Native Fish Need A Natural Flow Regime

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Water development has threatened the ecological integrity of riverine ecosystems. Increasing water demand, persistent drought, and climate change exacerbate the effects of habitat degradation and loss in altered systems such as the Colorado River basin. Today, biologists are challenged to identify management actions that benefit native fishes while not hindering water development or management. Herein, we discuss the importance of the natural flow regime for functioning riverine ecosystems and provide examples from four tributaries to the Green River, a major headwater branch of the Colorado River. These tributaries represent a gradient of impacts ranging from water abstraction to the point of complete seasonal desiccation to a relatively natural flow regime, and consequently have maintained different levels of instream habitat complexity and native fish persistence. Despite decades of management, endangered species lack self-sustaining populations and other native species have been extirpated from over half their ranges, which begs the question: can water development and fish conservation be balanced under current water laws and climate change-driven declines in runoff? Given the continued decline in freshwater biodiversity and abundance occurring across the globe, we contend that immediate designation of rivers with natural flow regimes as freshwater conservation areas will enhance native species recovery.

It is well established that a natural flow regime is important for the ecological health of rivers (Poff et al. 1997; Palmer and Ruhi 2019). The natural flow regime is the habitat template for riverine organisms, including fishes, and plays a vital role in building and maintaining complex instream habitats (Bunn and Arthington 2002; Yarnell et al. 2015). Although all components of the natural flow regime are important, there is no more important attribute than the simple existence of water in the channel. One of the most striking examples of this truism is the transformation of the Colorado River delta, once among North America’s most productive and biologically diverse regions that is now a dry, sandy, ephemeral channel confined by levees (Glenn et al. 1996). Assuming this most basic criterion of the flow regime is achieved, other components of the flow regime (magnitude, frequency, duration, timing, and rate of change) are important determinants of habitat and cues for native fishes. For example, peak flows play an especially important role in providing complex habitat, flushing fine sediments, and facilitating lateral connections to riparian areas (Benke 2001; Lytle and Merritt 2004). Reduction of peak flow magnitude and duration typically leads to simplification of instream habitat, channel narrowing, and encroachment by riparian vegetation, which diminishes water and sediment fluxes among the river channel, riparian area, and upland ecosystems (Gauman et al. 2005; Merritt and Poff 2010; Grams et al. 2020). For fishes, complex instream habitat and habitats created during floodplain inundation are important spawning and rearing habitat (Humphries et al. 2020), but these habitats are often limiting where channels are confined by levees, have incised or simplified, or have been significantly dewatered (e.g., Bestgen et al. 2011). Given the degradation of many riverine ecosystems and continuing impacts of climate change, any opportunity to conserve natural flows will likely enhance native species recovery (Palmer and Ruhi 2019).

The Colorado River basin (CRB) epitomizes loss of riverine ecological integrity through water development. Water in the CRB is overallocated and does not reach the Gulf of California in most years (Wheeler et al. 2021). The effects of water development in the CRB from dams and diversions that deliver water for human use include reductions in flow magnitude (instantaneous, flood, and total annual flow), habitat alteration and degradation, and increased fragmentation. As such, declines in native fishes in the Colorado River and its tributaries have been profound and persistent (Minckley and Deacon 1968; Budy et al. 2015; Propst et al. 2021). Additionally, native fish populations were further impacted by intentional poisoning of rivers to aid establishment of nonnative fishes in newly created reservoirs (Holden 1991; Minckley and Deacon 1991). Eventually, basinwide declines in native fishes prompted the creation of several management and recovery programs and multi-state conservation agreements across the basin, such as the Glen Canyon Dam Adaptive Management Program (https://on.doi.gov/3wRK7R9), the San Juan River Basin Recovery Implementation Program (https://bit.ly/3oF23eq), and the Upper Colorado River Endangered Fish Recovery Program (https://www.coloradoriverrecovery.org/).

The goal of the San Juan and Upper Basin programs is to recover native species while water supply allocation and management proceeds in accordance with state and federal laws and interstate compacts. Each program was created following negotiation among water supply, hydropower, fish and wildlife, and environmental interests. Today, management
and recovery program biologists are challenged to identify strategies that benefit endangered fishes while not interfering with water development or management. That challenge may be impossible to meet under current water laws, particularly with persistent, basinwide reductions in snow melt runoff (Udall and Overpeck 2017; Milley and Dunne 2020; Wheeler et al. 2021) and ongoing debate about the magnitude of sustainable uses and losses in the upper CRB (e.g., Schott 2021). Thus, it is not necessarily surprising that endangered fishes such as Bonytail *Gila elegans*, Colorado Pikeminnow *Ptychocheilus lucius*, and Razorback Sucker *Xyrauchen texanus* still lack self-sustaining populations (Osmundson and White 2017; USFWS 2018), despite intense management by state, federal, tribal, and private organizations during the past several decades. Without federal stocking programs, some species surely would be extinct (Bestgen et al. 2017; USFWS 2018). Similar challenges are also present outside the CRB. For example, recovery efforts of Pacific salmon *Oncorhynchus* spp. in the Columbia River basin continue to be strained by dams (NOAA 2017), and water withdrawals in the watershed of the northern branch of the Rio Grande cause widespread intermittency of the river in New Mexico, stranding endangered Rio Grande Silvery Minnow *Hybognathus amarus* in isolated pools that eventually dry (Archdeacon and Reale

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**Figure 1.** Four major tributaries to the Green River in the upper Colorado River basin in the southwestern USA. Inset plots are historical (gray) and present flow regimes based on mean daily flows (USGS 2021). Solid lines represent medians and the bands represent the 25th and 75th percentiles. Period of record differs among gaging stations for historical flows: White and Green rivers (1929–1949), Price and San Rafael rivers (1945–1949), and Duchesne River (1942–1949). Present flows are from 2000–2020. White triangles represent locations of U.S. Geological Survey gauging stations. Negative numbers represent the percent reduction in median spring discharge (March–June) between historical and present time periods. Highlighted reaches of river represent the extent where large woody debris was quantified (presented in Figure 2).
2020). Thus, this issue is not unique to the CRB and begs the question: Can continued water development and fish conservation be balanced when watershed runoff is decreasing with a more arid climate? Herein, we present our perspective on the importance of conserving the natural flow regime and the critical need to prevent further unnatural reductions in flow in tributaries of the CRB. We demonstrate this need with data on flow, habitat, and fish occurrence in four tributary rivers that represent a gradient of water abstraction and associated habitat degradation.

A critical piece of the puzzle is the link between habitat complexity and flows, as is exemplified by major tributaries of the Green River, one of three headwater branches of the Colorado River, along with the upper Colorado and San Juan rivers (Figure 1). The Green River has two coequal headwater branches, the upper Green and the Yampa rivers, and these two branches have approximately the same mean annual flow at their confluence. In fact, the mean annual flow of the Yampa River was 11% greater than the upper Green between 2001 and 2020. Downstream of the confluence of the two headwater branches, there are four large tributaries—the Duchesne, Price, San Rafael, and White rivers (Figure 1). Although these tributaries have experienced declines in discharge because of flow regulation, water withdrawals, and persistent, basinwide drought since 2000 (Salehabadi et al. 2020; Table 1), only the White River retains a relatively natural flow regime (Figure 1).

The number of days with flow less than the 25th percentile of daily discharge has increased by 288% and 164% in the Price and San Rafael rivers, respectively, and the number of days with zero flow has more than doubled in the San Rafael River from the early and mid-20th century to the early 21st century (Table 1). The mean total annual flow of the Duchesne River since 2000 is only 38% of the estimated flow between 1914 and 1957 and is 59% and 45% for the Price and San Rafael rivers, respectively. In contrast, mean total annual flow of the White River between 2000 and 2018 was 76% of the estimated total flow of the early and mid-20th century, and this tributary is the one to experience unaltered spring snow melt floods on a fairly regular basis. The White River is also the only major tributary that has complex habitat required for recruitment of all life stages of native fishes. For example, as an important index of habitat complexity, we coarsely estimated large woody debris densities (i.e., log piles, submerged trees, and fallen trees) in each tributary using aerial imagery in Google Earth. We used imagery from 2015 for the Price and White rivers and 2019 for the Duchesne and San Rafael rivers, based on availability. Densities of large woody debris were two to six times higher in the White River relative to the other tributaries. Specifically, large woody debris density, measured as the total number of log piles, submerged trees, and fallen trees per total river kilometers assessed, was 2.45, 1.38, 0.73, and 0.37 in the White, Duchesne, San Rafael, and Price rivers, respectively. Reaches of the White River meander through wide floodplain with viable native Fremont cottonwood Populus fremonti galleries that contribute to recruitment of wood into the stream that form abundant, large complexes (e.g., submerged trees, wood piles)—a process representing a healthy, functioning river system. Another measure of the loss of habitat availability and complexity is channel narrowing. Channel width of the White River has decreased by 30%, on average (1936–2016; unpublished data from the authors) compared to reductions of 81% in the Price River (1938–2016; unpublished data from the authors) and 83% in the San Rafael River (1938–2009; Fortney 2015). Particularly for the White River, the natural flows play a critical role in the regeneration of cottonwoods (as seen by multiple cohorts), which in turn are critical in the formation and maintenance of complex instream habitats (Figure 3). It is perhaps unsurprising, but telling, that many native fishes that have been extirpated elsewhere or persist at very low levels still thrive in the White River, where flows are relatively unaltered and complex habitat remains (Figure 3; Anderson et al. 2019). We consider the White River to be one of the few remaining functioning riverine ecosystems in the entire CRB.

Tributaries provide important habitat for both resident and migratory native fishes in the CRB (e.g., Cathcart et al. 2015; Hooley-Underwood et al. 2021), particularly those with more natural flow regimes (Laub et al. 2018; Anderson et al. 2019). Of the four tributaries of the Green River considered herein, adult endangered Colorado Pikeminnow and Razorback Sucker attempt to use all of them (https://streamsystem.org); yet only portions of the lower White River are designated critical habitat (USFWS 1994; Bottcher et al. 2013; Webber and Bestgen 2013). For example, endangered fishes use the White River for spawning (Webber et al. 2013; Anderson et al. 2019), and densities of adult endangered Colorado Pikeminnow in the White River are some of the highest in the Green River watershed (Bestgen et al. 2018; Anderson et al. 2019). Young-of-the-year Roundtail Chub G. robusta, Bluehead Sucker Catostomus discobolus, and Flannelmouth Sucker C. latipinnis are consistently collected in the White River (Figure 3), despite having been extirpated from more than 50% of their ranges (Budy et al. 2015). Alternatively, Roundtail Chub have not been captured in the Price River in more than 40 years (Chart and Mohrman 2012), and although relatively common in the San Rafael River during sampling in 2008–2010 (Walsworth 2011), they were not captured in the same reaches during 2020; an extremely dry year when water abstraction dewatered the river downstream of several diversions (T. Remiszewski, U.S. Geological Survey Utah Cooperative Fish and Wildlife Unit, unpublished data). We assert that the continued presence and recruitment of otherwise imperiled (and endangered) native

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<th>Tributary</th>
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<th>Median summer baseflow (ft³/s; July–September)</th>
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<th>Mean number of days with zero flow</th>
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<td>14</td>
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<tr>
<td>White</td>
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Table 1. Flow metrics from four major tributaries to the middle Green River in the upper Colorado River basin in the southwestern USA. Period of record differs among U.S. Geological Survey (USGS) gauging stations for historical flows and are reported in Figure 1. The period of record for the present is from 2000–2020 for all stations (USGS 2021).
fishes in the White River is a function of its relatively natural flow regime and associated habitat availability and complexity. Alteration to any component of a river’s flow regime has ecological consequences (Acreman and Dunbar 2004), and environmental flows from dams are a commonly proposed method to attempt to benefit native species or at least reduce negative impacts of flow alteration following water development projects (e.g., Davies et al. 2013; Acreman et al. 2014; Yarnell et al. 2015). Although these flows may benefit some aspects of native fish life histories, we assert that environmental flows are unlikely to mitigate the adverse effects of large diversions of streamflow. The effectiveness of environmental flows that match some aspects of the natural flow regime (e.g., timing), but ignore others (e.g., magnitude, duration; Chen et al. 2020), to increase abundance of many native fishes is questionable based on the current state of many populations across the CRB (e.g., Bestgen et al. 2018; USFWS 2018). Furthermore, there are important components of a natural flow regime for native species beyond instream habitat, such as spawning cues and interaction with productive floodplain habitat, and there are likely others we do not yet understand. To increase lateral connectivity in the Green River, managers time flow releases coinciding with larval fish presence to entrain larvae into productive floodplain wetlands with some success (e.g., Bestgen et al. 2011, 2017), but this has only occurred in mainstem habitats, and it remains unclear if localized entrainment is enough to overcome broadscale recruitment bottlenecks. The ability of managers to provide environmental flows and native fish response to flow regime mimicry and management in the CRB is meager. Where environmental flows have been secured, the magnitude of these flows is often far from flow magnitudes during historical floods because of additive and interactive effects from damming, water abstraction, floodplain development, drought, and climate change. For example, flows in the San Juan River have been managed since 1993 to mimic the timing of snowmelt runoff in the Animas River and the average magnitude of pre-dam spring floods in the San Juan River (Gido and Probst 2012), but only the recommended frequency of the lowest magnitude flow target has been met between 2006–2020. Endangered fishes have spawned nearly every year since monitoring began in the San Juan River (Farrington et al. 2019), suggesting that perhaps flow regime mimicry is cueing fishes; however, populations are sustained by stocking and not by natural recruitment.

The scientific evidence for declines in snowmelt runoff in the CRB is unequivocal, and the upper basin states have expressed their interest in continuing to increase consumptive uses, consistent with their interpretation of the Law of the River. Water depletions have severely impacted riverine communities in three out of the four major tributaries to the Green River through habitat loss and degradation, as described above. Given the known importance of the natural flow regime in creating and maintaining complex instream habitat and floodplain connectivity for viability and persistence of native species (aquatic and terrestrial), additional depletions from rivers such as the White River have the potential for significant compounding effects on the remaining native fishes, such as what has occurred in the Duchesne River (Anderson et al. 2019). Additionally, natural flow regimes are important for overall health of riparian vegetation that results in valuable wildlife habitat (Tonkin et al. 2018), so any further unnatural alteration to the flow regime of the White River would also impact terrestrial communities. If the White River were to be depleted to the extent experienced by the other three tributaries of the Green River, then there would be no tributary downstream from the confluence of the upper Green and Yampa rivers with complex habitat and a natural flow regime to provide refuge and spawning habitats for native fishes. However, further depletions of flow of the White River are currently being proposed (e.g., https://bit.ly/3x50eeB).

Figure 2. Photos from (A–C) the White, (D) Price (several passive integrated transponder tag antennas are also visible), (E) San Rafael, and (F) Duchesne rivers. Relatively unaltered flows in the White River are critical to maintenance and formation of complex habitat in the river and riparian area. Conversely, water abstraction in the Price, San Rafael and Duchesne has severely altered habitats, sometimes leading to (E) complete channel drying. Photo credits: M. Breen (A, B, C, F) and Emma Doden (D, E).
Prioritizing rivers with a semblance of a natural flow regime for immediate conservation by giving them protected status as freshwater conservation areas (e.g., Williams et al. 2013) would have substantive benefits for native species. Obviously, this is an issue that extends beyond the CRB and the few examples presented herein (e.g., NOAA 2017; Archdeacon and Reale 2020; Tickner et al. 2020). The science is clear as to the benefits of natural flow regimes for native species. These benefits include adequate flows to support dynamic riverine landscapes, which provide complex and complimentary habitats able to support all life stages of fish (and other wildlife), which are lacking from rivers that are overallocated for human water use. Historically, the CRB was a highly dynamic and connected riverine landscape, and native species evolved through periods of wet and dry cycles; however, contemporary riverine habitat has been altered such that many flow regimes are decoupled from conditions in which native fishes evolved. While conservation of a natural flow regime might not completely alleviate all of the stresses facing lotic systems (Saunders and Tyus 1998), maintaining water in the channel under a natural flow regime likely enhances native species resilience to other stressors, such as nonnative species establishment (e.g., Merritt and Poff 2010; Kiernan et al. 2012). Unless we prioritize conservation of riverine ecosystems, native species populations will likely continue to decline as flows are further reduced by climate change and human water use.

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REFERENCES


