FRESHWATER ECOLOGY

Hydropeaking intensity and dam proximity limit aquatic invertebrate diversity in the Colorado River Basin

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Abstract. River biodiversity is threatened globally by hydropower dams, and there is a need to understand how dam management favors certain species while filtering out others. We examined aquatic invertebrate communities within the tailwaters 0–24 km downstream of seven large hydropower dams in the Colorado River Basin of the western United States. We quantified aquatic invertebrate dominance, richness, abundance, and biomass at multiple locations within individual tailwaters and across the basin and identified biological community responses associated with dam operations and distance from dam. We found that each tailwater was dominated by 3–7 invertebrate taxa, accounting for 95% of total abundance. Half of these dominant taxa were non-insect, non-flying species and thus were unavailable to terrestrial consumers. Consistent with previous studies, aquatic insects and sensitive taxa were negatively associated with hydropeaking intensity (magnitude of daily flow fluctuations associated with hydropower generation), which limits the composition and potentially the quality of the invertebrate food base. While total invertebrate abundance and biomass did not change with increasing distance downstream from dams, insect and sensitive taxa richness, abundance, and biomass all increased, suggesting that impacts of hydropeaking are most acute immediately downstream of dams. Our results demonstrate that tailwaters experiencing hydropeaking support high abundances of aquatic invertebrate, but the diversity of these communities is low.

Key words: Colorado River; dam; dominance; environmental flows; hydropeaking; invertebrate.

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INTRODUCTION

Rivers are biodiversity hotspots, but two-thirds of the world's longest rivers (>1000 km) are no longer free-flowing (Grill et al. 2019). These rivers face unique biodiversity threats, particularly from hydropower dams (Nilsson et al. 2005, Winemiller et al. 2016). In the United States, there are >2500 hydropower dams that impact biodiversity across river basins, and the number of hydropower dams is growing globally (Stanford and Ward 2001, Hadjerioua et al. 2012, Zarfl et al. 2014). Large hydropower dams change the physical nature of a river by creating barriers to dispersal and altering dissolved oxygen levels, nutrients, temperature, suspended sediment

loads, and flow regimes (Friedl and Wüest 2002, Graf 2006, Tortajada et al. 2012, Maavara et al. 2020). Altered flow regimes are of particular interest due to the critical role flow plays in both ecological and evolutionary processes (Poff et al. 1997, Bunn and Arthington 2002, Lytle and Poff 2004).

Hydropower dams alter flow regimes by either reducing or amplifying variation in flow, depending on the timescale being examined. On the seasonal or annual scale, homogenization of flow occurs through reduction of seasonal flow extremes (Poff et al. 2007). On the diel scale, fluctuations between high and low flows can be amplified to meet sub-daily changes in electricity demand, a procedure known as hydropeaking (Førsund 2015). Thus, organisms occupying tailwater habitats downstream of hydropower dams can be subject to both decreased flow variability at seasonal timescales and increased flow variability at daily timescales (Moog 1993). Because biological responses to altered flow regimes can vary regionally, there is a need to assess flow management impacts at both the regional scale across entire river basins and the local scale downstream of individual dams (Mac Nally and Quinn 1998, Brosse et al. 2003, Poff and Zimmerman 2010).

Anthropogenic disturbance may confer a competitive advantage to certain species, leading to numerical dominance by one or a few species (Seabloom et al. 2003). For example, weedy plant species may become dominant as a result of human-induced increases in atmospheric nitrogen deposition (Tilman and Lehman 2001). Likewise, flow alterations in rivers may lead to dominance by obligate aquatic taxa and exclude invertebrates with complex life cycles. These latter groups have aquatic larval and terrestrial adult life stages, and most deposit eggs along river margins during their aerial adult phase (Kennedy et al. 2016, Ruhi et al. 2018). Under hydropeaking conditions, these eggs are subject to daily cycles of desiccation. Indeed, Kennedy et al. (2016) showed that the relative abundance of taxa with complex life cycles in the sensitive groups Ephemeroptera, Plecoptera, and Trichoptera (EPT) was negatively related to hydropeaking intensity. By causing a shift from biodiverse communities of terrestrially available taxa to communities dominated by just a few

obligate aquatic taxa, hydropeaking could have consequences for the amount of biomass available to terrestrial consumers such as birds and bats, as well as the diversity of prey available to fish and other aquatic predators.

The Colorado River Basin provides an opportunity to study both local and basin-wide impacts of hydropower dams on biodiversity. This river basin stretches over seven U.S. states, supplying drinking water to 40 million people, irrigating 5.5 million acres of cropland, and generating approximately 11 gigawatt hours of energy annually (Maupin et al. 2018). To serve these purposes, the Colorado is one of the most heavily regulated river basins in the world, with 19 large dams and >100 smaller dams in its basin, many of which are operated for hydropower (Bishop and Porcella 1980, Graf 1985).

Our study quantified invertebrate dominance, richness, abundance, and biomass at multiple sites within the tailwaters downstream of seven major Colorado River Basin dams that span a range of hydropeaking intensities. Specifically, we sought to determine (1) whether hydropower dams influence patterns of invertebrate dominance and community structure, (2) whether hydropeaking intensity affects the proportion of insect and EPT taxa, and (3) how dominance, richness, abundance, and biomass change with increasing distance from dams. We predicted that a few highly abundant non-insect taxa would dominate invertebrate communities both within each tailwater and across the Colorado River Basin. We also predicted that hydropeaking intensity would disfavor taxa with complex life cycles, thereby reducing the proportion of insect and EPT taxa in the aquatic community terms of richness, abundance, and biomass. Finally, due to attenuation of dam impacts with distance downstream, we predicted that distance downstream of a dam would be inversely related to dominance and positively related to local richness, abundance, and biomass of the entire invertebrate community.

METHODS

Study sites

We sampled 5–8 sites located from 0 to 24 km downstream of seven large dams in the Colorado River Basin ($N = 52$ sites; Fig. 1). We use the
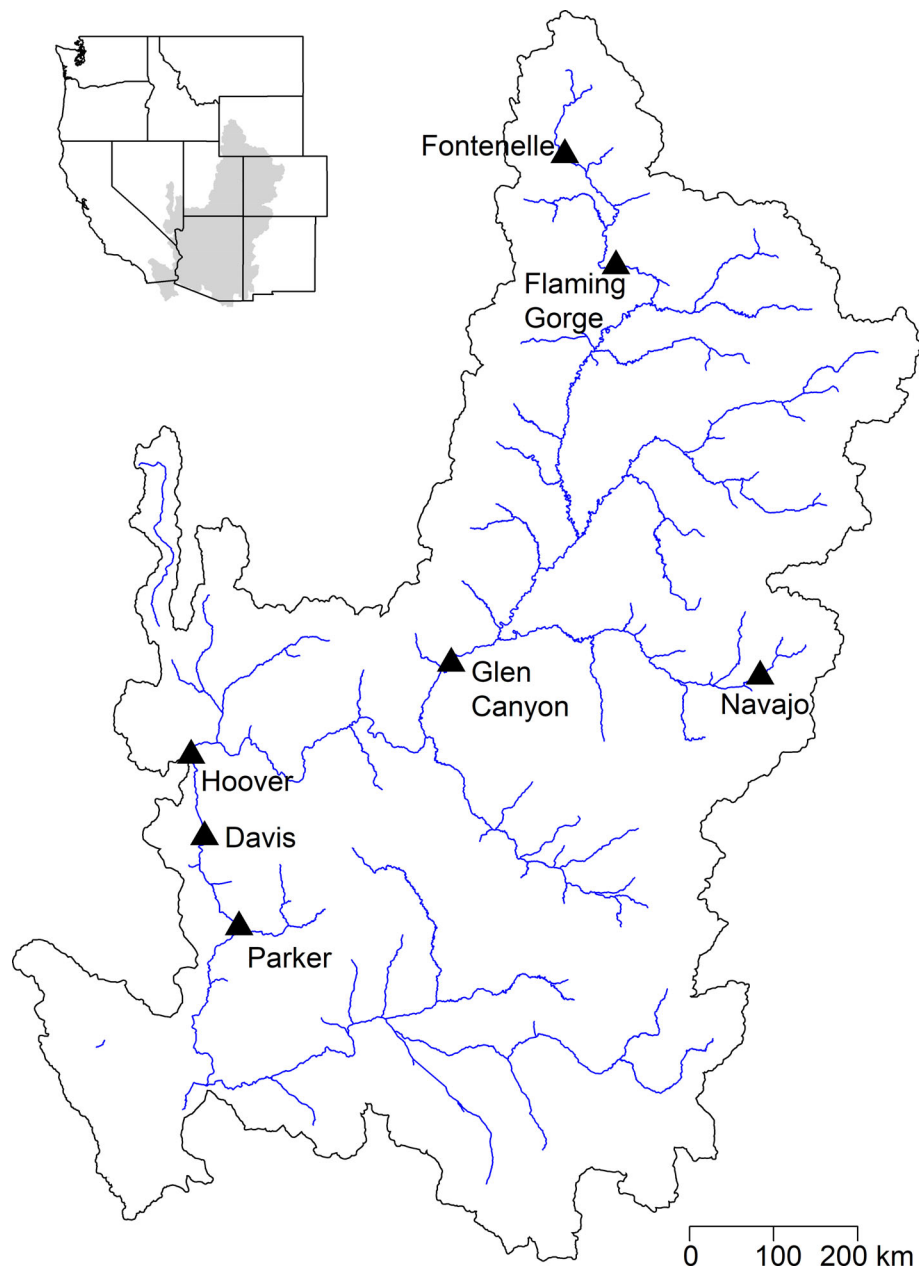
Fig. 1. Map of the Colorado River Basin showing major tributaries and the dams upstream of the tailwaters sampled for this study.

term tailwater to refer to the entire 0–24 km reach sampled downstream of each dam. The dams were built from 1931 to 1966 and range in height from 42 to 221 m. They differ in structure (earthfill, concrete thin-arch, or concrete arch-gravity), primary purpose (hydropower, storage, or flood-control), and reservoir length and capacity (see Appendix S1: Table S1 for more dam-specific information). We calculated hydropeaking intensity for each dam as the mean of the standard deviation of daily flow divided by the mean of daily flow for the five years preceding sample collection (Dibble et al. 2015).

Sample collection and processing

Sampling took place from May to June 2015 except at Glen Canyon Dam, which was sampled in May 2013. We collected 3–5 replicate benthic samples from the permanently submerged zone at each of the 52 sites. We sampled using the best method for the substrate present. At Fontenelle, Navajo, and Flaming Gorge Dams where water was wadeable and substrate was predominantly larger gravels and small cobbles, we used Surber sampling. Where water was wadeable and substrates were alternately dominated by finer sediments or larger cobbles, we used Hess sampling and rock scrubbing, respectively (Glen Canyon, Davis, Parker, and Hoover Dams). To sample sand or vegetation substrate in deep water, we used petite Ponar dredge sampling (average depth 4 m, range 1–9 m). We determined the area sampled at each site based on the sampling device used or the surface area of the scrubbed rocks, calculated from photographs (average sampled area 0.4 m^2, range 0.03–1.4 m^2). We then filtered samples through a 250-μm sieve and stored them in 95% ethanol.

To facilitate processing in the laboratory, we combined and rinsed the 3–5 replicates from each site before transferring them to a Caton tray sampler for subsampling. We randomly chose a single square of the gridded Caton tray, representing 1/30th of the sample, and removed it from the Caton tray. We then picked all invertebrates from the debris. If the subsample did not yield >500 invertebrates, we repeated the process on another 1/30th subsample, and so on until a count of 500 invertebrates was achieved or the entire sample was picked. Once subsampling was complete, we performed a visual scan of the Caton tray for large-bodied and rare invertebrates missed by subsampling. We identified invertebrates to the lowest feasible taxonomic level, usually genus. We measured the body length of the first 30 individuals and used allometric equations from the published literature to calculate biomass (Hódar 1996, Benke et al. 1999).

Data analysis

To explore whether responses differed across major taxonomic groups, we organized data into three partitions: all invertebrates (full dataset, including non-insects without a terrestrial phase), insects only (these generally have a complex life cycle with a terrestrial phase), and EPT only (the insect orders considered most sensitive to disturbance; Lenat and Penrose 1996). We calculated richness, abundance, biomass, and dominance for each site. Dominance values for each site were determined from the Simpson index (Simpson 1949) using the simpson function in the R software vegan package (R Core Team 2016, Oksanen et al. 2019). Simpson's D is a measure of dominance that has a range of $1/R$ to 1, where R is the number of taxa. To characterize invertebrate community structure in different tailwaters, we used the metaMDS function in the vegan package with the Bray-Curtis dissimilarity index to create nonmetric multidimensional scaling (NMDS) plots of log-adjusted abundance at the order level (or the lowest taxonomic level above order). We constrained the ordination to two dimensions and fit vectors onto the ordination for the 10 most abundant taxa, hydropeaking intensity, and dam height using the envfit function in the vegan package, which also calculates the squared correlation coefficient (r^2) for vectors. To further compare tailwater communities, we performed a permutational multivariate analysis of variance (PERMANOVA) using the adonis function in the vegan package.

We examined how environmental factors (distance from dam, hydropeaking intensity, and dam height) affected dominance, richness, abundance, and biomass for all invertebrates, insects only, and EPT only using generalized linear mixed models (GLMM). We used the glmmTMB and glmmADMB functions in the R packages of the same names (Fournier et al. 2012, Kristensen et al. 2016, R Core Team 2016). When modeling count (hereafter referred to as abundance) or biomass data, we included an offset term in our models, rather than using count or biomass data standardized by meter squared, in order to account for sampling uncertainties within (as opposed to outside) the models (Gelman and Hill 2007). We calculated this offset term for each site by multiplying the area of benthic substrate sampled by the area of the Caton tray subsampled. We compared Akaike information criterion (AIC) scores among a null model (no explanatory variables) and models with tailwater identity or an environmental factor (distance from dam, hydropeaking intensity, or dam height) as a fixed

effect. We chose the model family based on the distribution of the data; ultimately, the models used were either negative binomial or gamma for discrete (richness and abundance) and continuous (dominance and biomass) data, respectively.

Data generated during this study are available as a USGS data release (Muehlbauer and Abernethy 2021).

RESULTS

Patterns of dominance and community structure

Within each tailwater, 3–7 taxa dominated the communities, accounting for 95% of total abundance. The ten most abundant families accounted for ~99% of total abundance (Table 1). Of the ten most abundant taxa within each tailwater, eight taxa occurred in at least four tailwaters. Five of those widespread taxa belonged to the class Insecta: Baetidae (Order: Ephemeroptera), Chironomidae (Order: Diptera), Hydropsychidae (Order: Trichoptera), Hydroptilidae (Order: Trichoptera), and Simuliidae (Order: Diptera; Appendix S1: Table S2). Three of the widespread taxa were non-insects: Acari (Class: Arachnida), Hyalellidae (Order: Amphipoda), and Platyhelminthes (Appendix S1: Table S2). Across all sites, we found that dominance values ranged from 0.19 to 0.95 (average 0.55), invertebrate genus richness ranged from three to 26 (average 10 genera), abundance ranged from 415 to >170,000 individuals/m^2 (average 42,125 individuals/m^2), and biomass ranged from 0.3 to 125 g/m^2 (average 12.9 g/m^2).

Tailwater invertebrate communities in the Colorado River Basin were distinct from each other at the order and family levels in terms of both abundance and biomass. For these analyses, we chose to examine abundance data at the ordinal level (rather than genus, etc.) which was most accurate for all groups, including non-insects for which finer taxonomic resolution was not possible, and observed patterns were consistent regardless of the taxonomic resolution used (Fig. 2). There were clear differences in community composition between tailwater communities ($F = 26.07$, $P = 0.001$), as well as between insect and non-insect orders along NMDS axis 1. Hydropeaking intensity was associated with this axis ($r^2 = 0.62$), while dam height was associated with NMDS axis 2 ($r^2 = 0.59$). Insect orders with complex life cycles (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera) were associated with the three tailwaters experiencing lower hydropeaking intensity, while non-insect orders (e.g., Lumbriculida, Gastropoda, and Veneroida) were generally associated with the four tailwaters experiencing higher hydropeaking intensity.

Effects of hydropeaking intensity

Hydropeaking intensity had a greater impact on insect and EPT taxa relative to the full aquatic invertebrate community. Based on GLMM results for the full community dataset (i.e., all invertebrates, including non-insects), hydropeaking intensity did not improve model fit compared to the null model for dominance or genus richness, and only slightly improved fit for abundance and biomass (Appendix S1: Table S3). However,

Table 1. Patterns of dominance within tailwaters throughout the Colorado River Basin.

Tailwater	Dominance	No. taxa to reach 95% abundance	Percentage abundance contributed by 10 MAT	No. insect taxa of 10 MAT	Percentage of biomass contributed by insects	Total biomass (g/m^2)
Fontenelle	0.32 (0.06)	5	99.0	9	96.3	5.0 (1.62)
Navajo	0.60 (0.08)	4	99.5	5	95.2	3.7 (0.91)
Flaming Gorge	0.51 (0.01)	3	99.8	8	19.3	18.4 (2.67)
Glen Canyon	0.64 (0.06)	3	100	3	50.1	15.8 (3.7)
Davis	0.58 (0.1)	3	99.6	5	2.2	4.0 (1.45)
Parker	0.48 (0.09)	7	99.0	5	0.6	39.8 (19.05)
Hoover	0.36 (0.03)	4	100	3	26.9	3.2 (1.85)

Note: Dominance and total biomass are expressed as mean with SE in parentheses.
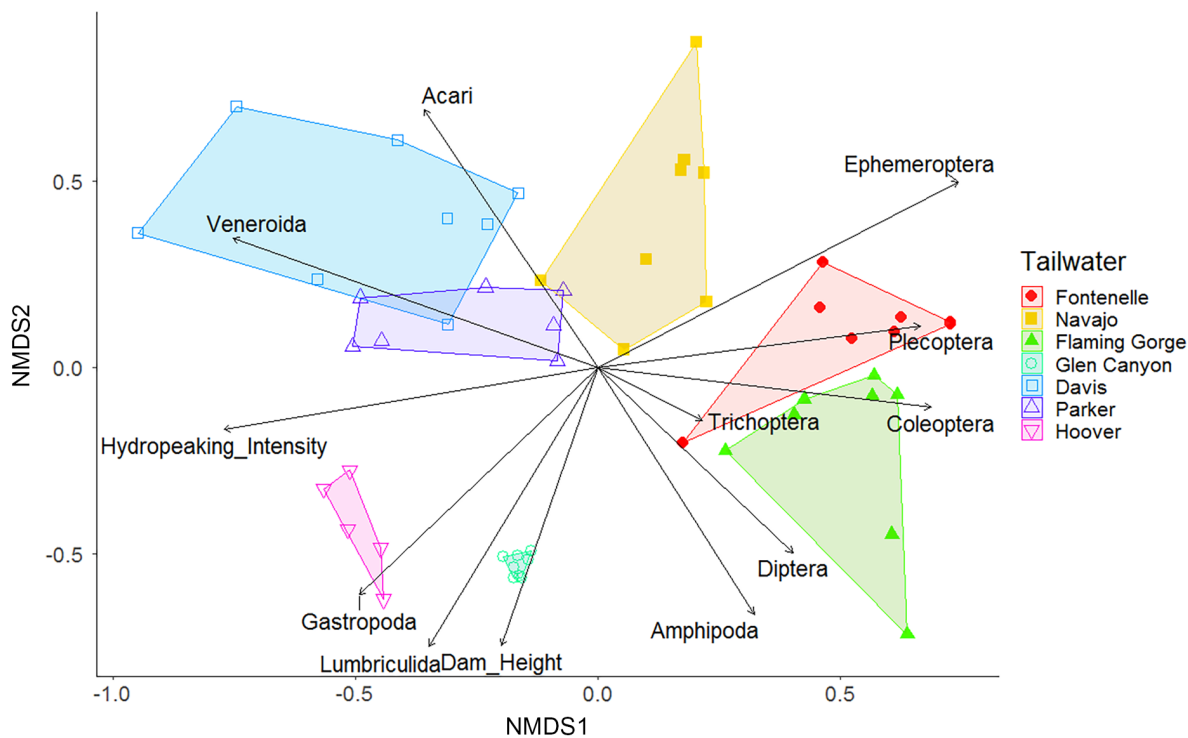MAT, most abundant taxa.

Fig. 2. Nonmetric multidimensional scaling plot (stress value 0.18) showing the log-adjusted abundance at the order level (or the lowest taxonomic level above order) with vectors showing the 10 most abundant taxa. Tailwaters are ordered from lowest to highest hydropeaking intensity in the legend.

models examining the insect and EPT data partitions showed that hydropeaking intensity clearly improved model fit, negatively impacting richness, abundance, and biomass (Appendix S1: Tables S4 and S5). Biotic response variables for insects and EPT were generally lower in tailwaters experiencing high hydropeaking (Glen Canyon, Davis, Parker, and Hoover; Appendix S1: Table S1). For example, the percent biomass contributed by insects relative to non-insect invertebrates was 2–160 times higher in tailwaters experiencing the lowest levels of hydropeaking (Fontenelle and Navajo; Appendix S1: Table S1; Fig. 3a). For EPT taxa, this effect was even more exaggerated, indicating that even small amounts of hydropeaking greatly diminish EPT biomass (Fig. 3b). For most models, tailwater identity and dam height improved fit; these variables serve as proxies for a multitude of environmental variables such as temperature, nutrient loads, reservoir size, and latitude/longitude.

Proximity to dams negatively affects communities

Distance from dam predominantly impacted richness regardless of the data partition used (i.e., full community, insect, or EPT). For the full community dataset, including distance from dam in the model improved fit for genus richness and dominance, but not for abundance and only slightly for biomass (Appendix S1: Table S3). For the insect and EPT-only data partitions, incorporating distance from dam improved fit for genus richness, but not for abundance or biomass (Appendix S1: Tables S4 and S5). Within most tailwaters, genus richness increased with increasing distance from dam and did so for all three data partitions. When examining the full community dataset, this positive trend was significantly different from zero for Fontenelle ($P = 0.017$) and Navajo ($P = 0.012$; Fig. 4). It was even more pronounced for the insect and EPT-only data partitions, for which four and five tailwaters (respectively) showed significant
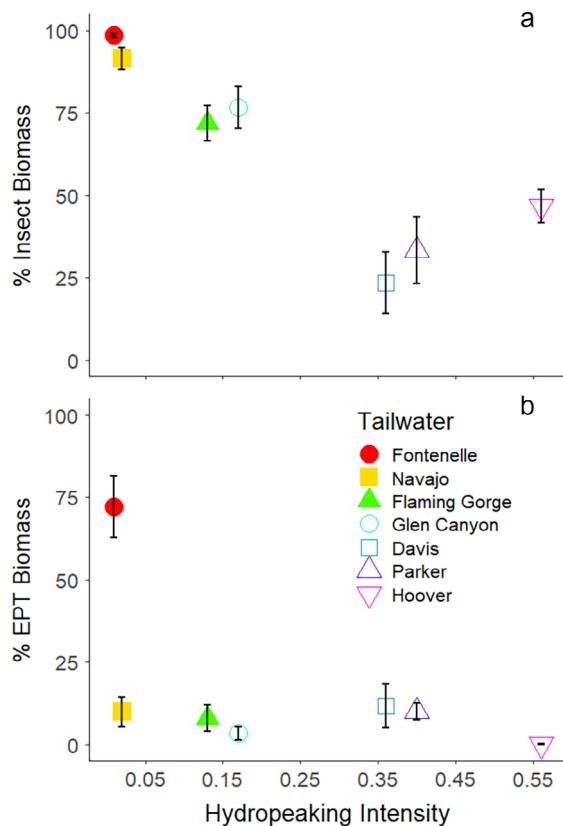
Fig. 3. Proportion of (a) insect and (b) Ephemeroptera, Plecoptera, and Trichoptera (EPT) biomass shown as an average across all sites collected downstream of each dam graphed against hydropeaking intensity. Bars represent standard error. Tailwaters are ordered from lowest to highest hydropeaking intensity in the legend.

increases in genus richness with increasing distance from dam. Exceptions to these positive trends were observed at Glen Canyon, where community richness was low and static throughout the tailwater, and Hoover, where community richness was low and decreased with increasing distance from dam.

Discussion

Our study showed that tailwaters downstream of large dams in the Colorado River Basin are dominated by just 3–7 taxa. These dominant taxa accounted for 95% of the total invertebrate abundance within individual tailwaters (Appendix S1: Table S2). Half of these taxa were non-insect, non-

flying species and thus were unavailable to terrestrial consumers (i.e., seven of the 14 dominant taxa are non-insects). Consistent with previous studies, aquatic insects and sensitive EPT taxa were negatively associated with hydropeaking intensity, which puts limits on the composition and perhaps the quality of the invertebrate food base available to higher consumers. While total invertebrate abundance and biomass did not change throughout tailwaters, insect and EPT richness, abundance, and biomass all increased, suggesting that the impacts of damming are most acute immediately downstream of dams.

Tailwaters favor the dominance of a few taxa

Hydropeaking dams generate highly modified and disturbed environments, which affect the suite of organisms that can inhabit both downstream tailwaters and upstream reservoirs (Céréghino et al. 2002, Havel et al. 2005, Johnson et al. 2008, Kennedy et al. 2016, Kjærstad et al. 2018). Our study showed that in the highly modified tailwaters in the Colorado Basin, only a few invertebrate taxa dominated communities (largely Chironomidae, Baetidae, and Dreissenidae). These invertebrate families include generalist species that are likely to occur across a variety of flow conditions, analogous to weedy terrestrial plant species. The quagga mussel (Dreissenidae: *Dreissena bugensis*) is a dominant invasive species that now occurs within four of the studied tailwaters and is also capable of persisting in a variety of flow conditions including periodic desiccation (Ricciardi et al. 1995). The dominance patterns we observed were the result of species loss closer to the dam rather than reductions in total abundance, further suggesting that the presence of extreme ecological conditions, and not reduced productivity (as in Hall et al. 2015), was the mechanism favoring a few generalist species. This taxonomic dominance by only a few species was evident across the basin: Seven of the ten most abundant taxa occurred at over half of the tailwaters.

While two of the most abundant taxa in Colorado River Basin tailwaters do have a terrestrial phase during their life cycle (Chironomidae and Baetidae), half of the most abundant taxa we observed were non-insects that do not (13 of the 26 taxa in Appendix S1: Table S2 are non-insects). This prevalence of non-insects has important consequences for ecosystem function,
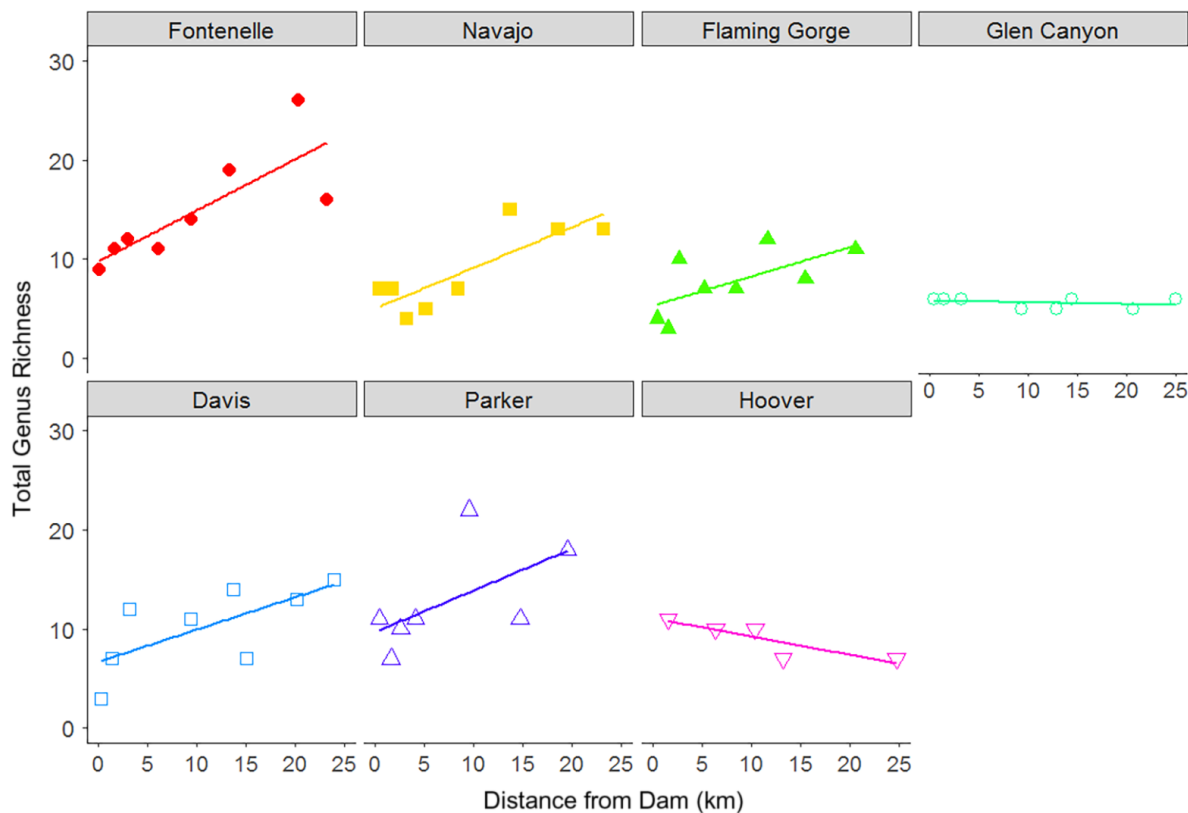
Fig. 4. Genus (or the lowest feasible taxonomic level) richness as a function of distance from dam for all taxa observed at each site. Colors represent different tailwaters.

particularly by decreasing energy flow into the terrestrial environment, and represents a shift away from communities primarily composed of insect taxa that occur in undammed Colorado River tributaries (Blinn and Cole 1990). Insects are the primary food base for many organisms both within and adjacent to rivers, contributing energy to riparian and terrestrial consumers (Baxter et al. 2005). Ultimately, the dominance of a few invertebrate taxa locally and across the basin has negative implications for aquatic biodiversity within tailwaters, a type of habitat now widespread globally (Zarfl et al. 2014), even while total productivity may have remained unchanged.

Hydropeaking intensity negatively impacts aquatic insects

As predicted, hydropeaking intensity had a negative effect on insect and EPT richness,

abundance, and biomass, although this effect diminished with increasing distance downstream from dams. This suggests that hydropeaking could play a role in excluding EPT and other insect taxa, particularly immediately below dams. Similarly, insect and EPT biomass was lowest in tailwaters experiencing high amounts of hydropeaking, suggesting that a lower amount of biomass will be available to riparian consumers at these tailwaters. We did not observe a negative relationship between hydropeaking intensity and biomass when all invertebrates were considered together, suggesting that hydropeaking puts limits on the type and perhaps quality of the invertebrate food base rather than overall secondary production. In fact, the highest average biomass occurred downstream of a high hydropeaking intensity dam (Parker Dam; ~40 g per m^2) in the form of a hyper-abundance of large, invasive quagga

mussels. Although we reported biomass as standing stock, rather than secondary production, the high invertebrate assemblage biomass values we observed suggest that these tailwater systems are highly productive (Fisher et al. 1982, Huryn and Wallace 2000, Tonkin et al. 2009, Tonkin and Death 2013).

Richness increases within 24 km downstream of dams

We show that richness increased and dominance decreased within the 24 km downstream of the dams, while neither abundance nor biomass changed substantially. Tailwater communities nearest the dams were largely dominated by non-insect taxa (e.g., Dreissenidae) or generalist insect taxa (e.g., Chironomidae). As distance from the dam increased and the dominance of certain taxa decreased, more taxa joined the community, yet whole community abundance and biomass remained relatively constant. A possible explanation is that more suitable conditions (increases in periphyton, planktonic drift, primary production, substrate size, or changes in thermal and flow regime) could exist for EPT taxa farther from the dam. Similar to our findings, Ellis and Jones (2014) observed shifts in the relative abundance of invertebrate taxa, with filter feeders dominating communities directly downstream of dams. Whereas Ellis and Jones (2014) observed a recovery plateau within 5 km, we continued to see increases in richness throughout the 24 km sampled in many tailwaters.

Two tailwaters, Glen Canyon and Hoover Dam, instead showed a constant or a slight decrease in richness throughout each 24 km stretch. Unlike the other tailwaters, neither Ephemeroptera nor Plecoptera taxa were present in the downstream-most samples from these tailwaters. Within the sampled reach below Hoover, the river merges with the reservoir pool behind Davis Dam. Thus, it is not surprising to find fewer macroinvertebrate taxa as this large river system shifts from a lotic to a deep-water lentic environment. In Glen Canyon, we did not observe recovery of EPT taxa at the spatial scale of our study (24 km). However, Kennedy et al. (2016) previously documented diversity changes in Glen-Grand Canyon at the scale of hundreds of kilometers, driven by the timing of daily hydropeaking events that attenuates very slowly through the long, narrowly confined canyon reach. Given that these trends exist within the Glen Canyon tailwater only at this larger spatial scale, it becomes even more interesting that we did observe species recovery within other tailwaters at a smaller spatial scale.

Conclusions

Our study provides a spatially extensive dataset of the aquatic invertebrate communities in the Colorado River Basin and illustrates how hydropeaking intensity and distance from dam may be structuring the insect and non-insect components of aquatic communities, which can be used to inform management with respect to the invertebrate food base of rivers. Although our study examined communities at one time point, long-term datasets from tailwaters may eventually elucidate how subtle shifts in more complex environmental conditions (i.e., temperature and nutrient loads) affect insect populations and communities temporally (Ruhi et al. 2018). These data can then help parameterize predictive models for dam practitioners to tailor their management actions to particular targets (Shenton et al. 2012, Yen et al. 2013, Tonkin et al. 2018, Rogosch et al. 2019). For example, downstream of Glen Canyon Dam experimental flow releases are being implemented specifically for the benefit of aquatic insects (Duke 2018). While focusing management actions too narrowly on specific taxa (e.g., EPT taxa and insects) may have drawbacks for other members of the aquatic community, identifying how dam management practices impact specific biotic components can ultimately inform holistic ecosystem management.

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SUPPORTING INFORMATION