado River and other TMDs have been attributed to differences in watershed characteristics (Oberlin et al. 1999), mainstream flow variability (Hofknecht 1981; Kennedy et al. 2016), sediment deposition and water quality (Newcombe &MacDonald 1991; Stevens et al. 1997; Wood& Armitage1997), mainstream failure of key life history phases (Kennedy et al. 2016), fish predation (Shaw &Richardson 2001), and other mechanisms. Kennedy et al. (2016) emphasized the negative impacts of mainstream hydro peaking flows on BMI egg survivorship, limiting mainstream colonization primarily to nematoceran Dipteraspecies that lay eggs on the water surface and thus avoid desiccation related to fluctuating flows. While that explanation may partially explain the long-recognized depauperate condition of the mainstream BMI assemblage (Blinn &Cole 1991; Stevens etal.1997; Cross etal.2013), the high frequency of TMDs in Grand Canyon suggests that mainstream colonization failure occurs among larvae and some adult BMI (e.g., elmid beetles) that drift from tributaries into the mainstream, rather than suppression of egg survivorship by fluctuating mainstream flows. Additional research is needed to identify potential flow and/or non-flow management options to improve foodbase production and fisheries management in the Colorado River and other regulated rivers.

Figure1. *Aerial image and inset map of Tapeats Creek and the six microhabitats sampled in 2017: DOC - downstream outflow channel, LCR - lower Colorado River (downstream from the creek mouth), TC - Tapeats Creek, UCR - upper Colorado River (control not influenced by Tapeats Creek), UOC - upstream outflow channel, and UVC - upper varial channel.*

Here we present data from field measurements and experiments at the confluence of a large, cool water, nearly pristine tributary in central Grand Canyon to improve understanding how and why BMI assemblage composition, structure, and development differs from the adjacent, intensively regulated Colorado River (Fig.1). A smaller stream than the Colorado River, Tapeats Creek nonetheless has water quality and relative flow variability that closely match water released from Glen Canyon Dam, making it the only tributary in Grand Canyon at which such an ecological comparison can be made. Similar in temperature and geochemistry to water released from the dam, Tapeats Creek has elevated EPT density, a benthic fauna greatly contrasting that in the adjacent mainstream (Hofknecht 1981;Blinn &Cole 1991; Stevens etal. 1997;Oberlin et al. 1999; Cross et al. 2013). However, the causal factors for this abrupt discontinuity remain unclear.

Although unique among the approximately 50 perennial tributaries to the Colorado River in Grand Canyon, these patterns make the Tapeats Creek confluence a compelling site at which to understand the mechanisms creating a biological discontinuity from an unregulated stream to a regulated river, and to advance understanding of why and where TMDs may be expected to occur, as well as implications on foodbase and fisheries management in regulated rivers.

METHODS

Study Area

Tapeats Creek is a 4th order, cool stenothermic stream draining a 214 km2basin on the North Rim of Grand Canyon, located at Colorado River Mile 134R (Rkm 215.6R; N 36.3705°, W 112.4694°, 590 m elevation), 240 km downstream from Glen Canyon Dam (Fig. 1). Tapeats Creek is fed by three main springs complexes (Crazy Jug, Tapeats, and Thunder River Springs). Flooding typically contributes to discharge during springtime (February-May) snowmelt spates and summer monsoon storms (Cooley et al. 1977).

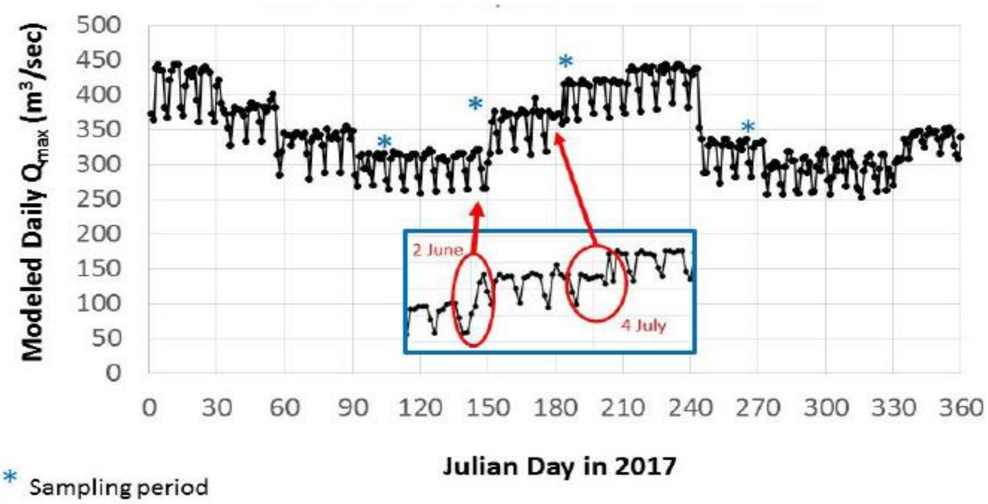

Figure2. *Flow of the Colorado River mainstream at Lees Ferry from 1 January through 31 December 2017, spanning the duration of this study*

Debris flow floods in Grand Canyon tributaries commonly deposit large boulders in the center of tributary channel mouths. Consequently, the mouths of most large tributaries in Grand Canyon develop a low-gradient upstream outflow channel and a steeper downstream outflow channel (e.g., Cooley et al. 1977; Melis 1997; Fig.1). This geomorphic configuration influenced our sampling design.

We sampled six aquatic microhabitats in and near the Tapeats Creek confluence:1) Tapeats Creek (TC) upstream from the impacts of normal Glen Canyon Dam operations; 2) the lower gradient upstream varial channel (UVC) microhabitat lying immediately above the creek mouth area, which is stalled and inundated when mainstream flows exceed 500 m3/s; 3) the low-gradient upper outflow channel (UOC) microhabitat in lower Tapeats Creek, which is inundated by mainstream flows >250 m3/s; 4) the high-gradient downstream outflow channel (DOC) microhabitat in lower Tapeats Creek, which carries approximately two thirds of Tapeats Creek outflow and, like the UVC begins to be inundated when mainstream flows exceed 500 m3/s;5) the lower Colorado River (LCR) mainstream microhabitat downstream from the DOC and which receives BMI drift from Tapeats Creek; and 6) the upper Colorado River (UCR) mainstream microhabitat, a control site lying upstream from and is not influenced by the creek.

DATA COLLECTION AND ANALYSES

Site Visits

We conducted four expeditions to the confluence study area in 2017. The mid-April 2017 visit was a reconnaissance to determine confluence microhabitat distribution. A 12-day May-June site visit was timed to characterize microhabitats and BMI assemblage characteristics, and specifically to observe the May-June mainstream monthly hydropower flow regime shift. A22-day June-July site visit was conducted to re-measure physical and biological characteristics, conduct fluctuating flow simulations, and observe the June-July mainstream monthly flow regime shift. During a five-day mid-September site visit, we measured physical and biotic characteristics after the return of the mainstream to low autumn flows.

Mainstream and Tapeats Creek Discharge

We estimated mainstream Colorado River flow at Tapeats Creek by establishing a staff gauge and modeling the stage-to-discharge relationship between the study site and the mainstream flow at the U.S. Geological Survey Lees Ferry stream flow gauge (USGS station 09380000); model R2 = 0.975). While several large tributaries potentially influence flow between that gauge and Tapeats Creek, mainstream water year (WY) 2017 was strongly dominated by clear water and few tributary floods. The Lees Ferry period of historic flow records extends back to 1922,allowing us to back cast mainstream inundation frequency at the TC confluence in pre-dam time. Hydro peaking peaking flows were greatly reduced after 1991 to 0.5 m/day to conserve fine sediment mass balance for recreational river running and native fish shoreline habitat conservation (U.S. Department of the Interior 1995, 2016). Oblique photographs taken by the senior author reveal little evidence of geomorphic change of the confluence since 1980, but backcast flow estimates should be interpreted with caution. Tapeats Creek peak flow was estimated by the National Park Service on 15 April 2017. We measured Tapeats Creek flow 150 m upstream from the mouth in May,June, July, and September in 2017 using a wading rod and SwofferTM flow meterat 0.5 m intervals across the creek, with data integrated to estimate flow during each sampling visit.

Water Quality

We measured water temperature, pH, specific conductance, salinity, and alkalinity in TC and mainstream microhabitats during each expedition using a calibrated Hanna Combo meter and a LaMotteTM alkalinity test kit. Both Tapeats Creek and the mainstream are cool, whitewater streams with near-saturation levels of dissolved oxygen.

Bmi

We characterized physical conditions and BMI assemblages using a Hess sampler (0.5 mm mesh, basket diameter 21.4 cm, area 0.036 m2), documenting benthic substrate composition and benthic invertebrate abundance(number of individuals/m2), species richness, and species density (number of species/m2) in each microhabitat. The Hess sampler was placed at randomly selected points in each microhabitat, and the bed was vigorously disturbed for one minute. Six or more Hess samples were collected in each microhabitat during daytime during each site visit, velocity was measured with a Swoffer™ flow meter, and depth and bed sediment characteristics were recorded as the visually estimated % cover (VE%C) of silt, sand, fine gravel, coarse gravel, and small to large boulders. We calculated embeddedness as the VE%C of sand or finer particles at each Hess sampling point. Embeddedness data were relegated to ordinal classes consonant with definitions by Platts et al. (1983), Sylte &Fischen rich (2002), and Sennatt et al. (2006).Invertebrate samples were stored in 85% ethanol in separate Whirlpak™ bags and returned to the laboratory for sorting under 10X magnification, identification, and enumeration. We sampled during specific mainstream hydropower flow transition periods, which were scheduled according to monthly hydroelectric power contracts. Two of the largest stepped increases during the growing season occurred at springtime and early summer monthly flow transitions. Given the 1.5-day lag in the kinematic wave arrival from Glen Canyon Dam to Tapeats Creek (Wiele &Smith 1996), and the occurrence of low flows on weekend days and holidays, we planned on, and sampled the suite of microhabitats before, during, and immediately after monthly transitions at 15:00 on the 2nd of June, and on the 4thof July in 2017. Sampling during those periods provided insight into whether and how stepped mainstream flow changes directly affected benthic and drifting BMI in the creek and mainstream.

Drift

Following the recommendations of Muehlbauer et al. (2017), we conducted a preliminary insitu analysis of drift in relation to sampling duration using a LaMotte 153 µm nylon plankton tow net, with a throat diameter of 12.7 cm and net area of 127 cm2. The net was deployed at the top of the DOC, and we drift sampled over intervals of 60 to 1200 s. Tapeats Creek has highly transparent water, but the net clogged with fine organic matter after 1000 s, so we standardized drift sample duration at 500 s.We sampled Tapeats Creek drift with four replicates during day and night each visit, focusing on the mainstream flow shift periods. We measured current velocity using a SwofferTM flow meter for each sample. Drift samples were stored in 85% ethanol and returned to the laboratory for sorting under 10X magnification, identification, and enumeration.

Colonization and Simulated Fluctuating Flow Experiments

We investigated benthic colonization and BMI responses to simulated fluctuating flows using artificial basket samplers constructed of 12 mm mesh hardware cloth, and measuring 10 x 20 x 15 cm.Each basket was filled with a measured volume of sterilized gravel-cobble stream substrata (1 to 20 cm in diameter). We tested BMI colonization in five microhabitats, except the UCR due to safety concerns, deploying six samplers for 20 d during the June-July sampling period. After 20 days, each sampler was surrounded by netting and carefully removed from its location. BMI were flushed from each basket, placed in 85% ethanol in separate WhirlpakTM bags, and returned to the laboratory for sorting, identification, and enumeration. We calculated BMI abundance/L of rock substrata and species richness/L of substrata from each artificial sampler. Eight additional baskets were placed in the UVC to test BMI colonization rate, with four UVC baskets were harvested after one week, after two weeks, and for the original six baskets after 20 days.

We experimentally simulated flow fluctuations in TC, testing the impact of flow variation on BMI assemblage abundance and species richness. We deployed four replicates of six basket baskets in the TC microhabitat, with treatments including: 1) a control set of six baskets placed at approximately 0.5 m depth that was not moved for 20 d; 2) another control set that was moved twice daily to near the surface and back to the bottom depth of 0.5 m; 3) a set moved from 0.5 m depth at night up to just under the surface during the day; and 4) a set that was kept near the surface at night and lowered to 0.5 m depth during daytime. Samplers were moved slowly over the course of several minutes to prevent flushing of BMI. One day of treatment interruption occurred during a crew change during the 20-day experimental period. Baskets were retrieved and processed after 20 days, as described above. Field surveys and experiments were analyzed using Kruskal-Wallis, simple linear regression, and other descriptive statistics (Zar1984).

RESULTS

Discharge and Hydrography

The flow of Tapeats Creek is not regularly monitored, but we assembled available data to depict its hydrograph in 2017. The mid-April 2017 snowmelt spate elevated Tapeats Creek's flow to approximately 14 m3/s, larger than the historic flood of 11.2 m3/s in December 1966 (Cooley et al.1977). Flow decreased by mid-June to 2.3m3/s, reaching a base flow of approximately 1.5 m3/sin mid-September. Daily stage flow variation was negligible in Tapeats Creek, except for a brief 0.25 m stage change that occurred during mid-July. As a result, Tapeats Creek water transparency remained high for nearly the entire growing season. Overall, Tapeats Creek discharge ranged over an order of magnitude during the course of the year, with little non-spate flooding disturbance during our sampling and experimentation.

Mainstream discharge in 2017 varied predictably in relation to hydroelectric power production releases and the location of Tapeats Creek in relation to the daily kinematic wave produced by Glen Canyon Dam releases (Fig. 2). Daily mainstream flows at the mouth of Tapeats Creek ranged from 240-440 m3/s in May 2017, stepping up to a range of 285-485 m3/s in June, and up to 300-560 m3/s in July and August, then stepping back down to 240-440 m3/s in September. Due to the distance downstream from Glen Canyon Dam (240 km), the daily flow peak arrived in the early evening hours.

Daily low flows arrived in the mid-morning, lasting several hours. Weekend low flows dropped to near the minimum monthly range. The May-to-June and the June-to-July stepped increases arrived on schedule, providing the maximum daily mainstream stage changes that occurred during 2017. Daily mainstream flows at Tapeats Creek consisted of, on average, 0.5 m of stage change, with the exception of the 2 June and 4 July monthly flow regime up-steps when daily flow stage increased to 0.75 m. Using the modeled relationship between the Lees Ferry gauge and our study site gauge, we back cast mainstream flow hydrography from 1922-2017, using water years (WYs) 1958, 1979 under pre-1990 regulated and highly fluctuating flows, and 2017 as example years (Table 1). Hydrograph modeling indicated that predam annual high flows frequently inundated or stalled flow throughout lower Tapeats Creek, and inundated the UOC microhabitat 33% of the time. During the early post-dam period from 1965-1991, including the time of Hofknecht's (1981) study, Glen Canyon Dam was managed to maximize hydroelectric power production. Hydropower peaking flow sent daily "tides" of up to 3 m/day passing through the Colorado River corridor. Flows during that period (e.g., WY 1979) would have ponded and inundated the UOC microhabitat nearly 39% of the time, an increase over pre-dam inundation due to increased post dam base flow. Except for rare, brief post-1996 planned high flows for sediment management, post-1990 mainstream flows stalled flow and/or inundated the UVC microhabitat only 9.4% of the time, although the UOC was inundated nearly 35% of the time.

Table1. *Percent of time that lower Tapeats Creek (TC), the upper varial channel (UVC), and the upstream outflow channel (UOC) microhabitats were stalled or inundated by mainstream Colorado River flows in representative Water Years 1958 (predam), 1979 (early post-dam), and 2017 (contemporary).*

Water Year	**UOC**	**UVC**	**TC**
1958	33.3	24.3	22.6
1979	38.8	26.9	18
2017	34.5	9.4	1.24

Water Quality

Water quality was similar between Tapeats Creek and the mainstream Colorado River throughout our study (Table 2). Springs that feed Tapeats Creek source at approximately 10^0 C (Tobin et al. 2017), warming slightly during summer as the stream flows approximately 4 km to the mainstream. There, creek water averaged 15^0 C during the course of our study. Mainstream Colorado River water temperature also was relatively constant during the study, averaging 15.5^0 C. We did not measure water temperature during the winter months in this study; however, water temperatures in lowermost Tapeats Creek were 12^0 C in November 2015, and 13^0 C in April 2018 (LES, unpublished data), indicating a slight cooling of the tributary during winter. A similar level of cooling occurs in the mainstream (Wright et al. 2008).

Tapeats Creek average pH and alkalinity also were strikingly similar to that of the mainstream, while specific conductance was higher in the mainstream (741µS) than in the tributary (294µS; Table 2). Exploratory field experiments with dominant Tapeats Creek EPT revealed no obvious mortality effects due to exposure to mainstream water or experimentally elevated water temperature, and other recent studies have shown negligible negative proximal responses of BMI to mainstream water geochemistry or temperature (C. McDaniel, Brockport SUNY, written commun.)

Table2. *Average water quality and BMI data by microhabitat in the Tapeats Creekconfluence area in 2017.Abbreviations: DOC – downstream outlet channel; LCR – lower (downstream) Colorado River; TC - Tapeats Creek; UCR – upstream Colorado River; UOC - upstream outflow channel; UVC - upper varial channel; VE%C - visually estimated % cover. Mean embeddedness habitat condition definitions follow Sylte and Fischenrich (2002).*

	Microhabitat					
Variable	**TC**	**UVC**	**DOC**	**UOC**	**LCR**	**UCR**
Water Quality						
pH	8.5	---	---	---	---	8.4
Elect. Cond. (µS)	294.2	---	---	---	---	740.8
Total dissolved solids (ppm)	147.4	---	---	---	---	371.7
Water Temperature (°C)	14.8	---	---	---	---	15.5
Total Alkalinity (mg/L)	160.9	---	---	---	---	142.2
Velocity (m/s)	0.86	0.69	0.62	0.59	0.19	0.15
Sampling Depth (m)	0.32	0.25	0.2	0.28	0.34	0.33
Substrata						
Mean VE%C Silt	0	3	0	0	0	8.8
95% CI % Silt	0	0.128	0	0	0	0.194
Mean VE%C Sand	7.9	9.1	6.9	5	29.4	46.3
95% CI % Sand	0.21	0.114	0.101	0.095	0.485	0.467
Mean VE%C Fine Gravel	19.8	26.4	19.2	15.2	5.2	0
95% CI% Fine Gravel	0.193	0.124	0.14	0.11	0.115	0.203
Mean VE%C Coarse Gravel	29.1	36.6	32.9	39.4	2.9	0.4
95% CI% Coarse Gravel	0.212	0.181	0.199	0.192	0.087	0.144
Mean VE%C Small Boulder	43.2	24.5	32.6	40.4	47.1	44.6
95% CI % Small Boulder	0.352	0.235	0.281	0.256	0.577	0.535
Mean VE%C Large Boulder	0	0	7.1	0	15	0
95% CI % Large Boulder	---	---	0.193	---	0.433	---
Mean VE%C Embeddedness	7.9	12.1	6.9	5	29.4	55

Mean Habitat Condition	Optimal	Optimal	Optimal	Optimal	Sub-optimal	Marginal
V, D, Substrata, Hess N	36	54	70	60	26	30
Hess Samples						
Total No. Specimens	2350	4668	5877	3724	896	291
Mean Total density/m^2	1813.3	2401.2	2332.1	1724.1	777.8	336.8
Mean Species richness/sample	4.8	5	5.2	3.7	2.3	1.1
Mean density EPT/m^2	369.8	373.2	317.3	121.5	29.3	0
Mean No. EPT	13.6	13.7	11.6	4.5	1.1	0
Total No. EPT	424	702	747	271	26	0
Gravel Basket Samplers						
Total No. BMI Specimens	362	194	299	28	74	---
Mean No. BMI/Sampler	42.5	22	51.6	8.1	34.1	---
Mean BMI Richness/Sampler	3.1	3.5	6	1.7	3.1	---
Mean No. EPT/Sampler	15.1	19.4	33.2	4.7	9.3	---
Mean EPT Richness/Sampler	1.2	1.1	2.6	0.7	1.3	---
% EPT/L of Gravels	34.3	14.2	40.5	18.8	44.2	---
Gravel basket N	6	6	6	6	6	0

HESS SAMPLES

Microhabitat Assemblage Structure

We collected 276Hess samples among the six microhabitats (Table 2). Physical habitat factors varied to some extent among the Tapeats Creek microhabitats, but substantially between tributary and mainstream micro habitats. Velocity and depth were greatest at TC, decreasing to the UOC as creek outflow reached the mainstream. Kruskal-Wallis analyses revealed that the UVC sustained significantly reduced flow velocity and significantly increased depth with the onset of July mainstream flows (H1 =12.52, N= 58, P = 0.0004; H1=13.02, N=58, P = 0.0003, respectively).

Benthic habitat structure, measured as VE%C of substrate particle size in the creek were composed of gravels and cobble (Table 2; Fig. 3). Embeddedness (VE%C of sand and finer sediments from Hess samples) in Tapeats Creek microhabitats was low and optimal (sensuSylte & Fischenrich 2002); however, embeddedness in the UOC increased over the growing season. Fine gravel dominated that microhabitat following the April spate and through May, but increased summertime mainstream flows deposited fine sediment across the UOC surface.

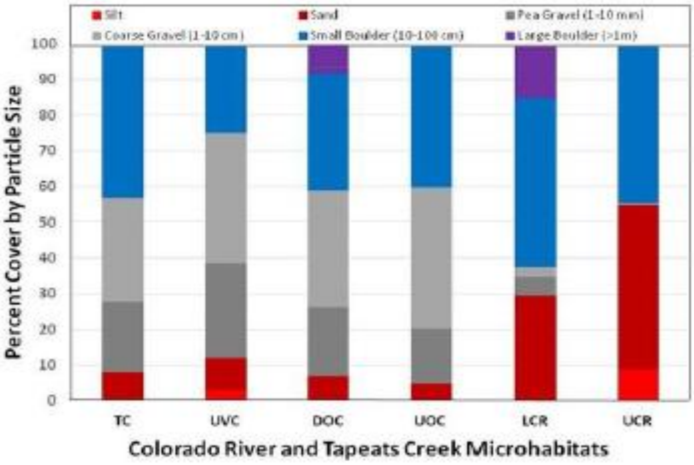

Figure3. *Particle size distribution among the six Tapeats Creek confluence microhabitats: DOC – downstream outlet channel in TC, LCR – lower Colorado River, TC – Tapeats Creek, UCR – upper Colorado River, UOC – upper outlet channel in TC, UVC – upper varial channel in TC.*

Velocity and depth of Hess samples were lower in the mainstream wave-washed habitat that dominates the shorelines. In contrast to Tapeats Creek, mainstream particle size distribution was distinctly bimodal, with large cobbles and boulders embedded in fine sand (Table 2; Fig. 3). Mainstream cobbles and boulders in the nearshore habitat displayed dorsal cover by Oscillatoria, with a lateral fringe of filamentous green algae that supported chironomid larvae (as described by Stevens et al. 1997). Fine and coarse gravels and small cobbles were conspicuously absent throughout the UCR and the lower LCR, a pattern that did not vary seasonally except a brief episode of upstream tributary-derived silt deposition in mid-summer.

Hess Biotic Data

We collected 17,805 BMI specimens in 15 families among 276 Hess samples. BMI total abundance varied from 0 in mainstream samples to 15,639 individuals/m2in creek samples (Table2;Figs. 4a, b). BMI were strongly dominated by larval Chironomidae in all settings; however, both abundanceand species densityof EPT taxa, larval Odonata, larval and adult elmid beetles, and Tipulidae were consistently higher in Tapeats Creek than in the mainstream. Kruskal-Wallis tests revealed differences among EPT species across microhabitats(excluding the UCR) from Hess sample data [H4=55.932, N=246, P = <0.0001).The creek BMI assemblage included relatively high density, richness, and percent of EPT species, and EPT density was consistently lower or absent in the LCR. The only BMI arthropod taxa detected in the mainstream UCR upstream from the confluence area were Chironomidae, Simuliidae, and rare introduced Gammaridae (Gammarus lacustris).

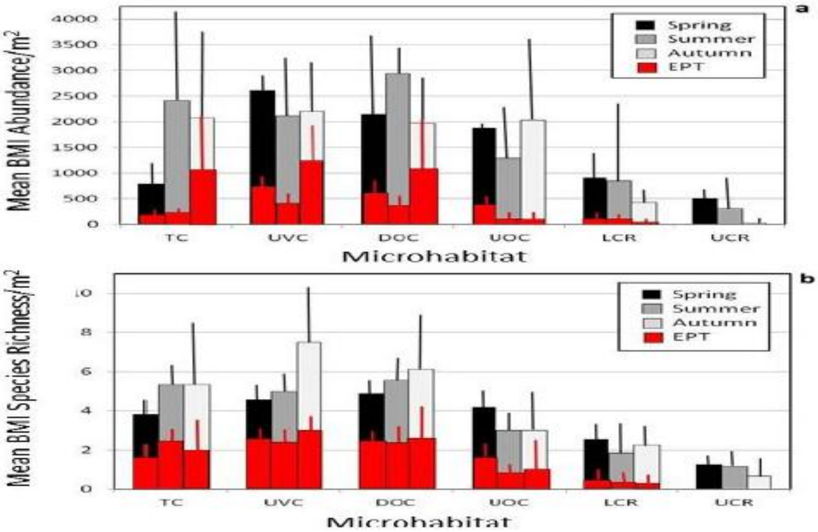

Figure4. *a) Mean Hess sample BMI and EPT abundance/m2, and b) mean BMI and EPT species richness/sample among six creek and mainstream microhabitats. DOC – downstream outlet channel in TC, LCR – lower Colorado River, TC – Tapeats Creek, UCR – upper Colorado River, UOC – upper outlet channel in TC, UVC – upper varial channel in TC.N> 6 replicates/microhabitat/site visit. Error bars represent 95% confidence intervals.*

The UOC and DOC diverge around the Tapeats Creek mouth island, and the DOC flows for an additional 35 m before mixing with the main stream in the LCR microhabitat. The UOC was frequently inundated by the mainstream, while the DOC remained relatively unaffected by the Colorado River until mainstream flows exceeded 425 m3/sin mid-summer. Mean EPT abundance, density, and species density were low in the UOC, but remained high in the DOC (Table 2, Figs. 4a, b). Mean EPT abundance decreased from 1165/m2 at the upstream end of the DOC downstream to 0 to 25/m2 at its confluence with the main stream, and to 0/m2 downstream, as that microhabitat became increasingly subject to mainstream sediment, flows, and wave action. Tapeats Creek BMI and EPT abundance, density, and species density varied through the growing season, increasing through the growing season in all creek microhabitats except the frequently-inundated UOC. Ephemeroptera dominated there in April and May (240 individuals/m2), but decreased over the growing season to 25-50 individuals /m2, a change attributed to increasing embeddedness and life history phenology. Thus, BMI abundance, species richness, and species density declined in the UOC through the growing season, in contrast to the DOC. Mainstream BMI species richness and density remained low throughout the growing season (Table 2). Slightly decreased mainstream BMI occurred during higher mid-summer flows, which increased suspended sediment loads, and shoreline velocity and wave magnitude.

Drift

Drifting BMI taxa are subject to increased probability of mortality (Brittain & Eikeland 1988), and we expected and found BMI drift rates to be low under the steady flows in Tapeats Creek. The grand mean BMI drift rate was 0.0007BMI/L, with one standard deviation of 0.0009 BMI/L (N=46; Table 3). High variability resulted in non-significant differences among drift sampling period across microhabitats and sampling periods (H4 = 6.356, N=47, Kruskall-Wallis P = 0.174).Chironomid midge larvae were the dominant drifting BMI, and the grand mean EPT drift rate was 0.00007 (1 sd = 0.0002), <11% of the total drifting BMI. Drift rate increased by 3.9- to 7.9-fold during the June-July monthly stepped flow increase as compared to that immediately prior. Diurnal drift was 1.4- to 4.1-fold higher during day than at night during the flow transition, and was up to 7.9-fold higher during nighttime for all metrics in September during normal autumn flow conditions.

Table3. *Mean (N, 95% CI) of diurnal and nocturnal drift of total BMI and EPT abundance/L and species density/L at the upstream end of the downstream outlet channel at the mouth of Tapeats Creek in June, during the June-July stepped flow increase, and in September, 2017.*

Variable	Time	June	July pre-rise	July transition high flow	September
Mean BMI abundance/L	Diurnal	0.71 (14, 0.21)	0.19 (4,0.38)	1.36 (10, 1.12)	0.23 (6, 0.26)
Mean BMI abundance/L	Nocturnal	---	---	0.33 (6, 0.19)	0.33 (6, 0.19)
Mean EPT abundance/L	Diurnal	0.01 (14, 0.02)	0.01 (4,0.00)	0.08 (10, 0.18)	0.04 (6, 0.07)
Mean EPT abundance/L	Nocturnal	---	---	0.03 (6, 0.07)	0.33 (6, 0.33)
Mean BMI no. spp/L	Diurnal	0.23 (14, 0.06)	0.11 (4,0.21)	0.57 (10, 0.29)	0.16 (6, 0.15)
Mean BMI no. spp/L	Nocturnal	---	---	0.21 (6, 0.13)	0.22 (6, 0.17)
Mean EPT no. spp/L	Diurnal	0.01 (14, 0.02)	0.01 (4,0.00)	0.04 (10, 0.09)	0.04 (6, 0.07)
Mean EPT no. spp/L	Nocturnal	---	---	0.03 (6, 0.07)	0.14 (6, 0.16)

Basket Sampler Results

Among Microhabitat Comparisons:

BMI abundance in the UVC was variable, but stabilized during the latter half of the basket experiment, varying non-significantly between weeks (P>0.05). Proportional representation of EPT in each of the samplers averaged 10%of total BMI detected after 20 days, roughly equivalent to Hess sample results. Total mean BMI species richness/L of substrata increased across the interval, while EPT abundance stabilized, averaging 20% of the total BMI. Comparison of Hess and basket sampler data among microhabitats (below) indicated that 20 days was sufficient for equilibration of BMI colonization.

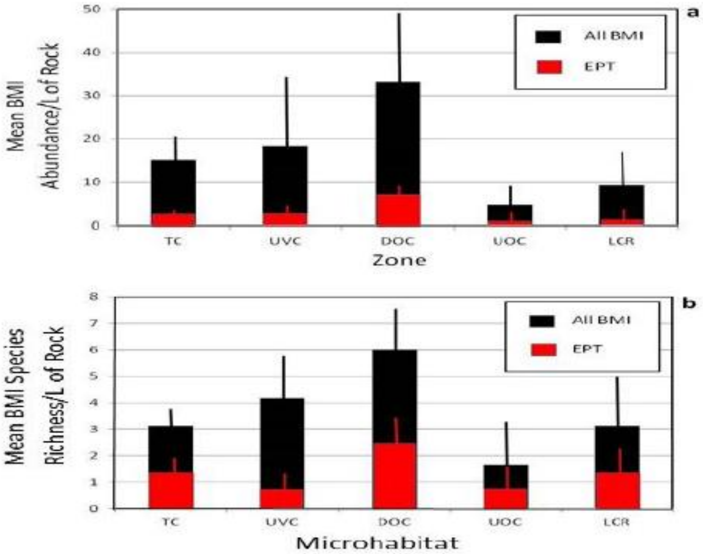

Figure5. *Artificial basket sampler results after 20 days by Tapeats Creek microhabitat in June-July 2017. a) Mean BMI and EPT abundance/L of gravel and b) species richness/L gravel. DOC – downstream outlet channel in TC, LCR – lower Colorado River, TC – Tapeats Creek, UOC – upper outlet channel in TC, UVC – upper varial channel in TC. Error bars are 95% confidence intervals.*

Artificial basket sampler and Hess data were similar, with maximum BMI and EPT abundance/L and species density/L of gravel in the DOC (Figs. 4a, 4b, 5a, 5b). BMI and EPT colonization were high in all Tapeats Creek microhabitats except the UOC, likely in response to fine sediment deposition under high summertime flows (Figs. 5a, 5b). Experimental introduction of non-embedded gravel habitat in the upstream-most LCR sites where drifting EPT colonization potential was elevated resulted in BMI and EPT abundance/L and species density/L roughly equivalent to those in TC.

Simulated Fluctuating Flows in TC

The flow variation experiment in TC revealed mean BMI density (1025 individuals/L rock m2) was 43% of the average abundance/L detected using the Hess sampler, well within the 95% confidence interval for that period, indicating that the 20-day time period was adequate for analysis of fluctuating flow simulations (Table 4). However, the experiment failed to reveal clear differences among treatments in either BMI or EPT abundance/L of rock or species density/L of rock (H3 = 3.934, N = 23, Kruskall-Wallis P = 0.269 for abundance; and P>0.05 for EPT species density/L).Slight but non-significant differences of greater BMI abundance/Loccurred in the control treatment, and slightly greater species density in the day-up treatment, the latter possibly in response to increased photosynthetically active solar radiation and benthic productivity (e.g., Yard et al. 2005).

Table4. *Experimental artificial basket sampler flow variation results on benthic macro invertebrates (BMI) and combined Ephemeroptera, Plecoptera, and Trichoptera (EPT) abundance/L of rock and species richness/L of rock after 20 days of exposure to four treatments in Tapeats Creek, Grand Canyon, Arizona (N = 6).*

Assemblage	Treatment	Mean Abundance/L	Abundance/L 95%CI	Mean No Spp/L	No. Spp/L 95%CI
All BMI	Control	126.01	48.94	3.84	0.64
EPT	Control	23.38	24.08	1.6	0.978
All BMI	Move/replace	76.81	31.03	4.1	0.82
EPT	Move/replace	29.29	21.06	2.07	0.572
All BMI	Day up	93.96	35.51	5.27	0.6
EPT	Day up	37.86	11.54	2.52	0.463
All BMI	Night up	73.51	33.36	4.35	1.24
EPT	Night up	29.26	21.62	1.83	1.272

DISCUSSION

Factors Influencing Tributary Confluence Bmi Assemblages

Water Quality Impacts

Water temperature, geochemistry, and other variables are widely known to affect BMI assemblages (Campbell 1982; Wilson &McTammany 2014). We selected Tapeats Creek for this study specifically because of its similarity to the water temperature and geochemistry of the Glen Canyon Dam tail water (Stevens et al. 1997; Table 2). Water temperature variation in Tapeats Creek is similar to that in the cool stenothermic mainstream throughout the year, and thus is unlikely responsible for the BMI TMD. Seasonal water temperature variation can stimulate for completion of the life cycle among temperate BMI (e.g., Ward &Stanford 2003; Csercsa et al. 2018). However, photoperiod canbe more influential than temperature on BMI life cycles (Stoks et al. 2014). Thus, seasonal warming does not appear to be astimulus for adult BMI emergence in either Tapeats Creek or the adjacent Colorado River mainstream. However, other, large, low-gradient tributaries in Grand Canyon, such as the Paria River, and Nankoweap and Kanab Creeks undergo large seasonal changes in water temperature. For example, Stevens et al. (unpublished data) measured water temperature in the lower Paria River on 10 July 2005 at 37^{0} C, and summertime fish kills are regularly observed there and in Kanab Creek. Temperature extremes in such tributaries likely influence BMI life cycles, but few of the BMI species there co-occur in either Tapeats Creek or in the mainstream (Oberlin et al. 1999; Stevens et al. 1997; Cross et al. 2013).

The geochemistry of several other Colorado River tributaries in Grand Canyon (e.g., the travertine-depositing Little Colorado River and Havasu Creek) also differ strongly from that in Tapeats Creek and the mainstream (Oberlin et al. 1999). While BMI assemblages in those tributaries similarly are slightly richer than the mainstream, tributaries with more chemically enriched water and embeddedness is due to travertinesealing of interstitial space support fewer and less abundant BMI and EPT than do cool stenothermic streams with low embeddedness, such as Bright Angel, Shinumo, and Tapeats Creeks(Oberlin et al. 1999).Overall, neither water temperature nor geochemistry are responsible for the striking TMD of BMI from Tapeats Creek into the mainstream.

Hydrograph Impacts

Predam mainstream discharge varied nearly two orders of magnitude monthly, seasonally, and among years, but little within days (Topping et al. 2003). Mainstream high flows prior to 1963inundated and ponded the Tapeats Creek confluence for prolonged periods during springtime and summer spates (e.g., WY 1958 in Table 1). LES witnessed extensive ponding of the Little Colorado River, Tapeats Creek and other Grand Canyon tributary mouths during the June-August high flows of 1983, observations documented at the Little Colorado River confluence by Protiva &Yard (2000 unpublishedU.S. Geological Survey report). Collectively, those observations indicate that high mainstream flows ponded tributary mouths up to the mainstream high flow stage, turning tributary mouths in wider reaches into low velocity habitats. Large changes in velocity and flow direction, such as occurred under predam high flows would have limit BMI occurrence and density.

For example, many net-spinning lotic system Trichoptera require consistent, unidirectional flow to capture drifting detritus (e.g., Tachet et al. 1992; Feio et al. 2005; Merritt et al. 2008). Therefore, flows that inundate tributary confluences or create wave-washed shorelines likely strongly reduce Trichoptera foraging success, abundance, and assemblage composition in Tapeats Creek, other tributary mouths, and along the mainstream shoreline.

Large daily hydropower production tides characterized the mainstream Colorado River in Grand Canyon from 1965 through July 1990 (Topping et al. 2003). Flow variability during that period exceeded 500 m3. s-1 . day-1 every month of the year, ponding and draining tributary confluences on a daily basis in mid-summer and mid-winter (e.g., WY 1979, Table 1). Those mainstream hydrographic conditions were encountered by Hofknecht (1981), who first reported numerous TMDs. Thus, during both predam times and the first half of the postdam period, less than half of the growing season was available for BMI assemblage development due to tributary or mainstream flooding and confluence ponding. Reduced postdam daily flow fluctuations after 1990 reduced fine sediment export and hydrographic impacts on tributary mouth habitats, and although contemporary planned floods briefly pond tributary mouths, the area and duration of benthic habitat stability of tributary mouths is now far greater than ever before.

During our study, mainstream flows ranged from 240-440 m3/s in May 2017, stepping up to a June range of 285-485 m3/s, and to 300-560 m3/s in July and August, then steppedback down to 240-440 m3/s in September (Fig. 2). In contrast, daily flow variation was minimal in Tapeats Creek, changing slowly after the end of the springtime spate, except for one brief, flood-related 0.25 m stage change in mid-July.

Thus, the Tapeats Creek BMI assemblage was subject to essentially steady flow conditions, while that in the mainstream sustained regular minor flow variation of half a meter of stage change/day. Repeated daily dewatering flows of the UOC, springtime emergence phenology of Ephemeroptera, and increasing embeddedness reduced the BMI assemblage in that microhabitat during the 2017 growing season. In relation to our previous work (Stevens et al. 1997) and in terms of the Thorp &DeLong (1994) and Thorp et al. (2008) river productivity model, mainstream flow regulation in Grand Canyon likely has increased the productivity and ecological interactivity of often highly productive tributary confluences.

Drift operates in complex, often species-dependent ways (Brittain &Eikeland 1988; Wilson &McTammany 2014). For example, experimental leaf litter packs in artificial streams revealed rapid, curvilinear drift-based colonization, but with BMI diversity maintained by turnover rather than simple accumulation (Connolly &Pearson 2018).

Also, BMI may move by crawling both upstream and downstream, rather than risking entrainment in the water column. We measured low levels of drift in Tapeats Creek, with chironomid larvae9.1-fold more abundant than EPT. June-July mainstream stepped flow increases stimulated only a brief, minor increase in drift (Tabled 3). While Tapeats Creek BMI drift in low densities into the mainstream, BMI colonists, particularly EPT do not persist there.

Basket sampler results and flow variation experiments results corroborated Hess survey results, and high levels of BMI abundance and species richness in non-embedded creek microhabitats, with rapid colonization of experimental samples in the creek, but not in the mainstream. Simulated daily flow fluctuation experiments in Tapeats Creek demonstrated no strong differences in BMI or EPT abundance or richness among fluctuating flow treatments versus the control treatments (Table 4), indicating that EPT occupied and readily colonized available habitat in the creek. However, BMI, including Trichoptera colonized artificial samplers in the regulated main stream LCR microhabitat at the upper end of that reach, EPTrichness decreased sharply to zero over distance from the creek mouth in the artificial samplers.

On the basis of the above measurements and experiments we conclude that relatively minor daily flow fluctuations, such as those occurring under contemporary dam operations do not account for the conspicuous difference in the BMI assemblage between Tapeats Creek and the regulated Colorado River mainstream. The area of creek and mainstream shoreline dewatered under contemporary low fluctuating flows is relatively trivial in relation overall channel areas. However, mainstream flows during periods of high suspended sediment loading reduce aquatic PAR and BMI density and composition (Stevens et al. 1997; Yard et al. 2005).

Habitat Impacts

Of the three factors tested, the most compelling explanation for Tapeats Creek BMI transition is the natural difference in embeddedness between the creek and the mainstream. The predam Colorado River was named for its legendary fine sediment transport. While McKee (1938) reported turbulent predam flood sediment stratigraphy at the mouths Grand Canyon tributaries in narrow reaches, fine sediment deposition dynamics are more laminar in larger tributary mouths in wider reaches, like Tapeats Creek and other major perennial tributaries. Post-dam fine sediment transport in the mainstream near the dam has been largely eliminated, but fine sediments continue to be delivered by the Paria and Little Colorado Rivers (Andrews 1991; Topping et al. 2000, 2003), and the mainstream remains sand and cobble/boulder floored river. The BMI assemblage at Tapeats Creek is dominated by larval Chironomidae, Simuliidae, and non-native Gammarus lacustris that feed on epiphytic diatoms on macrophytic growth on the surface of embedded boulders (Stevens et al. 1997; Cross et al. 2013). As a natural characteristic of the river, fine sediment mass balance remains a primary objective for dam management (U.S. Bureau of Reclamation 1995, 2016). In contrast to the mainstream, the Tapeats Creek channel has a unimodal grainsize distribution, dominated by gravel to small boulder particle sizes with much interstitial space. Such substrata are required by EPT for protection from high velocity currents and predators. Thus, due to natural embeddedness, the mainstream Colorado River does not provide suitable habitat for many BMI taxa, particularly EPT.

The general absence of mainstream EPThas been attributed to failed BMI egg hatching success (Kennedy et al. 2016). However, our findings indicate that the absence of suitable larval habitat is another important factor contributing to the depauperate condition of the mainstream. Our measurements and experiments demonstrate that the sand-and-boulder dominated mainstream does not provide sufficient interstitial benthic space to support EPT. Oscillatoria-covered mainstream cobbles and boulders with marginal fringes of filamentous green algae is the dominant firm substratum in the mainstream and does not provide suitable habitat for EPT. Furthermore, given the large annual sediment transport (60 M metric tonnes/year, Andrews 1991; Topping et al. 2000, 2003), there is no evidence that the predam river provided such habitat. Our experimental habitat manipulations revealed that EPT can occupy the main stream when suitable, non-embedded habitat is provided in the confluence outflow, but such habitat does not occur there more than briefly following tributary floods. A drastic change in mainstream substrata would be required to support native EPT in the mainstream, and such a change would be contrary to contemporary management for fine sediment mass balance for recreation and fisheries habitats.

Other Factors

Predation by non-native rainbow trout (Oncorhynchusmykiss) or other fish, as well as macro invertebrate life history phenology may influence BMI in the study area (e.g., Shaw

&Richardson 2001, Wesner 2010). However, rainbow trout were observed only in low numbers in both the mainstream and lower Tapeats Creek during the study, and the high densities of BMI in the tributary indicates that trout predation is unlikely to play a significant role in EPT distribution there. Other potential EPT predators or competitors include waterfowl, American Dipper (Cinclus mexicanus), and larval Odonata, which occur in low densities. Gammarus lacustris has been proposed to compete with Cheumatopsyche oslari(Haden et al. 1999); however, the experimental samplers showed that the caddisfly can occupy the mainstream if appropriate substrata are present.

Life history factors influence BMI assemblage composition (Merritt et al. 2008; e.g., Wilson &McTammany 2014). Dispersal strategy affected BMI assemblage composition in the Middle Danube River (Hungary), where taxa with temporally stable strategies exhibited more robust seasonal structuring than did those with temporally varying strategies (Csercsa et al. 2018). BMI life history patterns in Tapeats Creek involved decreasing larval Ephemeroptera abundance during mid-summer, and increasing Isoperla density over the growing season. In contrast, Cheumatopsyche oslari caddisfly larvae were continuously abundant during the growing season, with adult emergence throughout the summer. We found relatively few larval or adult elmid beetles or turbellarian flatworms during our studies in 2017, taxa that dominated the UVZ in November 2015 (Stevens unpublished data). Such variation indicates inter annual as well as seasonal life history structuring. Ubiquitous benthic and hyporheic anoxia in the Glen Canyon Dam tail waters upstream from Lees Ferry (McDaniel et al.,inprep.), and the rapidly advancing non-native quagga mussel (Dreissina bugensis) invasion throughout the Colorado River corridor in Grand Canyon may further limit mainstream EPT colonization.

MANAGEMENT IMPLICATIONS

We selected the Tapeats Creek confluence to better understand the factors influencing BMI assemblage limitations in the regulated Colorado River, and dam management options for enhancing the tail waters aquatic food base. Schmidt et al. (1998) concluded that science can provide adaptive ecosystem managers with clarity on ecosystem processes and components, and advisement on feasibility and tradeoffs of those options. Maintaining a sediment mass balance in the Colorado River downstream from Glen Canyon Dam for recreational sandbar area and native fish habitat integrity are stated management goals (U.S. Bureau of Reclamation2016), and are appropriate to maintain the natural fluvial ecological conditions (Wohl et al. 2015).However, those goals are at odds with enhancing natural EPT occurrence in the river ecosystem.

Kennedy et al. (2016) proposed that Diptera egg survivorship was limited by fluctuating flows that desiccate egg masses, and that the food base therefore can be enhanced by steadier flows. This argument may apply to selected chironomid and simuliid taxa, which comprise the bulk of the present fisheries food base in the tail waters, but not to EPT that require non-embedded habitat. Outbreaks of nuisance Smidicrea and Nectopsyche Trichoptera and at least one mayfly species in the lower Colorado River basin appear attributable to specialized deep-water egg-laying behaviors in cobble-gravel substrata(LES unpublished data). However, natural embeddedness presents an insuperable barrier to larval EPT presence upstream in the mainstream in Grand Canyon. Kennedy et al.’s (2016) thesis allows for management for both fine sediment mass balance and an enhanced nematoceran Dipterafoodbase, while our findings reveal natural limits to EPT population enhancement. Furthermore, due to tributary-derived fine sediment loading, mainstream EPT presence likely will be restricted to species with specialized life histories, except in times of prolonged clear water flows. Thus, not all desired ecosystem conditions may be technically and simultaneously feasible. Our results clarify potential foodbase management options and limits to improve well-informed stewardship of the Colorado River ecosystem in Glen and Grand Canyons.

ACKNOWLEDGEMENTS

We thank Argonne National Laboratory for funding Project No. 6F-31242, especially Kirk LaGory and Mario Salerno, the Western Area Power Administration, and the Museum of Northern Arizona. Particularly Jeri Ledbetter and Lynn Yeager for administrative oversight. The National Park Service provided research and back county camping permits, and we kindly thank Ms. Ronda Newton for her support of this project (NPS Research Permit No.

GRCA-2017-SCI-0008). This project benefitted greatly from the generous support of the staffs of Arizona Raft Adventures Inc., Canyoneers Inc., Hatch River Runners Inc., O.A.R.S. Inc., and Tour West, Inc.

We thank Jeff Jenness of the Museum of Northern Arizona's Springs Stewardship Institute for map illustration, and Louise Fuchs, Sam Goddard, and David Sinclair. John Hayse of ANL provided much appreciated reviews that improved the final manuscript. The authors have no conflicts of interest to declare.

REFERENCES

[1] Andrews, E.D. (1991).Sediment transport in the Colorado River basin. In: Marzolf, G.R. (ed),*River Ecology and Dam Management*, 54-74. National Academy Press, Washington.

[2] Blinn, D.W., &Cole, G.A. (1991) Algae and invertebrate biota in the Colorado River: Comparison of pre- and post-dam conditions. In Marzolf, G.R. (ed), *Colorado River Ecology and Dam Management*, 85-104. National Academy Press, Washington.

[3] Brittain, J.E., &Eikeland, T.J. (1988) Invertebrate drift – a review. *Hydrobiologia*, 166, 77-93.

[4] Bruns, D.A., Minshall, G.W., Cushing, C.E., Cummins, K.W., Brock, J.T., & Vannote, R.L. (1984) Tributaries as modifiers of the river continuum concept: Analysis by polar ordination and regression models. *Archiv für Hydrobiol.*, 99, 208-220.

[5] Campbell, I.C., MacMillan, L.A., Smith, A.J., &McKaige, M.E. (1982) The benthic macro invertebrates of the Yarra River and its tributaries. *Victoria Ministry for Conservation Environmental Studies* Series No. 362, Victoria. https://r hithroecology .com/wp-content/uploads/2013/04/Yarra-Report-Part1.pdf (accessed 1 Dec 2018).

[6] Connolly, N.M., &Pearson, R.G. (2018) Colonization, emigration and equilibrium of stream invertebrates in patchy habitats. *FreshwaterBiol.*,63.doi:10.1111/fwb.1372.

[7] Cooley, M.E., Aldridge, B.N., &Euler, R.C. (1977) Effects of the catastrophic flood of December 1966, North Rim area, eastern Grand Canyon, Arizona. *U.S. Geol. Surv.* Prof. Pap. 980, Washington.

[8] Cross, W.F., Baxter, C.V., Rosi-Marshall, E.J., Hall, R.O. Jr., Kennedy, T.A, Donner, K.C., Wellard-Kelly, H.A., Seegert, S.E.Z., Behn, K.E., &Yard, M.D. (2013) Food-web dynamics in a large river discontinuum. *Ecol. Monogr.*, 83, 311–337.

[9] Csercsa, A., Krasznai, E., Varbiro, G.& 10 co-authors. (2018). Seasonal changes in relative contribution of environmental control and spatial structuring on different dispersal groups of stream macro invertebrates. *Hydrobiol.*doi:10.1007/s 10 750-018-3806-6

[10] De Jalon, D.G., Sanchez, P. &Camargo, J.A. (1994) Downstream effects of a new hydropower impoundment on macrophyte, macroinvertebrate and fish communities. *River Res. Appl.*, 9, 253-261.

[11] Feio, M.J., Vieira-Lanero, R., Ferreira, V., &Graça, M. (2005)The role of the environment in the distribution and composition of Trichoptera assemblages in streams. *Archiv fur Hydrobiol.*,16, 493-512.

[12] Haden, A., Blinn, D.W., Shannon, J.P., &Wilson, K.P. (1999) Interference competition between the net-building caddisfly *Ceratopsyche oslari* and the amphipod *Gammarus lacustris*. *J. Freshw. Ecol.*, 14, 277-280.

[13] Hofknecht, G.W. (1981) Seasonal community dynamics of aquatic invertebrates in the Colorado River and its tributaries within Grand Canyon, Arizona. *Northern Arizona University MS Thesis*, Flagstaff.

[14] Katano, I., Negishi, J.N., Minagawa, T., Doi, H., Kawaguchi, Y., &Kayaba, Y. (2009) Longitudinal macroinvertebrate organization over contrasting discontinuities: Effects of a dam and a tributary. *Freshw. Sci.*, 28, 331-351.

[15] Kennedy, T.A., Muehlbauer, J.D., Yackulic, C,B, Lytle, D.A., Miller, S.W., Dibble, K.L, Kortenhoeven, E.W., Metcalfe, A.N., &Baxter, C.V. (2016). Flow management for hydropower extirpates aquatic insects, undermining river food webs. *BioSci.*, 66, 561-575.

[16] Kiffney, P.M., Greene, C.M., Hall, J.E., &Davies, J.R. (2006) Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstream rivers.*Can. J. Fish. Aqu. Sci.*, 63, 518-2530.

[17] McDaniel, C., Stevens, L.E., Holway, J.H., &Ellsworth, C. Distribution and effects of hyporheic anoxia in the Colorado River below Glen Canyon Dam. *Rivers Res.Appl.*

[18] McKee, E.D. (1938). Original structures in Colorado River flood deposits of Grand Canyon. *J. Sed.Petrol.*, 8, 77-83.

[19] Melis, T.S. (1997) Geomorphology of debris flows and alluvial fans in Grand Canyon National Park and their influences on the Colorado River below Glen Canyon

Dam, Arizona. *University of Arizona PhD dissertation*, Tucson.

[20] Merritt, R.W., Cummins, K.W., & Berg, M.B. (eds). (2008)*An Introduction to the Aquatic Insects of North America.* 4th edition. Kendall/Hunt, Dubuque, Iowa.

[21] Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S., &Leonard, N.E. (2007) The contribution of headwater streams to biodiversity in river networks. *J. Amer. Water Res. Assoc.*, 43, 86-103. doi: 10.1111/j.1752-1688.2007.00008.x.

[22] Newcombe, C.P., &MacDonald, D.D. (1991) Effects of suspended sediment on aquatic ecosystems. *N. Amer. J. Fish. Manag.*,11, 72-82.

[23] Oberlin, G.E., Shannon, J.P., &Blinn, D.W. (1999) Watershed influences on the macroinvertebrate fauna of ten major tributaries of the Colorado River through Grand Canyon, Arizona. *Southwestern Nat.*, 44, 17-30.

[24] Platts, W.S, Meghan, W.F., &Minshall, G.W. (1983) Methods for evaluating stream riparian and biotic conditions. *U.S. Department of Agriculture Forest Service* General Technical Report INT-1983, Ogden.

[25] Protiva, F., &Yard, M.D. 2000. Stage-to-discharge relationship of the Colorado River at the confluence of the Little Colorado River, Grand Canyon, Arizona. Unpublished *U.S. Geol. Surv, Rep*, Flags taff.

[26] Rice, S.P., Greenwood, M.T., &Joyce, C.B. (2001) Tributaries, sediment sources, and the longitudinal organization of macroinvertebrate fauna along river systems. *Canadian J. Fish.Aqu.Sci.*, 58, 824-840.

[27] Schmidt, J.C., Webb, R.H., Valdez, R.A., Marzolf, G.R., &Stevens, L.E. (1998). Science and values in river restoration in the Grand Canyon. *BioSci.*, 48, 735-747.

[28] Sennatt, K.M., Salant, N.L., Renshaw, C.E. &Magilligan, F.J. (2006) Assessment of methods for measuring embeddedness: application to sedimentation in flow regulated streams. *J. Amer. Water Res. Assoc.*, 42, 1671-1682.

[29] Shaw, E.A., &Richardson, J.S. (2001). Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Can. J. Fish. Aqu. Sci.*, 58, 2213–2221.

[30] Stevens, L.E. (2012)The biogeographic significance of a large, deep canyon: Grand Canyon of the Colorado River, southwestern USA. In Stevens, L.E. (ed). *Global Advances in Biogeography*, 169-208. In Tech Publications, Rijeka. ISBN: 978-953-51-0454-4.

[31] Stevens, L.E., Shannon, J.P., &Blinn, D.W. (1997) Benthic ecology of the Colorado River in Grand Canyon: Dam and geomorphic influences. *Regul.RiversRes. Man.*, 13, 129-149.

[32] Stoks, R., Geerts, A.N., &DeMeester, L. (2014) Evolutionary and plastic responses of freshwater invertebrates to climate change: Realized patterns and future potential. *Evol. Appl.* 7:42-55.

[33] Sylte, T.L., &Fischenrich, C. (2002) Techniques for measuring substrate embeddedness. *ERDC* TN-EMRRP-SR-36. Available online at: www.dtic.mil/get-tr-doc (accessed 11 Dec 2017).

[34] Tachet, H., Pierrot, J.P., Roux, C., &Bourmand, M. (1992) Net-building behavior of six *Hydropsyche* species (Trichoptera) in relation to current velocity and distribution along the Rhône River. *J. N. Amer. Benth. Soc.*, 11, 350-365.

[35] Thorp, J.H., &DeLong, M.D. (1994) The riverine productivity model: An heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, 70, 305–308.

[36] Thorp. J.H., Thomas, M.C., &Delong, M.D. (eds). (2008). *The Riverine Ecosystem Synthesis: Towards Conceptual Cohesiveness in River Science*. Academic Press, London.

[37] Tobin, B.W., Springer, A.E., Kreamer, D.K., &Schenk, E. (2017) Review: The distribution, flow, and quality of Grand Canyon Springs, Arizona (YUSA). *Hydrogeol. J.*doi 10.1007/s10040-017-1688-8.

[38] Topping, D.J., Rubin, D.M.,&Vierra, L.E. Jr. (2000). Colorado River sediment transport 1. Natural sediment supply limitation and the influence of Glen Canyon Dam.*Wat. Resour. Res.* 36:515-542.

[39] Topping, D.J., Schmidt, J.C., &Vierra, L.E. Jr. (2003) Computation and analysis of the instantaneous-discharge record for the Colorado River at Lees Ferry, Arizona -- May 8, 1921 through September 30, 2000. *U.S. Geol. Surv. Prof. Pap*. 1677.

[40] U.S. Bureau of Reclamation. (2016) Glen Canyon Dam Long-term Experimental and Management Plan Environmental Impact Statement. U.S. Department of the Interior, Washington. Available on-line at: http://ltempeis.anl.gov/documents/final-eis/ (accessed 21 March 2018).

[41] Vinson, M.R. (2001) Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecol. Appl.*, 11, 711-730.

[42] Ward, J.V., &Stanford, J.A. (1983) The serial discontinuity concept of lotic ecosystems. In Fontaine, T.D., & Bartell, S.M. (eds). *Dynamics of Lotic Ecosystems*, 29–42. Ann Arbor Science Publishers, Ann Arbor.

[43] Ward, J.V., & Stanford, J.A. (2003) Thermal responses in the evolutionary ecology of aquatic insects. *Ann. Rev. Ent.*, 27, 97-117.

[44] Wesner, J.S. (2010) Aquatic predation alters a terrestrial prey subsidy. *Ecol.*, 91, 1435-1444.

[45] Wharton, G., Mohajeri, A.H.,& Righetti, M. (2017) The pernicious problem of streambed colmation: A multidisciplinary reflection on the mechanisms, causes, impacts, and management challenges. *Wiley Interdisc. Rev. Wat.*, 4, e 1231. https: //doi .org/10.1002/wat2.1231.

[46] Wiele, S.M., &Smith, J.D. (1996) A reach-averaged model of diurnal discharge wave propagation down the Colorado River through the Grand Canyon. *Wat. Res. Res.*, 32, 1375-1386.

[47] Wilson, M.J., &McTammany, M.E. (2014) Tributary and mainstream benthic macroinvertebrate communities linked by direct dispersal and indirect habitat alteration. *Hydrobiol.*, 738, 75-85. doi: 10.1007/s1-750-014-1920-7.

[48] Wohl, E., Bledsoe, B.P., Jacobson, R.B., Poff, N.L., Rathburn, S.L., Walters, D.M.,& Wilcox, A.C. (2015) The natural sediment regime in rivers: broadening the foundations for ecosystem management. *BioSci.*, 65, 358-371.https;//doi.org/10.1093/biosci/biv 002.

[49] Wood, P.J., & Armitage, P.D. (1997) Biological effects of fine sediment in the lotic environment. *Envir. Man.*,21, 203-217. https://doi.org/10.1007/s002679900019.

[50] Wright, S.A., Anderson, C.A., &Voichick, N. (2008) A simplified water temperature model for the Colorado River below Glen Canyon Dam. *Riv. Res. Appl.* doi: 10.1002/rra.1179.

[51] Yard, M.D., G.E. Bennett, S.N. Mietz, L.G. Coggins Jr., L.E. Stevens, S. Hueftle, & D.W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. *Ecol. Mod.*, 183:157-172.

[52] Zar, J.H. (1984) *Biostatistical Analysis*, 2nd ed.Prentice-Hall, Inc., Englewood Cliffs.

Citation: *Lawrence E. Stevens, Joseph H. Holway, and Craig Ellsworth.“ Benthic Discontinuity between an Unregulated Tributary and the Dam-Controlled Colorado River, Grand Canyon, Arizona, USA ”. Annals of Ecology and Environmental Science 4(2), pp 1-16, 2020.*