Articles

A Small Warm Tributary Provides Prespawning Resources for Colorado Pikeminnow in a Cold Dam-Regulated River

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Abstract

Riverine habitat mosaics, including tributaries, are an important reason the Green River subbasin supports the largest remaining population of federally endangered Colorado Pikeminnow *Ptychocheilus lucius* in the Colorado River Basin. Upstream Colorado Pikeminnow distribution is limited by Flaming Gorge Dam and few typically occurred in the reach immediately downstream of the dam, which is the reach most affected by thermal and hydrologic alterations. However, fish captures and passive integrated transponder (PIT) antenna sampling of previously tagged individuals from 2011 to 2021 revealed seasonal congregations of up to 75 Colorado Pikeminnow annually in the mouth of Vermillion Creek, a small tributary in the regulated reach. Approximately 11% ($N = 93$ individuals) of the entire 2017–2018 Green River basin population were encountered in Vermillion Creek over the 11-y study, an underestimate of use considering that untagged fish were not detected by antennas. Colorado Pikeminnow used Vermillion Creek primarily when Green River spring flows from Flaming Gorge Dam were high and cold in May through mid-June when the confluence was a large, deep backwater warmer than the main channel and supported forage fishes. Intra-annual encounters revealed seasonal residence times for individual Colorado Pikeminnow up to 91 d, and multiple inter-annual encounters indicated site fidelity. Frequent detections of individual Colorado Pikeminnow in a Yampa River spawning area soon after their detections in Vermillion Creek indicate this tributary may be an important resource for reproductive adults. The intensive and basin-wide PIT tagging and detection program for Colorado Pikeminnow enhanced our understanding of the importance of small habitat nodes such as Vermillion Creek in the Green River drainage network. Understanding and protecting these seasonally available riverine habitat mosaics used for prespawning conditioning may assist with recovery of Colorado Pikeminnow.

Keywords: Pikeminnow; tributary; dam; habitat; Green River

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Introduction

In large river networks throughout the world, tributaries provide important habitat and resources for aquatic biota (Leopold et al. 1964; Baker et al. 1991). For example, tributary streams contribute inorganic and organic materials to mainstem rivers; create heterogeneity in channel morphology, habitat, physicochemical makeup, and biota (Braaten and Guy 1999; Benda et al. 2004; Kiffney et al. 2006); and add complexity and redundancy to drainage networks. Fish populations primarily residing in mainstem rivers use tributaries for reproduction (Robinson et al. 1998; Van Haverbeke et al. 2013; Kluender et al. 2016; Fraser et al. 2017), nursery habitat (Brown and Coon 1991, 1994), foraging (Dames et al. 1989), and refuge from high flow events (Braaten and Guy 1999; Valdez et al. 2001). However, despite their importance in enhancing riverine mosaics for fishes, permanent as well as ephemeral tributaries are sometimes overlooked by managers and are legally underprotected in some settings (Sabo et al. 2012; Colvin et al. 2019; Hooley-Underwood et al. 2019).

The Upper Colorado River Basin supports several rare endemic warm water fishes whose distribution and abundance are restricted by cold water temperatures downstream of large dams (Muth et al. 2000; Johnson et al. 2008; Zelasko et al. 2016). These include Humpback Chub *Gila cypha*, Bonytail *G. elegans*, Colorado Pikeminnow *Ptychocheilus lucius*, and Razorback Sucker *Xyrauchen texanus*, all of which are listed as endangered by the U.S. Fish and Wildlife Service, pursuant to the U.S. Endangered Species Act (ESA 1973, as amended; USFWS 1987). Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *C. discobolus*, and Roundtail Chub *G. robusta* are also listed by states in the Upper Colorado River Basin as needing conservation (Bezzerides and Bestgen 2002).

Ecological studies of fishes in tributaries of the Colorado River Basin has focused largely on medium to large perennial streams including the Little Colorado River in Grand Canyon (Robinson et al. 1998; Van Haverbeke et al. 2013), and the Yampa and White rivers in the Green River subbasin (Holden and Stalnaker 1975; Tyus and Saunders 2001; Webber et al. 2013). Those large, perennial tributaries are used for purposes described above, but smaller tributaries may also provide resources for endemic species (Sabo et al. 2012; Kluender et al. 2016; Hooley-Underwood et al. 2019). Even ephemeral streams sometimes support reproduction and rearing of young (Chart et al. 1999; Hooley-Underwood et al. 2019) and tributary confluences in the Green and San Juan rivers are used by multiple life stages of native fishes (Tyus and Saunders 2001; Fresques et al. 2013; Cathcart et al. 2015, 2018, 2019).

The Green River subbasin, including the tributary White and Yampa rivers arguably support the most widely distributed populations of native fishes remaining in the basin (e.g., Bestgen et al. 2007, 2020a; Zelasko et al. 2010). However, even there, native fish distributions have been negatively affected by dams, including Flaming Gorge Dam on the Green River (Vanicek et al. 1970; Holden 1991; Bestgen and Crist 2000; Sabo et al. 2012). For example, Colorado Pikeminnow were displaced from the 106-km reach between Flaming Gorge Dam and the Yampa River confluence after closure of the dam (Vanicek and Kramer 1969; Vanicek et al. 1970), but reestablished there following flow and dam penstock modifications that increased downstream temperature (Holden and Crist 1981; Bestgen and Crist 2000; Muth et al. 2000). As a result, Tyus and Saunders (2001) suggested the reach between the dam and the Yampa River be reconsidered as critical habitat for Colorado Pikeminnow and other imperiled fishes. Close proximity of this reach to the lower Yampa River, one of the two regularly used Colorado Pikeminnow spawning habitats in the Green River basin to which individuals migrate (Tyus 1990; Irving and Modde 2000; Kitcheyan and Montagne 2005), adds to the value of the reach between Flaming Gorge Dam and the Yampa River.

Prior to 2011, there were few reports of Colorado Pikeminnow in the 75-km reach of the Green River upstream of Lodore Canyon despite active fish community sampling and telemetry studies (Tyus 1990; Irving and Modde 2000; Kitcheyan and Montagne 2005). However, opportunistic capture of eight individuals during a Green River electrofishing survey in spring of the high flow year 2011 in lower Vermillion Creek, a small, seasonally flooded tributary, drew attention to the stream as potentially important habitat. Those captures were unexpected because annual multiple-pass sampling in Lodore Canyon, a 32-river-km (rkm) reach immediately downstream of the confluence of Vermillion Creek and mainstem Green River, usually yielded just a few Colorado Pikeminnow (Bestgen and Crist 2000; Bestgen et al. 2007) and captures by other gears immediately upstream of Vermillion Creek were infrequent. The reach was not even included in Green River basin-wide abundance estimation sampling because few individuals were thought present (Bestgen et al. 2007). Here, we report on sampling from 2011 to 2021, which documented annual concentrations of Colorado Pikeminnow using the diminutive Vermillion Creek mouth, as well as prespawning site fidelity of long-distance migrants, to support the idea that small tributaries may play a role in supporting Colorado Pikeminnow in the Green River subbasin. We posit that this habitat, and perhaps others like it, provides prespawn conditioning for Colorado Pikeminnow, which may be an important but understudied life history strategy in the reproductive ecology of fishes.

Study Site

The Green River downstream of Flaming Gorge Dam flows through northeastern Utah and northwestern Colorado, and enters Browns Park National Wildlife Refuge about 26 rkm upstream of the northern boundary of Dinosaur National Monument at rkm 588 (Figure 1). The river in this area has a low-gradient, braided channel dominated by sand substrate and numerous vegetated off-channel backwaters throughout. During endangered fish recovery releases from Flaming Gorge Dam in spring (hereafter, spring peak releases), higher flows fill backwaters, tributary mouths, and form extensive wetland and inundated floodplain habitat. Spring peak releases from Flaming Gorge in May and June 2011–2021 were typically 131–255 m^3/s (Figure 2); base flows were typically 23–71 m^3/s (USGS Gauge 09234500, Greendale, Utah). Spring peak releases from Flaming Gorge Dam were designed mainly to inundate floodplain wetlands in the Green River well downstream of the Yampa River, to benefit early life stages of imperiled fishes including Razorback Sucker and Bonytail (Muth et al. 2000; Bestgen et al. 2017; LaGory et al. 2019).

Vermillion Creek is a small tributary that joins the Green River, in Browns Park National Wildlife Refuge 70 rkm downstream of Flaming Gorge Dam, and drains

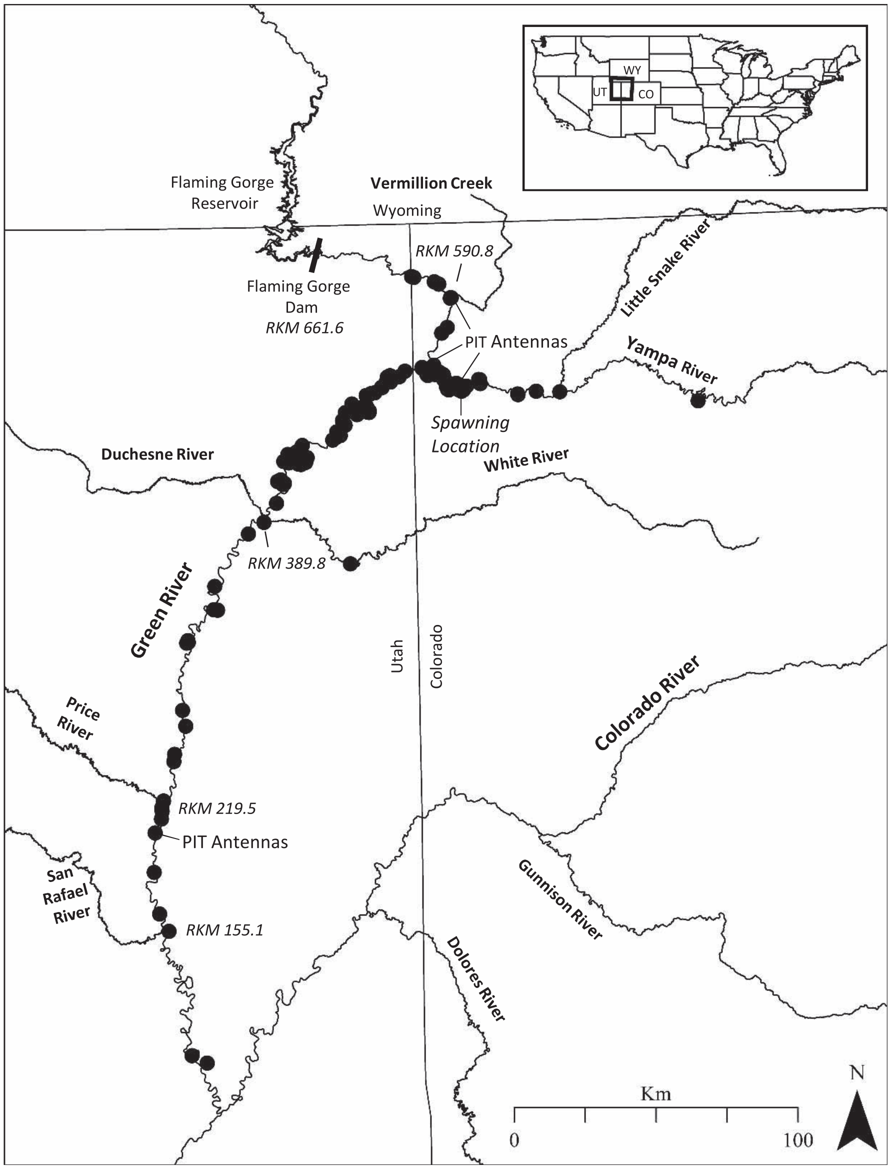

Figure 1. Study area in Upper Colorado River Basin. Black circles indicate locations at which at least one capture or detection of a passive integrated transponder (PIT)–tagged Colorado Pikeminnow *Ptychocheilus lucius* with a history of encounter in Vermillion Creek has occurred. PIT tag antennas were located at the mouth of Vermillion Creek (RKM 590.8), the mouth of the Yampa River (RKM 555.0), and at the Yampa River spawning location labeled on the map; sampling for physical capture of Colorado Pikeminnow minimally occurred throughout the Green, Yampa, White, and Colorado rivers in Colorado, Wyoming, and Utah as delineated on the map. Dates of encounter range from 1 May 1992 to 29 June 2021.

2,542 km^2 (Hansen 1986) in Colorado and Wyoming. Vermillion Creek at the Green River confluence has primarily soft silt substrate, and thus, is dynamic in depth and channel bed morphology during high flow events. Mean annual discharge was last gauged in 1981, but recent observations indicated periods of low (<0.1 m^3/s) or zero flow due in large part to agricultural diversions upstream. Mean spring discharge during snowmelt runoff about 30 rkm upstream of the mouth was 0.62 m^3/s for the period 1977–1981 (USGS Gauge 09235450) and flash floods are common during summer thunderstorms. Vermillion Creek contributes a substantial amount of sediment to the Green River (Grams and Schmidt 2005), and at low flows, silt deposits have been observed >0.5 m deep. At Green River base flows (about 57 m^3/s) and depending on silt deposition near the mouth, Vermillion Creek was flooded upstream to about 250 m from the mouth, with depths <0.5 m; but during higher spring peak flows (e.g., 245 m^3/s), approximately 600 m of the creek mouth was inundated and was >1 m deep (Figure 3). This slack water confluence and upstream habitat was warmer and more turbid than the Green River during high flow periods (Figure 4). Vermillion Creek was rarely accessible to large-bodied fishes from the mainstem during lower base flows

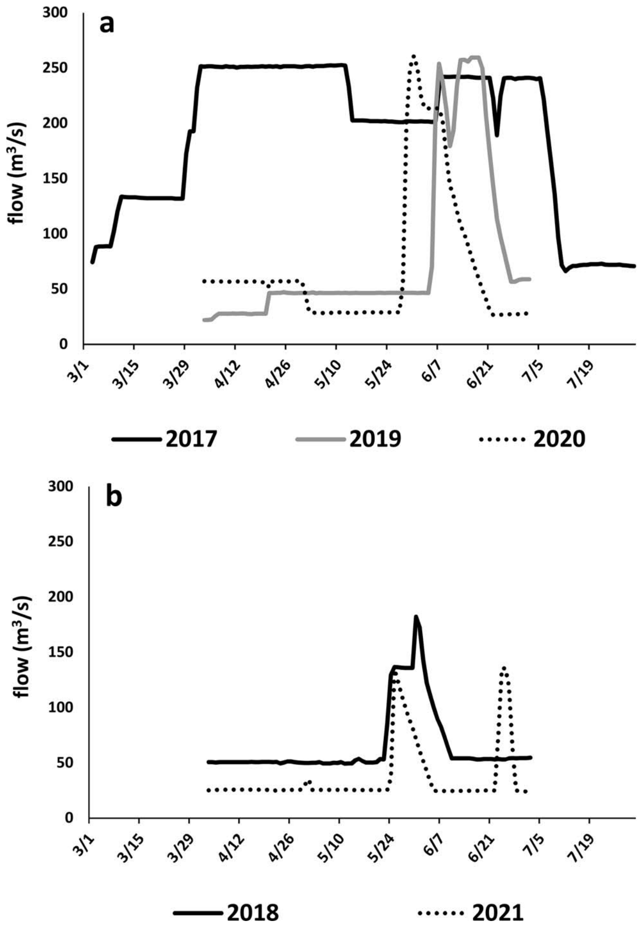

Figure 2. Green River mean daily flow from Flaming Gorge Dam as measured at U.S. Geological Survey Gauge 09234500 in Greendale, Utah, during **(a)** high peak flow years 2017, 2019, and 2020, and **(b)** low peak flow years 2018 and 2021. A discharge of approximately 85 m^3/s is required in most years for inundation of the mouth of Vermillion Creek to form backwater habitat.

although was usually connected to the Green River by a shallow lens of water.

Methods

Sampling and data collection

We initially observed Colorado Pikeminnow in Vermillion Creek during exploratory boat electrofishing throughout Browns Park National Wildlife Refuge in 2011. Subsequently, we sampled fish with trammel nets and occasionally fyke nets in Vermillion Creek and at other nearby locations on the Green River every year through 2021. We blocked the mouths of tributaries and backwaters with trammel nets to the extent possible, and set fyke nets such that fish would be captured both entering and exiting the backwater mouth. Beginning in 2015, we eliminated fyke nets and used trammel nets (15 m × 2 m × 25 mm) as the primary sampling gear in Vermillion Creek, given their effectiveness at capturing nonnative species targeted for removal (mainly Northern Pike *Esox lucius* and White Sucker *Catostomus commersonii*) as well as native species including Colorado Pikeminnow. We primarily sampled in May and June and usually began before the ascending limb of spring peak releases from Flaming Gorge Dam. We ended sampling after peak releases stopped and summer base flow was achieved, which resulted in longer sampling periods during wetter hydrologic years and shorter periods during drier years.

Colorado Pikeminnow captured throughout the Upper Colorado River Basin are tagged with 134.2-kHz passive integrated transponder (PIT) tags by us and other investigators. Thus, we monitored Colorado Pikeminnow use of Vermillion Creek via detection of PIT tags with antennas (detections) and physical captures (captures). We used flat-plate antennas on an exploratory basis in 2016 but limited read range of these devices (<0.1 m) led us to use those detection data only for developing Colorado Pikeminnow lifetime encounter histories (below). We deployed two submersible PIT tag antennas (1.0-m diameter, advertised read range 0.33 m; Biomark, Inc., Boise, ID) in lower Vermillion Creek in each year from 2017 to 2021: one in the creek mouth and one 200 m upstream, each in the deepest part of the channel. The antennas were active for 93 d (11 April–13 July) in 2017, 21 d (16 May–6 June) in 2018, 71 d (24 April–4 July) in 2019, 20 d (27 May–16 June) in 2020, and 27 d (13 May–9 June) in 2021. We deployed a single TidbiT temperature logger (Onset Computer Corporation, Bourne, MA) 200 m upstream of the mouth of Vermillion Creek for the duration of the five seasons. We used main channel Green River temperatures collected by TidbiT temperature loggers deployed and maintained by the U.S. Fish and Wildlife Service 8.7 rkm upstream of the mouth of Vermillion Creek.

The PIT tag records from throughout the Upper Colorado River Basin date back to 1992, the first year such tags were used. We used captures and detections to assemble a capture history for each Colorado Pikeminnow encountered in Vermillion Creek (Upper Colorado and San Juan River Endangered Fish Recovery Program database, maintained by the Colorado Natural Heritage Program [STReaMS 2021, https://streamsystem.org]). We censored data from STReaMS and our Vermillion Creek records to one detection or capture per day, except we retained both a detection and capture in the same day in the few instances this occurred; individual fish histories included records before and after first capture or detection in Vermillion Creek.

We used linear regression to describe the relationship between the number of individual Colorado Pikeminnow that annually used Vermillion Creek as a function of flow duration and magnitude. We chose the annual number of days that spring peak releases from Flaming Gorge Dam exceeded 85 m^3/s as our explanatory variable because that is an approximate threshold for Green River flows to inundate most of lower Vermillion Creek. In all 5 y of our PIT tag antenna study, mean daily discharge

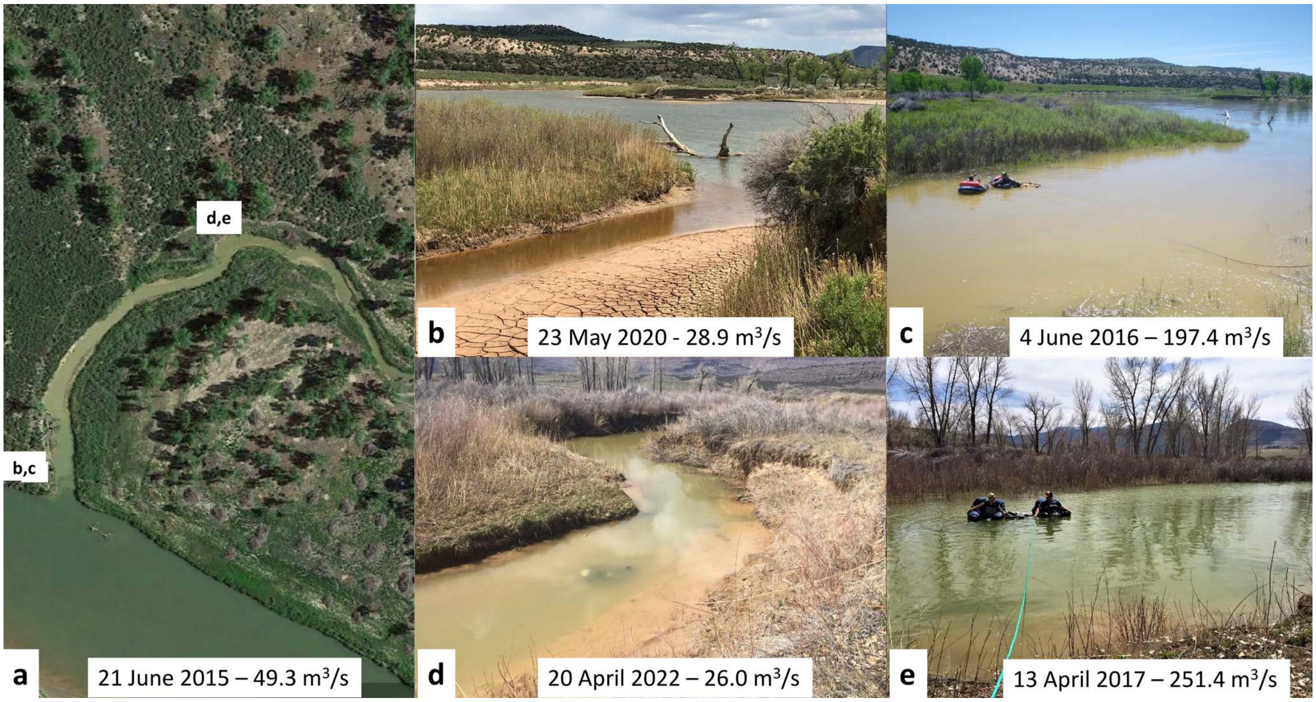

Figure 3. Lower Vermillion Creek and passive integrated transponder (PIT) tag antenna and water temperature monitoring locations (locations b–e, shown in image **a**) during Green River base and spring peak flows. Images **b** and **c** look downstream to the Vermillion Creek mouth at the Green River confluence (note tree in river), during base (**b**) and spring peak (**c**) flow. Mean daily flow levels are for the Green River measured that day at U.S. Geological Survey Gauge 09234500, Greendale, Utah, immediately downstream of Flaming Gorge Dam and 70 river km upstream of Vermillion Creek. Images **d** and **e** view the upstream site approximately 200 m from the mouth, at base (**d**) and spring peak (**e**) flows. Maximum depths are approximately 0.2 m in images **b** and **d** and approximately 2.0 m in images **c** and **e**. Image dates are as follows: (**a**) 21 June 2015; (**b**) 23 May 2020; (**c**) 4 June 2016; (**d**) 20 April 2022; and (**e**) 13 April 2017.

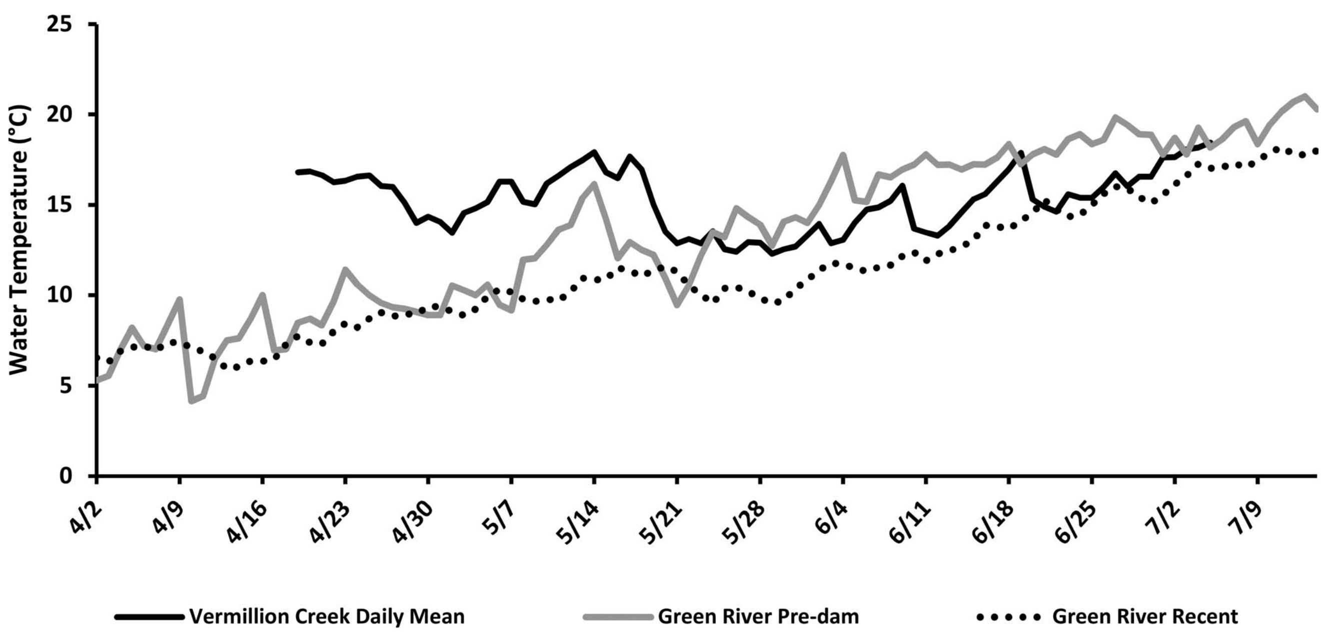

Figure 4. Green River and Vermillion Creek mean daily temperatures. Vermillion Creek daily means are from 2017 to 2021, Green River pre-dam means are from 1959 to 1962, and Green River recent means are from 2017 to 2021. Green River temperatures are measured by U.S. Fish and Wildlife Service at Browns Park National Wildlife Refuge, Colorado (8.7 rkm upstream of Vermillion Creek), downstream of Flaming Gorge Dam; and Vermillion Creek temperatures are measured 200 m upstream of the mouth, also in Browns Park National Wildlife, Colorado. See also Data S1, *Supplemental Material*.

exceeded 85 m^3/s the first day of spring releases from Flaming Gorge Dam (Figure 2).

Timing and duration of tributary use

We used individuals encountered annually both by capture and PIT tag antenna detections from 2017 to 2021 to describe timing and duration of Vermillion Creek use. We did not use Colorado Pikeminnow detections in Vermillion Creek prior to 2017 because flat-plate antenna read range was limited and the monitoring period was inadequate to estimate timing and duration of use. We report these results as number of unique fish detected per day. We defined average duration of use as the number of days elapsed between first and last detection for each individual, which is a conservative measure because of imperfect sampling or antenna detection. We assigned one day when a single annual detection was recorded. We also explored the linear regression relationship of average duration of use of Vermillion Creek by individual Colorado Pikeminnow, using data over all years, as a function of flow duration and magnitude, using the number of days that spring releases exceeded 85 m^3/s as the explanatory variable.

Lifetime encounters and range

We included all known lifetime capture and detection records of individuals encountered in Vermillion Creek between 2011 and 2021 in estimates of range. For each Colorado Pikeminnow, we calculated distance between the farthest upstream and farthest downstream locations of capture or detection over the lifetime of the individual's PIT tag (i.e., time between PIT tag implantation and most recent detection) to generate a total Green River subbasin range. For fish encountered in other streams (e.g., Yampa and White rivers), we calculated distance between the encounter farthest upstream and the mouth to generate a use length for that stream. We assigned both upstream and confluence antennas in Vermillion Creek to Green River rkm 590.8, the mouth of the creek.

Results

Sampling and data collection

We encountered 93 individual Colorado Pikeminnow in Vermillion Creek from 2011 to 2021. All individuals were adults (483–796 mm total length) and were either only captured ($n = 11$), only detected ($n = 47$), or were both captured and detected ($n = 35$). The 46 total captured fish were handled between one and four times each, with a mean of 1.5 captures/fish in Vermillion Creek over the 11-y period. Total number of individual Colorado Pikeminnow encountered in Vermillion Creek each year varied widely: 75 in 2017, 13 in 2018, 15 in 2019, 13 in 2020, and 2 in 2021. Number of unique Colorado Pikeminnow encountered each year in Vermillion Creek was well predicted by number of days during spring runoff that mean daily flow exceeded 85 m^3/s (Figure 5a), the limitations of only five data points and one large outlier (2017) notwithstanding.

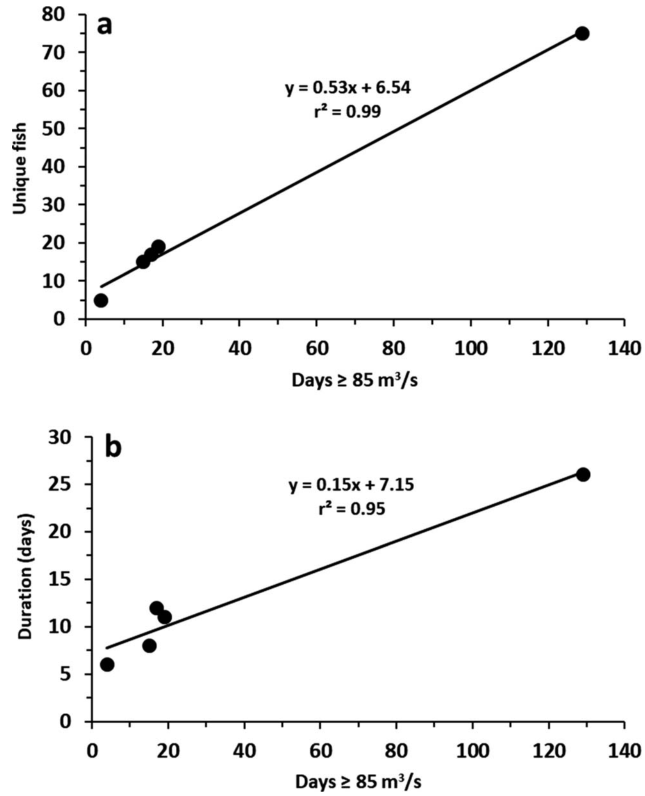

Figure 5. Number of unique Colorado Pikeminnow *Ptychocheilus lucius* encountered each year in Vermillion Creek **(a)** and mean duration of time (days) spent in Vermillion Creek **(b)** as a function of days of mean daily Green River flow ≥85 m^3/s from Flaming Gorge Dam. Flows were measured at U.S. Geological Survey Gauge 09234500 in Greendale, Utah, during spring peak releases for 2017–2021. Duration spent in Vermillion Creek is the mean number of days elapsed between first and last encounter among individuals encountered within each year. Most of lower Vermillion Creek was inundated and accessible for Colorado Pikeminnow when spring peak releases from Flaming Gorge Dam exceeded 85 m^3/s.

Many of the Colorado Pikeminnow encountered in Vermillion Creek were encountered there in >1 y ($n = 41$, 44%) between 2011 and 2021, thus exhibiting varying degrees of site fidelity. Of those returning in more than one year, we encountered 22 in 2 y, 8 in 3 y, 5 in 4 y, 2 in 5 y, and 4 in 7 y. During Green River fish community monitoring for other projects in the 52-rkm reach downstream of Vermillion Creek from 2002 to 2021, we encountered 128 individual Colorado Pikeminnow. Of those, only nine were encountered in Vermillion Creek at some point during their known lifetime, indicating that most of the fish found in Vermillion Creek were not simply residents of the adjacent reach.

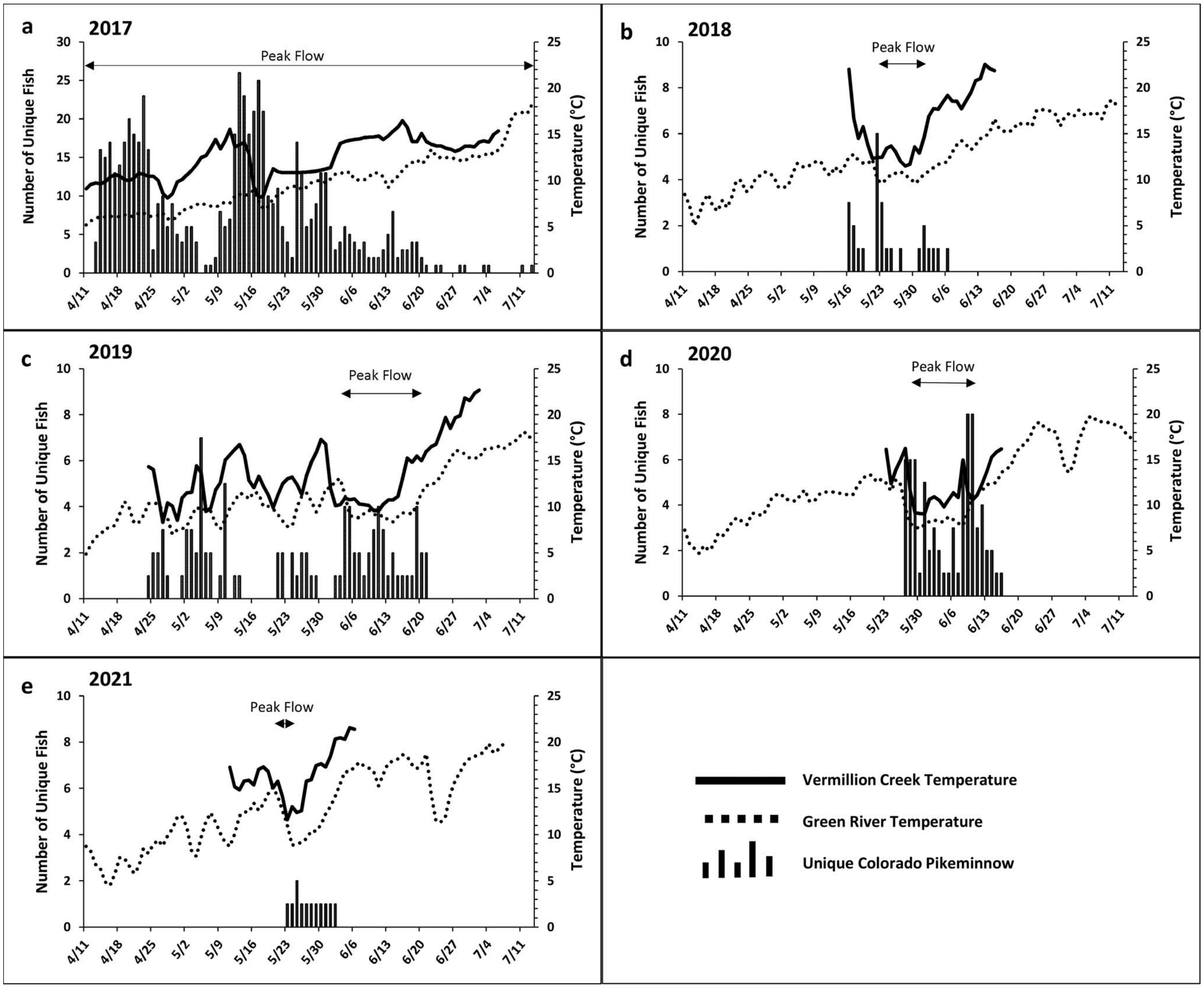

Figure 6. Water temperatures and number of individual fish detected by passive integrated transponder (PIT) tag antennas per day during monitoring periods in 2017–2021 in Vermillion Creek, Colorado. Antenna monitoring periods are the same as temperature monitoring periods. Note primary *y*-axis scale for 2017 is 3× greater than other years. "Peak Flow" denotes the period of annual spring peak releases (4,600–8,600 ft^3/s; see Figure 2) from Flaming Gorge Dam, Utah, on the Green River. Green River temperatures are measured at Browns Park National Wildlife Refuge (8.7 rkm upstream of Vermillion Creek) downstream of Flaming Gorge Dam; and Vermillion Creek temperatures are measured 200 m upstream of the mouth. Solid line indicates Vermillion Creek temperature, dotted line indicates Green River temperature, and vertical bars indicate number of unique Colorado Pikeminnow *Ptychocheilus lucius*. See also Data S1, *Supplemental Material*.

Timing and duration of tributary use

Spring hydrology of the Green River in the study area differed substantially over the period 2017–2021 (Figure 2) during intensive monitoring of Vermillion Creek. For example, early, high, and prolonged spring peak releases from Flaming Gorge Dam in 2017, the result of high upstream snowpack (>200% of average), were from early March to early July (130 d exceeding base flow) and flows were $\geq$200 m^3/s for 96 d, with a maximum flow of 255 m^3/s. In contrast, peak flow in 2021 was very brief and relatively low, with only 2 d $\geq$124 m^3/s. Spring peak flows in 2019 and 2020 were similar to each other in magnitude and duration, while 2018 flows were most similar to 2021.

Antenna monitoring periods varied by year and were primarily determined by timing and duration of spring peak releases (Figure 6). In all years except 2020 and 2021 (Figures 6a–6c), antennas detected Colorado Pikeminnow on the day they were deployed or very soon after, indicating earlier fish presence in Vermillion Creek, and also rendering habitat use duration estimates conservative. In those years, detections began as soon as the tributary mouth was inundated and habitat was available (Figure 6e). Increases in daily number of unique fish detected occurred concurrently either with temperature increases in Vermillion Creek relative to the mainstem Green River or with sustained high Green River flow (2017; Figure 6a) or increases in flow (2018, 2020, and 2021; Figures 6b, 6d, and 6e). In contrast, Vermillion Creek use by Colorado Pikeminnow in 2019 was relatively high well before spring peak releases (Figure 6c). In all study years, use declined in late June even when high flows sustained habitat. For example, Vermillion Creek remained accessible into July during 2017, but the majority of individuals emigrated well before spring peak releases declined to base flow. Each year from 2017 to 2021, average daily temperatures in Vermillion Creek during Colorado Pikeminnow presence exceeded those in the mainstem Green River by an average of 3.6°C (2.4°C warmer in 2020 to 5.7°C warmer in 2021; Data S1, *Supplemental Material*; Figures 4 and 6). Daily temperature differences for that period were up to 10.0°C warmer in Vermillion Creek. Although exact Colorado Pikeminnow residence time in Vermillion Creek could not be determined because detection efficiency was likely $<$100%, average duration of use (time between first and last encounters for individuals) was 26 d in 2017, 8 d in 2018, 11 d in 2019, 12 d in 2020, and 6 d in 2021. These average durations of use per year varied with magnitude and duration of flow and showed a strong positive relationship (Figure 5b).

The majority of Colorado Pikeminnow encountered in Vermillion Creek during our 2011–2021 lifetime range study period ($n = 63$, 68%) were also encountered in the Yampa River during their PIT-tagged lifetime, which included encounters before our study. Of those Yampa River encounters, 32 were detected by PIT tag antennas placed near or at known spawning areas approximately 26 rkm upstream of the mouth and 0.6 rkm upstream of the mouth in a narrow section of the river in which fish migrating upstream to spawn are concentrated. Each year from 2015 through 2020, individuals encountered first in Vermillion Creek during the prespawn period were also encountered soon after in the Yampa River during monitoring focused on the spawning period ($n =$ 1, 3, 8, 4, 6, 4 from 2015 to 2020, respectively). No Colorado Pikeminnow encountered in Vermillion Creek in the low-use year 2021 were encountered in the Yampa River. Despite the relative rarity of these within-year paired encounters, the timing of highest encounters in Vermillion Creek in May and earlier June was followed closely by highest use in the Yampa River in later June and July before or during the usual period of spawning. For example, our PIT tag detections and captures in Vermillion Creek from 2011 to 2021 reveal a peak in Colorado Pikeminnow presence around 13 May. The peak date for Colorado Pikeminnow encounters near the Yampa River spawning area for this same group of fish over the same period was 25 June (Figure 7). Additionally, the mean first date of Colorado Pikeminnow larvae capture in the Yampa River for 2011–2019 was 1 July (Bestgen and Smith 2019), which (after correcting for egg incubation and larvae emergence time of 12 d) equates to an estimated average first spawning date of 19 June (Bestgen and Hill 2016).

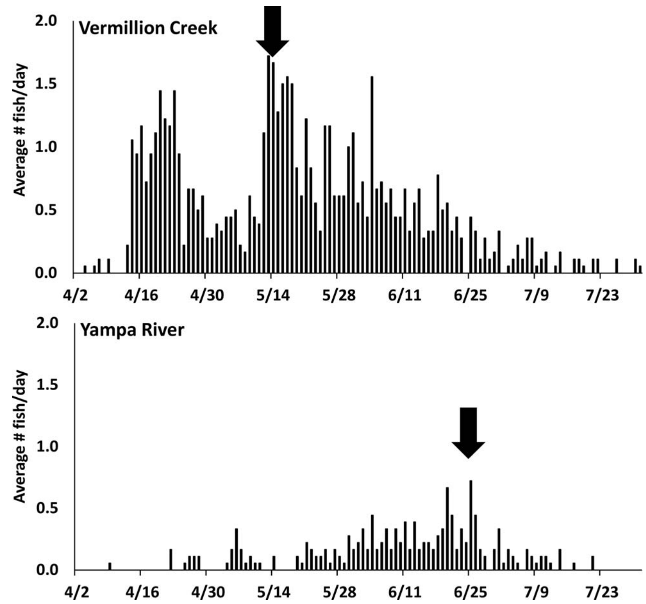

Figure 7. Mean number of individual Colorado Pikeminnow *Ptychocheilus lucius* encountered per date in both Vermillion Creek (**top**) and later in the Yampa River (**bottom**) for the period 2011–2021 in Colorado. Encounters include physical captures and detections from passive integrated transponder (PIT) tag antennas and include only the 93 Colorado Pikeminnow encountered during this study. Arrow denotes mean date of highest number of Colorado Pikeminnow captured.

Lifetime encounters and range

Colorado Pikeminnow encountered in Vermillion Creek ranged widely throughout the Green River basin, many with encounter histories beginning earlier than our study. Based on tag-recaptures and antenna detections collected from 1992 to 2021, Colorado Pikeminnow found in Vermillion Creek were encountered an average of nine times each (captures $\bar{x} = 2.6$, 0–8; detections $\bar{x} =$ 15.5, 0–53) throughout the Green River basin in their lifetime. Average time between first tagging and most recent encounter was 10.6 y (0–29, n = 89), and individuals used $\geq$166 rkm of the Yampa River, 62 rkm of the White River, and were throughout the 615 rkm of the Green River, essentially the reach from the upstream Colorado–Utah state line downstream to the Green River–Colorado River confluence. The average distance between the most upstream and downstream encounters was 190 rkm (12–599 rkm). Vermillion Creek was the farthest upstream encounter location or very near it (within 14.5 rkm) in the lifetime range (Figure 1).

Discussion

A large number of Colorado Pikeminnow from throughout the Green River basin in Colorado and Utah used the small tributary mouth of Vermillion Creek near the upstream extent of the species' distribution and Flaming Gorge Dam. Many individuals encountered in Vermillion Creek during our 11-y study showed site fidelity, returning multiple times over several years. Our data demonstrating site fidelity to Vermillion Creek are supported by Kitcheyan and Montagne (2005), who documented four adult Colorado Pikeminnow overwintered nearby in Browns Park National Wildlife Refuge, and found two that remained in the reach for more than a year. Colorado Pikeminnow consistently used this location in relatively large congregations immediately before moving downstream to the Yampa River, one of two known spawning habitats in the Green River basin (Irving and Modde 2000). Colorado Pikeminnow movements throughout the basin included use of two of the Green River's largest tributaries, the Yampa (166 rkm used) and White (62 rkm used) rivers.

In addition to high site fidelity of Colorado Pikeminnow to Vermillion Creek, a relatively large proportion of fish in the entire Green River basin have used this small habitat at least once. For example, the 93 individuals encountered there represent about 11% of the total number of adult Colorado Pikeminnow present in the Green River (about 850 adult fish) as of 2018 (Bestgen et al. 2020b). This estimated proportion is also conservative because antennas would not detect untagged Colorado Pikeminnow in Vermillion Creek. This suggests both basin- and population-wide importance of resources found in habitats such as Vermillion Creek, especially between Flaming Gorge Dam and the Yampa River confluence, which is the reach most affected by dam regulation.

Fidelity to spawning locations is common among potadromous species and well-documented for Colorado Pikeminnow (Tyus 1990; Irving and Modde 2000; Bestgen et al. 2007), but less is known about fidelity to prespawning habitat found in specific locations. Similarly imperiled or vulnerable large river species such as Paddlefish *Polyodon spathula* (Stancill et al. 2002), Zulega *Prochilodus argenteus* (Godinho and Kynard 2006), Robust Redhorse *Moxostoma robustum* (Grabowski and Isely 2006), and Alligator Gar *Atractosteus spatula* (Kluender et al. 2016) sometimes used the same prespawn staging habitats in multiple years, and those were relatively near spawning areas made accessible by seasonally influenced hydrology. The fidelity of individuals in a population, including Colorado Pikeminnow in the Green River, to distinct prespawn and spawning locations reveals the population-level need for a variety of resources specific to reproduction beyond spawning habitat alone.

A key benefit provided by low velocity, relatively warm tributary mouths, such as Vermillion Creek during periods of high seasonal flow, is refuge from cold, high-velocity water. Prior to spawning, many riverine fishes use staging habitats (Godinho and Kynard 2006; Grabowski and Isely 2006; Douglas et al. 2009; Kluender et al. 2016) evidently to build energy stores and increase gonadal condition prior to spawning. This strategy is common to several riverine fishes (Braaten and Guy 1999; Valdez et al. 2001), especially when water temperatures are cold, flow is high or prolonged in duration, or both. With no apparent velocity and an average spring daily temperature 3.4°C higher than the mainstem Green River during our study period (Figures 4 and 5), Vermillion Creek may be an ideal location for Colorado Pikeminnow prespawning conditioning. In fact, tuberculate fish were captured in May 2011, several weeks prior to when spawning occurred in the Yampa River (Bestgen and Hill 2016). Similarly, Colorado Pikeminnow in the San Juan River use the mouths of at least five small tributaries (Cathcart et al. 2018) in a reach where water temperatures are affected both by seasonal snowmelt runoff and by Navajo Dam during spring peak releases (Miller and Swaim 2013). Such seasonally inundated tributary mouths facilitate use of a greater extent of regulated river reaches than would be expected in their absence because they offer necessary seasonal thermal resources for Colorado Pikeminnow (Osmundson 2011; Sabo et al. 2012). Both the number of individual fish using Vermillion Creek per year and their average residence time in the habitat vary with flow. Prolonged high flow makes the habitat available to more individual fish for longer, while years of short-duration low flow limit the number of fish accessing the habitat and the time they use it.

Colorado Pikeminnow may also be attracted to Vermillion Creek in spring because it supports large numbers of potential forage fish in greater concentrations than in mainstem habitats. Our sampling (unpublished data from 2007 to 2019) indicate abundant smaller catostomids (White Sucker, Flannelmouth Sucker) and cyprinids (Redside Shiner *Richardsonius balteatus*, Fathead Minnow *Pimephales promelas*, Speckled Dace *Rhinichthys osculus*) in lower Vermillion Creek, which offer foraging opportunities for prespawning adult Colorado Pikeminnow. This is similar to Cathcart et al. (2015), who found concentrations of forage species in several tributary mouths used by Colorado Pikeminnow that were higher in abundance than the mainstem San Juan River. Additionally, many Flannelmouth and White suckers were found spawning in Vermillion Creek during our study, small individuals of which are potential prey for large Colorado Pikeminnow.

Emigration of Colorado Pikeminnow from Vermillion Creek and their subsequent detection in the Yampa River spawning area suggest use of the two locations is linked by reproduction. While allowing that not every encounter of Colorado Pikeminnow in the Yampa River reflects reproductive behavior, the timing of peak encounters near known spawning habitats during the well-established reproductive period bolsters the assumption that spawning migrations by a large number of individuals have been annually documented. This is supported by previous findings that Green River Colorado Pikeminnow typically make large-scale migrations to spawning areas after peak flows (Tyus 1990; Irving and Modde 2000; Kitcheyan and Montagne 2005).

Even though there is some residual uncertainty as to the specific benefits of Vermillion Creek, finding substantial congregations of Colorado Pikeminnow there on an annual basis, long durations of use when flows are adequate, and fidelity of some fish to this site, indicate this relatively rare habitat is important. Other small tributaries of the Green River do exist (e.g., Duchesne River, Nine Mile Creek, Price River, Utah), but these are in downstream reaches in which temperature and hydrology are less affected by Flaming Gorge Dam operations and no reports of large congregations of Colorado Pikeminnow are associated with those streams despite consistent sampling targeting the species in the confluences. Protecting nodes of habitat that support seasonally available pre-dam conditions in a dam-regulated river may have a key mitigating effect on the thermal fragmentation caused by large mainstem dams for Colorado Pikeminnow and other fishes native to large regulated rivers of the western United States. Similar to lower Vermillion Creek, floodplain features in the middle Green River downstream of Jensen, Utah, also provide relatively warm and food-rich conditions for Colorado Pikeminnow and other large river species prior to reproduction (Muth et al. 2000; LaGory et al. 2019). Flow recommendations have considered inundation strategies for such habitat (Muth et al. 2000; Bestgen et al. 2011, 2020a), including tradeoffs between high flow magnitude and duration, given that prespawning habitat for Colorado Pikeminnow may aid successful reproduction a few weeks later. Indeed, the duration of the high flow period seems linked to the number of unique Colorado Pikeminnow and the duration of their stay in Vermillion Creek, indicating longer spring peak releases allow more fish, including untagged individuals that we did not detect, to benefit from that area.

Management of imperiled species in increasingly altered river mosaics throughout the world, especially those with small tributaries critical to sustaining the resident fish community, is a complex and increasingly difficult challenge. This is especially true in regions experiencing aridification, reduced flows due to climate change, habitat modification, and rapidly increasing human water use. Tools and methods that both strengthen and simplify population monitoring have great value for managers whose goal is conservation of rare species. We recommend continued use of such methods (e.g., PIT tag antennas) to better monitor vital rates of imperiled fish populations (Conner et al. 2020; Zelasko et al. 2020, 2022) and identify and protect habitat and resources important to their persistence (e.g., Bottcher et al. 2013; Webber and Beers 2014; Cathcart et al. 2015, 2018, 2019). In river systems in which dam operations affect seasonal habitat and resource availability, focused study of vulnerable species' use of the small tributary habitats that contribute to reproductive success in particular will greatly enhance conservation-based management. Such focused study to inform seasonal dam operations is especially important for long-lived species with a life history requiring long-distance annual migration to access critical reproductive resources, and continued success of these fish communities depends on thoughtful and informed management.

Supplemental Material

Please note: *The Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Daily mean temperatures for Vermillion Creek and the mainstem Green River 8.7 rkm upstream of the mouth of Vermillion Creek and number of unique Colorado Pikeminnow *Ptychocheilus lucius* encountered in Vermillion Creek per day during our 2017–2021 study period.

Available: https://doi.org/10.3996/JFWM-22-025.S1 (65 KB XLSX)

Reference S1. Bestgen KR, Crist LW. 2000. Response of the Green River fish community to construction and re-regulation of Flaming Gorge Dam, 1962–1996. Unpublished report to the Recovery Implementation Program for Endangered Fishes in the Upper Colorado River Basin. Larval Fish Laboratory Contribution 107.

Available: https://doi.org/10.3996/JFWM-22-025.S2 (1.143 MB PDF)

Reference S2. Bestgen KR, Haines GB, Hill AA. 2011. Synthesis of flood plain wetland information: timing of Razorback Sucker reproduction in the Green River, Utah, related to stream flow, water temperature, and flood plain wetland availability. Final report to the Recovery Implementation Program for Endangered Fishes in the Upper Colorado River Basin. Denver: U.S. Fish and Wildlife Service. Larval Fish Laboratory Contribution 163.

Available: https://doi.org/10.3996/JFWM-22-025.S3 (1.585 MB PDF)

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Available: https://doi.org/10.3996/JFWM-22-025.S4 (2.121 MB PDF)

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Reference S5. Bestgen KR, Zelasko KA, Hawkins J, White GC, Walford C, Breen M, Smith C, Creighton K. 2020b. Abundance estimates for Colorado Pikeminnow in the Green River Basin, Utah and Colorado. Denver: Annual Report to Upper Colorado Endangered Fish Recovery Program.

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Available: https://doi.org/10.3996/JFWM-22-025.S17 (445 KB PDF)

Reference S17. Zelasko KA, Bestgen KR, White GC. 2022. Incorporating passive antenna detections with physical recaptures in the Barker model improves survival rate estimates for Razorback Suckers *Xyrauchen texanus* stocked in the Upper Colorado River Basin. Denver: Final Report to the Upper Colorado River Endangered Fish Recovery Program. Larval Fish Laboratory Contribution 225.
Available: https://doi.org/10.3996/JFWM-22-025.S18 (1.847 MB PDF)

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