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Assessment of Potential Recovery Viability for Colorado Pikeminnow Ptychocheilus lucius in the Colorado River in Grand Canyon

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Abstract

Colorado Pikeminnow *Ptychocheilus lucius*, the Colorado River's top native predatory fish, was historically distributed from the Gulf of California delta to the upper reaches of the Green, Colorado, and San Juan rivers in the Colorado River basin in the Southwestern US. In recent decades Colorado Pikeminnow population abundance has declined, primarily due to predation by warmwater nonnative fish and habitat modification following dam construction. Small, reproducing populations remain in the Green and upper Colorado rivers, but their current population trajectory is declining and the San Juan River population is maintained primarily through stocking. As such, establishment of an additional population could aid recovery efforts and increase the species' resilience and population redundancy. The Colorado River in Grand Canyon once supported Colorado Pikeminnow, but until recently habitat suitability in this altered reach was considered low due to a depressed thermal regime and abundant nonnative predators. Climate change and ongoing drought has presented an opportunity to evaluate the feasibility of native fish restoration in a system where declining reservoir storage has led to warmer releases and re-emergence of riverine habitat. These changes in the physical attributes of the river have occurred in concert with a system-wide decline in nonnative predators. Conditions ten years ago were not compatible with reintroduction feasibility in Grand Canyon; however, due to rapidly changing conditions an expert Science Panel was convened to evaluate whether the physical and biological attributes of this reach could now support various life stages of Colorado Pikeminnow. Here, we report on the evaluation process and outcome from the Science Panel, which developed a science-based recommendation to the U.S. Fish and Wildlife Service on reintroduction feasibility. The Science Panel concluded that current habitat attributes in Grand Canyon could satisfy some, but perhaps not all, Colorado Pikeminnow life history requirements. This reach has the potential to support adult and sub-adult growth, foraging, migrations, and spawning, but low juvenile survival may limit recruitment. However,

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Keywords: climate change; Colorado Pikeminnow; drought; extirpated; habitat suitability; recovery viability; redundancy; restoration

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Introduction

Colorado Pikeminnow *Ptychocheilus lucius* (formerly 'Colorado Squawfish') evolved over millions of years in rivers of the Colorado River basin (Houston et al. 2010). In their undammed state, these rivers were warm for much of the year, silt-laden, and exhibited high seasonal and interannual fluctuations in turbidity and flow volume (Miller 1961). Historically as the top predator in the system, Colorado Pikeminnow reached up to 1.8 m and 45 kg, although most captured today rarely exceed 10 kg (Miller 1961; Snyder et al. 2016). Prior to dam construction they migrated up to several hundred kilometers to spawn (Mueller and Marsh 2002), with the species' range extending from the Gulf of California delta (hereafter, 'delta') into rivers in Mexico, Arizona, California, Nevada, New Mexico, Colorado, Utah, and Wyoming (Figure 1). The species also exhibited plasticity in its ability to occupy non-traditional habitats, such as ancient Lake Cahuilla (same location as present-day Salton Sea) and Prospect Lake, which was formed when lava flows dammed the Colorado River's flow in Grand Canyon (Gobalet et al. 2005).

In the southern portion of their range in the Colorado and Gila rivers and in the delta (Figure 1), Colorado Pikeminnow were noted as common to abundant and the most highly prized of native fishes available for capture (Gilbert and Scofield 1898; Mueller and Marsh 2002). To the north, they were present and relatively common in the upper Colorado, Green, and San Juan rivers and in major tributaries such as the Animas, Gunnison, White, and Yampa rivers (Jordan 1889; Koster 1960; Quartarone and Young 1995). The construction of Laguna Dam near the Mexican border in 1909 followed by Hoover Dam in 1935 restricted migratory movement from the highly productive delta into the upper portions of the system (Mueller and Marsh 2002), with populations in the upper basin declining after the 1920s and 1930s following the construction of dams and with implementation of large rotenone projects (Quartarone and Young 1995). Declines in abundance and the species range

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contraction across the basin led to its inclusion in the 1967 List of Endangered Species (FR 1967), and formal listing as 'endangered' under the US Endangered Species Act (ESA 1973, as amended).

Current species status

Colorado Pikeminnow historically occupied most of the major river segments in the Colorado River Basin. This basin has been divided into six analysis units as delineated by geographic subbasin, with only three subbasins currently supporting Colorado Pikeminnow populations (shaded blue, Figure 1; USFWS 2020b). The analysis units were defined based on the location of dams and were further refined to the subbasin level where demographic processes are likely independent and population size is estimated (USFWS 2020a). Wild, self-sustaining populations remain in the Green and upper Colorado rivers, with a population persisting in the San Juan River through an ongoing stocking program. At the present time, the Green River adult population (age 7+, ≥ 450 mm TL) is the largest and includes fish from the Green, Yampa, and White rivers (Figure 1). From 2001-2018 abundance in the Green River declined from 3,640 to 885 (Table S1). This was likely due to declines in recruitment linked to poor survival of age-0 fish after 2000 combined with nonnative fish predation (Bestgen et al. 2018). The upper Colorado River population (upstream from the Green River confluence) is smaller than the Green River population, numbering in the few hundreds (Table S1; Figure 1). The frequency of strong year classes has declined to the point that recruitment is inadequate to replace adult mortality over the long term.

The San Juan River population was considered functionally extirpated in the early 2000s (USFWS 2020b), but extensive stocking efforts of age-0 fish starting in 1996 increased the abundance of juveniles in the river. Low survival has rendered adult population estimates challenging (estimated to be < 140 individuals; Table S1; Ryden 2000; Diver and Wilson 2018). Spawning by stocked adults has been documented in the San Juan River since 2003, with small

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numbers of mesolarvae captured in backwaters, embayments, and zero- or low-velocity areas (Farrington et al. 2016). Stocking of juvenile fish and the inability to mark small fish has led to uncertainty about recruitment to larger size classes and the provenance of larger fish that are captured (i.e., some could be the result of wild-spawned fish).

The Verde and Salt rivers in the Gila River basin have been stocked experimentally, but no young have been documented and recruitment is presumed non-existent (gray shading, Figure 1; USFWS 2020b). Colorado Pikeminnow are presumed extirpated from the Colorado River in Grand Canyon and in the Lower Colorado River mainstem since the last capture was recorded near Havasu Creek in 1978 (ASU Ichthyology Collection, Catalog #: ASUFIC007087). As such, fish recovery efforts are focused on the three remaining populations through the work of the Upper Colorado River Endangered Fish Recovery and the San Juan River Basin Recovery Implementation programs.

Colorado Pikeminnow recovery goals focus on achieving self-sustaining populations so the species can be considered for downlisting (e.g., from endangered to threatened) or delisting (e.g., from threatened to not warranted) under the ESA, while also ensuring water development proceeds in compliance with applicable regulations, laws, and interstate compacts (USFWS 2002, 2020b). Colorado Pikeminnow Recovery Goals (2002) identified downlisting and delisting criteria using 5-7 years of adult population abundance estimates for the Green, upper Colorado, and San Juan river populations to determine whether recovery criteria have been met (USFWS 2002); these goals are currently in revision. While the Green and upper Colorado river populations have met or exceeded adult abundance goals in past years, adult populations have declined below target demographic criteria. With low adult abundances and declines in the two remnant wild populations (Green and upper Colorado river), the U.S. Fish and Wildlife Service recommended no change in its status as an ‘endangered species’ in its recent ESA five-year status review (a periodic review to ensure the

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listing remains accurate). This review identified several important management actions, including a recommendation to "*investigate potential conservation actions that might be implemented in the lower basin*" (USFWS 2020a). An additional population could aid recovery efforts and increase the species resiliency and redundancy should unforeseen circumstances or further population declines in the upper basin compromise the species' continued existence. With rapidly warming reservoir releases and re-emergence of riverine habitat due to climate change, the U.S. Fish and Wildlife Service commenced the evaluation process described herein to assess the potential for whether the Colorado River in Grand Canyon could again support a viable population of Colorado Pikeminnow.

Reintroduction feasibility in Grand Canyon

The river segment under consideration here commences at Glen Canyon Dam, flows 25 km through Glen Canyon National Recreational Area to Lees Ferry, and then flows approximately 481 km through Grand Canyon National Park to the inflow of Lake Mead (Figure 2), although this distance can vary depending on the water elevation of Lake Mead. This river segment has been highly impacted by the two largest dams and their associated reservoirs in the US, Glen Canyon and Hoover dams, which form Lake Powell and Lake Mead, respectively. These dams provide water storage and flood control while also generating hydropower. The quality and quantity of water released from Lake Powell influences the physical and biological aspects of the downstream river in Grand Canyon, while the elevations of Lake Mead determine the extent of free-flowing river available for fish in warmer parts of the western Grand Canyon (Figure 2).

Colorado Pikeminnow historically inhabited the Colorado River in and around Grand Canyon, as evidenced by archaeological deposits in Stanton's and Salt Can caves and in Native American midden piles at the Homolovi Ruins and Catclaw Cave (Euler 1978, 1984). Colorado Pikeminnow were also used as a food source in Grand Canyon by early explorers and river runners, including by

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the Stanton Party in 1889, where it was reported they consumed “Colorado River Salmon” at Christmas dinner (Measeles 1981; Smith and Crampton 1987; Minckley 1991; Mueller and Marsh 2002). Reductions in Colorado Pikeminnow and other native fish populations were likely due to river fragmentation from dams constructed in the lower basin (Mueller and Marsh 2002), combined with transformation of the physical and biological attributes of the river including a depressed thermal regime (e.g., Voichick and Wright 2007) and reductions in turbidity and fine sediment load relative to pre-dam conditions (e.g., Topping et al. 2000). Nonnative fish including Channel Catfish *Ictalurus punctatus* and Common Carp *Cyprinus carpio* were present prior to dam construction and may have exerted additional population pressure on native fish through piscivory and competition (Holden and Stalnaker 1975).

In the post-dam era, the Colorado River in Grand Canyon was considered suboptimal habitat for native fishes. Habitat suitability for native fishes has increased in the last 15 years, which has primarily been driven by warmer water releases from declining Lake Powell elevations and re-emergence of 100+ km of relatively warm river in western Grand Canyon due to the contraction of Lake Mead from ongoing drought. Native species such as Flannelmouth Sucker *Catostomus latipinnis* and Humpback Chub *Gila cypha* have expanded into western Grand Canyon and increased dramatically since 2015 (Van Haverbeke et al. 2017; Rogowski et al. 2018; Kegerries et al. 2020; Van Haverbeke et al. 2020), and Razorback Sucker *Xyrauchen texanus* has also been found in western Grand Canyon and at the inflow of Lake Mead (Albrecht et al. 2010; Kegerries et al. 2017; Kegerries et al. 2020). In addition, Pearce Ferry Rapid emerged as Lake Mead elevation declined, which may be providing a barrier to nonnative fish movement from Lake Mead into western Grand Canyon (Kegerries et al. 2020), further contributing to native fish recovery.

Because of rapidly changing riverine conditions and the resurgence of native fish in western Grand Canyon, combined with declines in upper basin populations, there is interest among federal,

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state, and tribal resource management agencies to assess the feasibility of reestablishing Colorado Pikeminnow in Grand Canyon. A potential reintroduction effort is supported by the Comprehensive Fisheries Management Plan for native and nonnative fishes in Grand Canyon, which was developed by Grand Canyon National Park and Glen Canyon National Recreation Area, in consultation with the Arizona Game and Fish Department (GCNP 2013). One of four main goals in the plan includes restoring self-sustaining populations of extirpated species including Colorado Pikeminnow, if feasibility studies determine it can be reasonably restored without impacting other listed species (GCNP 2013).

Reintroduction feasibility process. The Colorado Pikeminnow reintroduction feasibility study was facilitated by the U.S. Geological Survey as the science provider and guided by a Steering Committee comprised of natural resource and land managers who have authority over wildlife or water resources in the Colorado River in Grand Canyon or on adjacent lands. The Steering Committee included representatives from the Hualapai Tribe, Navajo Nation, Arizona Game and Fish Department, Nevada Department of Wildlife, U.S. National Park Service, U.S. Bureau of Reclamation, and the U.S. Fish and Wildlife Service (Table 1). The Steering Committee identified a group of university and federal scientists with expertise in Colorado Pikeminnow ecology to serve on a Science Panel that would evaluate habitat suitability in Grand Canyon and provide a formal recommendation on whether experimentation to assess reintroduction feasibility is warranted. Participants and their respective roles in this process are defined in Table 1.

Science Panelists and members of the Steering Committee reviewed summaries of Colorado Pikeminnow population status and life history requirements, and information on the physical and biological attributes of Grand Canyon prior to and during a 1-day workshop held in Flagstaff, Arizona on September 11, 2019. Panelists completed a structured Life History Survey (see Text S1) prior to the workshop to reach consensus on life stage requirements related to flow, temperature,

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nursery habitat, and prey using information from remaining populations in the upper basin. Modifications to this table were made during the workshop based on collective discussion (Table 2). Science Panelists then visually assessed the Colorado River during a 4-day river trip in western Grand Canyon in the Diamond Creek (rkm 389) to Pearce Ferry (rkm 479) reach from September 12-15, 2019. Following discussions in the field, panelists provided feedback on environmental and biological factors that may help or hinder the development of a self-sustaining population, developed a list of research questions to inform reestablishing a population in Grand Canyon, and provided U.S. Fish and Wildlife Service with a formal recommendation by consensus on whether experimentation to assess reintroduction feasibility (i.e., the next phase) was warranted.

This study provides the official report of the Colorado Pikeminnow Science Panel, but it is important to note this study does not represent an action document. Rather, the purpose of this study is to provide a summary of the science, and where the science is unclear or incomplete, fill in gaps via elicitation of expert opinion to provide managers with information to base future reintroduction decisions. In the following sections we synthesize literature on the five environmental and biological factors most likely to influence species viability (USFWS 2020b), discuss the extent to which the Grand Canyon could support the life history requirements of Colorado Pikeminnow at various life stages (egg, embryo, larvae, juvenile, sub-adult, adult), and provide the Science Panel assessment of whether they think the Colorado River in Grand Canyon could support a population of Colorado Pikeminnow given rapidly changing conditions in this part of the watershed. We focus our discussion on aspects that are *essential* for Colorado Pikeminnow to complete each life stage vs. those that are *preferred* or *non-essential* per the information in the Life History Survey (Table 2), so as to focus on attributes that could lead to potential life history bottlenecks in Grand Canyon.

Factors that Influence Species Viability

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The Species Status Assessment for Colorado Pikeminnow (USFWS 2020b) included five environmental and biological factors most likely to influence species viability: 1) peak flows, which maintain channel complexity, form backwater nursery habitats, and clean cobble bars to provide suitable spawning and rearing habitat and promote invertebrate production; 2) base flows, which facilitate hatching success, transport drifting larvae, maintain zero to low-velocity backwater nursery habitat, and provide connectivity between spawning and foraging areas for sub-adults and adults; 3) warm water temperature, which provides a thermal regime to trigger spawning and support egg hatching, larval development, and growth; 4) complex, redundant, low-velocity areas that support spawning, rearing, and foraging; and 5) an abundant forage base that exhibits low predation and competition from nonnative species (USFWS 2020b). The suitability of these habitat characteristics are associated with stable or increasing fish populations that may be more resistant to environmental disturbance. Resilient populations exhibit consistent reproduction, high survival rates, and recruitment rates that offset adult mortality leading to population growth. At the present time there are no subbasins containing the perfect combination of environmental and biological factors, which has contributed to the species' decline.

Peak flows

Colorado Pikeminnow evolved in a highly variable environment and exhibit life history characteristics that are intrinsically tied to the hydrologic cycle of winter precipitation and spring to early summer snowmelt originating from the Rocky Mountains in western North America. This species uses environmental cues, including declining spring flows and increasing water temperature, to trigger spawning migrations to specific areas and commence reproduction in late spring to early summer (Vanicek and Kramer 1969; Nesler et al. 1988; Tyus 1990; Bestgen and Hill 2016a). Long-distance spawning migrations routinely occur in the Green River, whereas in the upper Colorado

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and San Juan rivers spawning movements are generally more localized (McAda and Kaeding 1991; Ryden and Ahlm 1996). Peak flows provide suitable spawning substrate by scouring cobble and gravel of fine sediment, which facilitates egg attachment and development (Table 2). Deep interstitial spaces ensure proper aeration and oxygenation of embryos that increase the likelihood of successful incubation and hatching (Tyus and McAda 1984; McAda and Kaeding 1991; Bestgen and Hill 2016a). The removal of fine sediment also promotes invertebrate production, thereby providing better foraging conditions for larval and juvenile fish (Osmundson et al. 2002).

Peak flows are also important in developing and maintaining low-velocity and backwater environments that larval fish drift into and use after hatching and swim up (Table 2; Bestgen and Hill 2016a). These low-velocity, warmwater refuges provide food to support juvenile growth and development (Bestgen and Hill 2016a). Peak flows maintain channel complexity by preventing vegetation encroachment, channel narrowing, and accretion of channel substrate deposits along the riverbank (USFWS 2020b). These flows also reconnect main channels to the floodplain, which benefit adult fish before spawning because floodplains are warm and contain abundant prey that enhance the gonadal maturation process (Muth et al. 2000).

Peak flows in Grand Canyon. Prior to the construction of Glen Canyon Dam, peak flows occurred in early June (~Day 150), ranged from ~700-6,200 m^3s^{-1}, and were several months in duration (Schmidt et al. 2001). Flows in Grand Canyon are now primarily driven by Glen Canyon Dam operations as prescribed in the Glen Canyon Dam Long-Term Experimental and Management Plan Environmental Impact Statement (LTEMP EIS; USDOI 2016a), its associated Record of Decision (ROD; USDOI 2016b), and the 2007 Interim Guidelines for water shortages (USDOI 2007). Inclusion of peak flows similar to pre-dam conditions were considered but not chosen as the preferred alternative in the LTEMP EIS and ROD; however, sediment-triggered experimental flows

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such as spring High Flow Experiments (HFEs) and flows within powerplant capacity (up to 708 m^3s^{-1}) were included and could substitute as short-term disturbance events.

The primary objective of spring HFEs is to mobilize sediment from the bed for deposition on banks to rebuild sandbars or protect the sediment supply from equalization flows (Grams et al. 2010; Melis 2011), but they also may form backwaters that can be used by larval and juvenile fish (Dodrill et al. 2015). Sediment-triggered spring HFEs can release up to 1,274 m^3s^{-1} of water in March or April with longevity ≤96 hours (4 days), whereas proactive spring HFEs can release up to 1,274 m^3s^{-1} of water in April, May, or June with longevity up to 24 hours (USDOI 2016b, 2016a). Two sediment-triggered spring HFEs were tested in spring 1996 and 2008 (Figure 3), but proactive spring HFEs have not been implemented. Given current operational constraints associated with low reservoir elevations, future spring HFEs may be limited. In addition to sediment-triggered spring HFEs, flows up to 708 m^3s^{-1} within powerplant capacity can be released from Glen Canyon Dam. Such flows were released as part of a Spring Disturbance Flow in March 2021, which released low steady flows for five days (116 m^3s^{-1}) then higher flows for approximately 82 hours (~3.5 days; 572 m^3s^{-1}). Research is currently underway to evaluate the effects of this flow on the aquatic food base, primary production, nutrient cycling, fish populations, and channel geomorphology, among others.

Suitability of peak flows to support Colorado Pikeminnow in Grand Canyon. Spring HFEs may function as short-duration peak flows since they are designed to move fine-grained sediment off the bed and onto sandbars or to higher elevations (Schmidt et al. 2001) in the months just prior to presumed Colorado Pikeminnow spawning. As such, spring HFEs could improve spawning substrate and stimulate invertebrate production, but it is not clear whether they could reduce substrate embeddedness and create well-oxygenated cobble and gravel for egg development. Spring disturbance flows, such as one that occurred within powerplant capacity in March 2021, have the potential to scour the substrate and remove fine sediment from the bed. However, it is unclear the

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extent to which such relatively low magnitude flows will affect sediment resources in Grand Canyon. Given the magnitude of this flow relative to pre-dam floods that sometimes exceeded >6,200 m^3s^{-1} (Schmidt et al. 2001), it is likely fine sediment on top of and along the margins of cobble bars will be scoured, but a much larger flow (e.g., a spring HFE; Grams et al. 2010) would be needed to winnow out fine sediment that would provide deep interstices most needed for successful egg protection and incubation.

Spring HFEs or disturbance flows may cue spawning migrations by adult Pikeminnow, but these migrations may ultimately be more dependent on warming water temperatures and increasing photoperiod than a flow trigger (Fraser et al. 2019). During the spring 1996 HFE, flows had a minimal effect on the abundance, distribution, and movement of native fishes such as Flannelmouth Sucker, Humpback Chub, Bluehead Sucker *Catostomus discobolus*, and Speckled Dace *Rhinichthys osculus* around the Little Colorado River (Valdez et al. 2001). Native Flannelmouth and Bluehead Sucker and Humpback Chub undertake spawning migrations by moving into tributaries such as the Paria and Little Colorado rivers in late February and early March (Valdez et al. 2001), but they may be following temperature and not flow cues. Humpback Chub spawn in Havasu Creek, which lacks a snowmelt runoff, and move into Bright Angel Creek to spawn after spring runoff in May or June (B. Healy, pers. comm). Nonetheless, spring flooding has been found to be an important environmental cue that shapes native fish abundance in Bright Angel Creek, along with temperature (Healy et al. 2020), so a combined effect of spring flooding and more favorable thermal conditions may ultimately stimulate native fish spawning. Since Colorado Pikeminnow spawns in hatchery settings in the absence of a flow trigger (Hamman 1981), it is possible another cue like water temperature could trigger spawning if peak flows were muted or absent relative to a traditional spring peak.

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Base flows

Base flows are an important environmental factor because they provide a consistent water supply to support egg development and hatching while also transporting drifting larvae into downstream nursery habitats, where fish grow and remain for the first few years (Table 2). In the upper basin, spawning occurs from June to August and larvae emerge from the substrate 4-7 days post-hatch measuring ~7-9 mm TL (Snyder et al. 2016). This occurs on the declining limb of the spring hydrograph where flows move larvae downstream into nursery areas where they develop. In the Green River the majority of larvae captured in drift nets are 6-8 days old and 8-10 mm TL, indicating relatively close proximity to a spawning ground (Bestgen et al. 2006).

Stable base flows provide connectivity between foraging and spawning areas for sub-adult and adult fish but also inundate backwaters and low-velocity nursery habitats without reconnecting them with the main channel (Table 2). Moderate summer base flows in the middle Green (48-85 m^3s^{-1}) and lower Green (48-108 m^3s^{-1}) rivers are associated with high survival and abundance of age-0 fish, whereas few larvae and juveniles are produced when base flows are lower or higher (Bestgen and Hill 2016a). This is likely because moderate flow levels optimize the number, extent, and stabilize temperature of backwater areas, providing resources to increase survival (Bestgen and Hill 2016a). Overwinter survival is also linked to the magnitude of daily winter flows, with high survival associated with low flows and low survival associated with high flows (Haines et al. 1998). This effect is likely due to high flows inundating backwaters that eliminate their value as nurseries, flushing fish downstream during a time that is already energetically costly while also subjecting them to injury and predation (Haines et al. 1998).

Operational base flows in Grand Canyon. Base flows in Grand Canyon in the pre-dam period typically ranged from 100-200 m^3s^{-1} during late summer, autumn, and winter (Figure 3). Under current operating rules and regulations, dam releases are restricted to a minimum of 227 m^3s^{-1}

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during the day and 142 m^3s^{-1} at night, with maximum releases of 708 m^3s^{-1} within powerplant capacity that may be exceeded during HFEs. The daily range in flows is restricted to 227 m^3s^{-1}, which is lower than the post-dam period that exhibited high levels of hydropeaking (Figure 3). The daily stage change in Lees Ferry (Glen Canyon) is approximately 0.5 m and produces a high and low-water mark that attenuates downstream, resulting in backwaters that are less persistent in the Grand Canyon (e.g., Grams et al. 2010) than in the Green, upper Colorado, and San Juan rivers. As such, these variable flows do not help to maintain stable nurseries in summer. However, operational base flows in Grand Canyon would provide connectivity between spawning and foraging areas for adults and these flows would provide high levels of substrate oxygenation, should fine sediment be adequately scoured from cobble and gravel.

Stable operational base flows to benefit endangered species were not included as a management objective in the LTEMP EIS and ROD (USDOI 2016b, 2016a). However, there are two stable flow experiments designed to benefit Humpback Chub and other native fish species that may also benefit Colorado Pikeminnow, which include: 1) low summer flows; and 2) macroinvertebrate production flows (i.e., 'bug flows'). The objective of low summer flows is to increase Humpback Chub growth and recruitment during years of coolwater releases from Glen Canyon Dam by increasing water temperature to ≥14°C at the Little Colorado River confluence. Low summer flows include releases of 227 m^3s^{-1} with little daily fluctuation (28 m^3s^{-1}), spanning July-September. A low summer steady flow experiment occurred in 2000, but low summer flows have not been implemented under the LTEMP EIS and ROD because temperatures have exceeded 14°C at the Little Colorado River confluence since then (2000-2022).

Operational base flows in Grand Canyon follow a load-following pattern, with higher flows released twice a day to generate electricity during hours of peak demand (e.g., in morning and at night). Hourly changes in discharge can be substantial and produce kinematic waves that propagate

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downstream, creating an extensive intertidal zone along shorelines for more than 400 km (Wiele and Smith 1996) that affects invertebrate production (Kennedy et al. 2016). Macroinvertebrate Production Flows (i.e., ‘Bug flows’) were developed as an experiment to test the hypothesis that keeping flows low and steady at the weekly minimum on weekends will benefit aquatic invertebrate production by ‘giving bugs the weekend off’ from flow fluctuations due to hydropower generation. This is because high chironomid counts occur in areas where minimum flows occur at dusk, while low counts occur in areas where maximum flows occur at dusk. Since aquatic insects tend to lay eggs along the water’s edge at dusk, eggs laid near the low water mark are presumably submerged and have a higher likelihood of survival during the day, whereas eggs laid at the high water mark are desiccated when flows drop (Kennedy et al. 2016). Bug flows were implemented from May-August in 2018, 2019, and 2020, with results generally positive and indicative of increased aquatic invertebrate production and higher levels of gross primary production (T. Kennedy, USGS, unpub. data; Deemer et al. 2022). If implemented on a long-term basis these flows could provide stability in backwaters during the weekends and potentially improve the food base.

Suitability of operational base flows to support Colorado Pikeminnow in Grand Canyon. Stage change differs across the canyon and is primarily driven by channel width and other local geomorphological features. The area of gravel and cobble bars that are exposed when flows drop to below 227 m^3s^{-1} is higher in western Grand Canyon than in the middle canyon (Kaplinski et al. 2020, and M. Kaplinski, USGS, unpub. data). Releases are restricted to a minimum of 227 m^3s^{-1} during the day and 142 m^3s^{-1} at night, however, minimum daily flows released from Glen Canyon Dam are typically at or near 227 m^3s^{-1}. As such, the degree to which eggs may be de-watered depends on where in the canyon and during what time of day Colorado Pikeminnow may spawn.

Discharge from Grand Canyon Dam is high relative to other dams in the basin, which has the potential to flush newly-hatched drifting larval fish into Lake Mead prior to them finding a low-

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velocity refuge. However, fishes are opportunistic and diversify habitat use based on availability. For example, while juvenile Humpback Chub, Bluehead Sucker, Flannelmouth Sucker, and Speckled Dace density is highest in backwaters relative to other habitats available near the Little Colorado River, juvenile Humpback Chub and Speckled Dace abundance is highest in talus and debris fan habitats, respectively (Dodrill et al. 2015). Talus and debris fans may provide a velocity refuge that minimizes energetic costs and provides cover from predation (Crook and Robertson 1999). In contrast, Bluehead Sucker and Flannelmouth Sucker were most associated with sandy substrate and shallow areas in Grand Canyon (Dodrill et al. 2015), a finding with similarities to the San Juan River where catostomids in secondary channels have been associated with fine substrates (Gido and Propst 1999). In addition, small-bodied fish sampling using seines in a variety of shallow areas from Bright Angel Creek to Pearce Ferry from 2014-2018 indicates dominance by four native species (Kegerries et al. 2020). This indicates native fishes occupy areas other than backwaters in Grand Canyon (Converse et al. 1998; Dodrill et al. 2015). Importantly, nonnative predators such as Walleye *Sander vitreus*, Smallmouth Bass *Micropterus dolomieu*, Striped Bass *Morone saxatilis*, and Northern Pike *Esox lucius* are rarely detected and not established (Kegerries et al. 2020; Gilbert et al. 2022), which is in sharp contrast to other river segments in the basin.

Daily Glen Canyon Dam operations provide a reliable source of water that is unlikely to completely dry up due to drought or water allocation decisions. Humpback Chub were recently downlisted from Federally endangered to threatened status (FR 2021), in part due to the Grand Canyon Humpback Chub population. While Humpback Chub abundance at the LCR has declined and triggered LTEMP conservation actions, Humpback Chub has expanded into western Grand Canyon and is naturally recruiting (Van Haverbeke et al. 2017; Rogowski et al. 2018; Kegerries et al. 2020; Van Haverbeke et al. 2020). As such, Humpback Chub in Grand Canyon are doing relatively well in this highly altered ecosystem relative to upper basin populations that reside in

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areas with more natural hydrographs and warmer temperatures but experience high levels of predation (Dibble et al. 2021). If operational base flows were reduced in the future due to a decline in water availability, sandbars may reappear in the channel, creating low-velocity environments that could serve as refuge or nurseries.

Water temperature

Warm water temperature triggers spawning (along with flow and photoperiod cues) and enhances maturation of gametes in adult fish, while also supporting egg hatching, larval development, and growth across all life history stages (Table 2). Adult Colorado Pikeminnow in the Green and lower Yampa rivers migrate to suitable spawning grounds in late spring to early summer and spawn in groups on the descending limb of the hydrograph when water temperatures reach 16°C, and are rising (Vanicek and Kramer 1969; Nesler et al. 1988; Tyus 1990; Bestgen and Williams 1994; Bestgen et al. 1998). In the lower Green River spawning commences at ~19-25°C, but fish do not consistently spawn until mean daily water temperature exceeds 18°C for 13 to 39 days (Tyus and McAda 1984; Tyus 1990; Bestgen et al. 1998). In the upper Colorado River, spawning has commenced in late June to early September when water temperature reaches 18-22°C, water levels decrease, and flows are 15-30% of maximum annual flow (McAda and Kaeding 1991). In the San Juan River, back-calculations of age from mesolarvae captured in the western portion of the river indicated a limited amount of spawning by stocked adult fish in mid-July when temperatures ranged from 20-23°C (Farrington et al. 2016). Across all studies, the optimum temperature for spawning is ~18-22°C even though adults reproduce outside that range.

Similar to spawning, water temperatures of 18-26°C are needed to ensure egg survival, development into embryos, and a successful hatch (Hamman 1981; Bestgen and Williams 1994). In laboratory experiments, embryos consistently exhibited 100% mortality when incubated at 5, 10,

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15, and 30°C temperatures (Marsh 1985). Hatching occurred at 20 and 25°C; however, 20°C facilitated better embryo survival and hatching success, maximized protolarval size, and reduced spinal deformities and other abnormalities (Marsh 1985). In another study, Bestgen and Williams (1994) found that a range of temperatures (18, 22, 26°C) supported successful hatch rates (72, 67, and 62%, respectively) and larval survival rates 7 days post-hatch (68, 64, and 83%, respectively), but higher temperatures of 30°C yielded lower hatch and survival rates (38 and 13%, respectively; Bestgen and Williams 1994). Based on laboratory experiments the optimal temperatures for embryonic development and post-hatch survival ranges from 18-26°C. Once hatched, 14-day old laboratory-raised larval Pikeminnow are particularly vulnerable to cold shock, with a 15°C drop resulting in direct mortality and a 10°C drop resulting in behavioral changes that could result in indirect mortality (Berry 1988). As such, Green River flows are now regulated to minimize the temperature difference with the unregulated Yampa River during larval emergence and drift (<5°C; Muth et al. 2000).

Juvenile and adult Colorado Pikeminnow exhibit positive growth in water temperatures ranging from 22-30°C (Bestgen and Hill 2016a), with an optimal temperature for juveniles of 25°C (Black and Bulkley 1985a; Black and Bulkley 1985b). Colorado Pikeminnow grow slower in temperatures <22°C in laboratory settings (Bestgen 1996) and cease to grow at <13°C or lower (Osmundson 1987). Analysis of in-channel thermal suitability using mean daily water temperature and Pikeminnow growth relationships found that the distributional limits of adults occur when thermal regimes fall below a long-term average of 47-50 Annual Thermal Units (ATUs), which may include colder upstream reaches of the Colorado River and its major tributaries (Osmundson 2011).

Water temperature in Grand Canyon. In the pre-dam era, the Colorado River in Grand Canyon was seasonably variable and characterized by mean monthly water temperatures that varied from 1 to 29°C (Voichick and Wright 2007). Today, drivers of water temperature in Grand Canyon

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include Lake Powell elevation and inflow rates, discharge and flow volume from the reservoir, ambient air temperature, and solar radiation (Wright et al. 2009; Mihalevich et al. 2020; Dibble et al. 2021). However, the major driver of water temperature in Grand Canyon that affects fish populations on a macro-scale is Lake Powell (Figure 4a). When elevation is high and the reservoir is full, releases are cold and relatively consistent, but when lake elevation falls and the penstocks draw water from closer to the surface, release temperatures are warmer (Figures 4a, b), with many of the warmest years coinciding with warm inflows (e.g., 2011, 2019). Reservoir releases from 2017-2021 ranged from 8-17.2°C in May-October, the warmest months of the year. Mainstem water temperatures historically warmed to ~16°C near Diamond Creek (rkm 388) in western Grand Canyon in May and reached 18-20°C in June-October (Figure 5). Backwaters reach up to 30°C in downstream reaches (USGS 2013; Vernieu and Anderson 2013). However, 2022 reached an unprecedented level of warming throughout Grand Canyon due to low levels in Lake Powell, with reservoir releases reaching 21.1°C that peaked at 25.4°C near Spencer Creek (rkm 422).

We assessed the thermal suitability of the mainstem Colorado River in Grand Canyon for adult growth using the concept of ATU units (Osmundson 2011), which were calculated using mean daily water temperature and predictions from a recently published model (e.g., Dibble et al. 2021). During the 1980s and 1990s the Grand Canyon was unsuitable for the growth of sub-adult and adult Colorado Pikeminnow (i.e., <50 ATUs; Figure 6). However, during the last two decades, the river downstream from Diamond Creek has been suitable for growth in nearly every year, and this trend has increased over time (Figure 6). In eastern Grand Canyon, habitat from the dam to Bright Angel Creek has been unsuitable since 1988; however, there is an increasing trend in ATUs from 2000-2020 in the eastern reaches of the canyon. Years in which ATUs increase near 50 are 2005 and 2014, when releases were warmer (Figure 6; Figure S1). While temperatures are cooler in Grand Canyon than in the upper basin, the prolonged growing season allows for a relatively high degree of

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cumulative warming (Figure 6). With additional declines in Lake Powell due to drought (Udall and Overpeck 2017), or with allocation decisions that de-emphasize storage in Lake Powell (e.g., Schmidt et al. 2016), we would expect to see Grand Canyon increase in thermal suitability (Dibble et al. 2021).

Warmwater tributaries in western Grand Canyon such as Havasu Creek may provide additional support for Colorado Pikeminnow, but only if adjacent mainstem temperatures do not prevent upstream movement. There are multiple tributaries of the Colorado River in Grand Canyon that support native fish populations, including Havasu Creek, Kanab Creek, Tapeats Creek, Shinumo Creek, Bright Angel Creek, the Little Colorado River, and the Paria River (Figure 2). Although all except Tapeats Creek contain warm water, a few have natural barriers that would prevent upstream movement of more than a few hundred meters (e.g., Shinumo, Havasu creeks). According to our ATU analysis, no major tributaries currently fall next to the mainstem river that is consistently above 50 ATU. However, Havasu and Kanab creeks are located in between 127-Mile Creek (rkm 230) and National Canyon (rkm 293), which reached 44 and 49 ATUs, respectively, in 2019 (Figure 6; Figure S1). As such, it is possible fish near their upstream distributional range may use Havasu or Kanab creeks, which exhibit warmer thermal regimes that could support the growth of sub-adults or adults (Figure 7). These creeks, although small in flow volume (Figure 7), could also provide warm conditioning areas similar to that found in Vermillion Creek, a tributary to the Green River that is used prior to adult spawning in the Yampa River (Bestgen et al. 2017). These tributaries would also provide sources of native fish prey items like Bluehead and Flannelmouth Suckers and Speckled Dace, along with nonnative small-bodied fishes such as Fathead Minnow *Pimephales promelas*, an important food source for Colorado Pikeminnow in the upper Colorado River (Vanicek and Kramer 1969; Muth and Snyder 1995).

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Suitability of water temperature to support Colorado Pikeminnow in Grand Canyon. Annual release temperatures from Glen Canyon Dam historically ranged from 8-13°C, with more recent release temperatures spiking to 21.1°C due to low reservoir levels. As such, the thermal regime in western Grand Canyon (below National Canyon) could support Colorado Pikeminnow in all life history stages at the present time. Water temperatures in the mainstem river meet and exceed 16°C downstream from Diamond Creek in May and June, and summer temperatures >18°C could support egg development and the growth of larvae, juveniles, sub-adults, and adults, with further support from warmwater tributaries such as Havasu and Kanab creeks (Figures 5-7). Even though western Grand Canyon is characterized by a relatively low temperature range that only reaches the low 20s, the extended growing season relative to other rivers may lead to good growth conditions for sub-adults and adults through the accumulation of thermal units over time. In the upper Colorado River, the greatest concentration of adults occurs in the Grand Valley near the upstream limits of their range (Osmundson and White 2014), where the warmest summer temperatures rarely exceed 25°C, and more typically are between 20 and 23°C (K. Bestgen, CSU, unpub. data). For juveniles, slower-growing fish with lower lipid reserves going into winter have been associated with reduced survival when feed was withheld (Thompson et al. 1991). However, fish in western Grand Canyon are likely to feed during the warm winter months (also see Tyus and Haines 1991), so it is unclear the extent to which lower temperatures may ultimately influence recruitment.

Colorado River water temperatures in Grand Canyon are dependent on Lake Powell elevations, which may change resulting from declining inflows due to long-term drought and from renegotiation of the 2007 Interim Guidelines (USDOI 2007). Should water storage in Lake Powell increase, water temperatures could return to colder conditions present in the early 1980s and late 1990s (Figure 4b), conditions that were unsuitable for the growth of Humpback Chub near the Little Colorado River (Robinson and Childs 2001) that would also limit adult Colorado Pikeminnow

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growth (e.g., Figure 6). Alternately, if storage is de-emphasized in Lake Powell, a warming trend could improve thermal suitability for native fish as well as improve conditions for nonnative fish (Dibble et al. 2021). The system received a preview of such warming in 2022. A rapid decline in Lake Powell elevations from 2021-2022 resulted in unprecedented warming of the Grand Canyon, with release temperatures reaching 21°C and mainstem temperatures near Spencer Creek in western Grand Canyon reaching 25°C. Should such unprecedented warming continue in the future, the thermal regime throughout Grand Canyon would be suitable for Colorado Pikeminnow growth, survival, and reproduction. This warming trend coincided with higher catch rates of YOY Striped Bass, Smallmouth Bass, and Green Sunfish (T. Kennedy, D. Ward, pers. comm), a sign of nonnative fish expansion from Lake Powell and other sources.

In the upper basin, Colorado Pikeminnow recruitment has declined in part due to nonnative fish predation. Grand Canyon typically lacks or has reduced populations of warmwater predators most often associated with hindering endangered fish recovery efforts in the upper basin (e.g., Smallmouth Bass, Walleye, Northern Pike, Red Shiner *Cyprinella lutrensis* (Bestgen et al. 2006; Johnson et al. 2008). Low predator abundance may be due in part to the cool thermal regime in eastern Grand Canyon combined with the barrier to upstream fish movement formed by Pearce Ferry Rapid.

Pearce Ferry Rapid developed when Lake Mead elevation dropped below 346 masl and through superimposition the river cut a new channel that flows over a bedrock ledge. Fish biologists hypothesize this rapid is a barrier to movement of nonnative fishes from Lake Mead into warmer riverine habitat in western Grand Canyon (Kegerries et al. 2020) that is largely inhabited by native species (Rogowski et al. 2018; Van Haverbeke et al. 2020). The continued persistence of Pearce Ferry Rapid may be beneficial to prevent nonnative species from moving upstream, but it may also cut off native fish movement. This could result in a similar situation as the San Juan River, where

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age-0 fish are stocked but many migrate past Piute Farms Waterfall into Lake Powell as adults and can no longer move upstream into the river (Cathcart et al. 2018; Pennock et al. 2020). As such, examination of Pearce Ferry Rapid and its importance as a driver of current resource conditions is warranted.

Complex, redundant habitat

Colorado Pikeminnow require complex, redundant, low-velocity areas for foraging, spawning, and rearing (Table 2). Adult fish prefer large pools, deep runs, and eddies to forage, and select spawning sites characterized by riffles with clean cobble that are located upstream from multiple low-velocity channel or backwater habitats (Table 2; Tyus and McAda 1984; Ryden and Ahlm 1996; Osmundson et al. 1998; Osmundson 2006; Durst and Franssen 2014). Tagging studies indicate adult Colorado Pikeminnow have made spawning migrations of up to 800 km along the Green River and its major tributaries to visit two spawning grounds – Yampa Canyon in Dinosaur National Monument and Gray Canyon of the Green River (Tyus 1990; Irving and Modde 2000; Bestgen and Hill 2016a). This species shows some spawning site fidelity as evidenced by individuals returning to specific areas used in the year prior (Tyus 1990) or in river reaches exhibiting similar geomorphological traits (e.g., rubble gravel bars in unique riffle-pool sequences in the Yampa River; Wick et al. 1983). However, there is plasticity in this trait as spawning adults migrate shorter distances and have been found in close proximity to larvae <22 mm TL in reaches of the upper Colorado River, indicating spawning occurs in widely scattered locations as long as substrate and riverine conditions can support reproduction (McAda and Kaeding 1991). Colorado Pikeminnow in the San Juan River tend to either have small home ranges that include spawning sites (Ryden and Ahlm 1996), or they migrate comparatively shorter distances relative to those in the Green River (e.g., up to 145 km; Platania et al. 1991; Ryden and Ahlm 1996). This could be due to physical barriers to movement

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(e.g., dams, diversions, waterfalls) or thermal intolerances as fish move closer to hypolimnetic-release dams such as Navajo Dam. Impediments to long-distance migration have eliminated the ability of adults to navigate to historically occupied habitats to spawn, as suggested by recaptures of ripe adults at the base of Flaming Gorge and Taylor Draw dams (Irving and Modde 2000).

Larvae dispersed downstream can move up to 200 km via currents into low-velocity nursery habitats, where they arrive as soon as 8-10 days post-hatch and remain as juveniles for months or even years (Bestgen et al. 1998; Bestgen et al. 2006). Low-velocity areas are usually nearshore channel margin backwaters in the river channel characterized by warmer water and lower flow than the mainstem river (Vernieu and Anderson 2013), which provide refuge areas for foraging and conserving energy (Muth et al. 2000). Backwaters are shallow habitats in a river channel that are situated downstream from obstructions (e.g., sand or gravel bars) that have a direct surface water connection with the river (Haines and Tyus 1990; Tyus and Haines 1991). These habitats are often associated with increasing levels of shoreline complexity that enhance larval survival and growth. Age-0 fish stay in nursery habitats from the time they arrive as larvae in mid-summer to their first autumn, taking advantage of steady summer flows, warm temperatures, and abundant prey (Vanicek 1967; Vanicek and Kramer 1969; Bestgen and Hill 2016a). Age-1 fish continue to use shallow, channel-margin backwaters that are warm (>18°C) and turbid (Muth et al. 2000), although spring season flows can inundate backwaters, displacing juveniles to other locations. After fish transition to age-2+, they disperse from nursery habitats and move into the main river channel or into tributaries to forage (Muth et al. 2000).

Complex, redundant habitat in Grand Canyon. There is currently 480 km of unimpeded river available between Glen Canyon Dam and Pearce Ferry Rapid, with another 26 km between the rapid and the inflow to Lake Mead. This segment is largely composed of a series of high gradient riffles and rapids followed by low gradient deep pools and eddies (Leopold 1969; Grams et al.

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2007). Declining Lake Mead elevation has converted once-inundated sections of western Grand Canyon into free-flowing river that is notably warmer and possibly more productive than eastern Grand Canyon (Kegerries et al. 2020). In total, the length of unimpeded river in Grand Canyon is comparable to the amount of habitat available in the upper Colorado and San Juan rivers. At typical temperatures (to 2020) the river only becomes suitable for sub-adult and adult growth near National Canyon (293 km from dam), so there is ~187 km of river available upstream from Pearce Ferry Rapid and another 26 km to the Lake Mead inflow. Tributaries such as Havasu and Kanab creeks are 15 and 37 km upstream from National Canyon, potentially putting them in range for use by Pikeminnow for growth, conditioning, or spawning, particularly during warmer years associated with declining Lake Powell elevations that remain above minimum power pool (e.g., 2022).

Spawning adults seeking loose, oxygenated substrate may use debris fans and cobble bars throughout Grand Canyon, but there is a large increase in the area of gravel bars in the eastern part of the canyon (~105-180 km from Glen Canyon Dam) and another large increase in western Grand Canyon from National Canyon to Diamond Creek (~315-390 km from the dam; Kaplinski et al. 2020; M. Kaplinski, NAU, unpublished data). This is river habitat that would be available to spawning adults with inundation above the minimum operational flows for typical operations (227 m^3s^{-1}) that is re-worked during the occasional spring or fall HFE. Large stochastic tributary flooding events during monsoon season (Figure 7) deposit new sources of gravel and cobble from side canyons into the mainstem river that also clean and rebuild existing debris fans. There are more than 750 ungaged ephemeral tributaries between the dam and the downstream end of Grand Canyon that transport approximately 2,800,000 metric tons of boulders, cobbles, pebbles, sand, and silt onto debris fans in the mainstem Colorado River annually (Webb et al. 2000). This sediment is poorly sorted, with finer grained sediment in the matrix of debris fans. In the pre-dam era large floods would free fine-grained sediment through debris fan reworking, leaving larger-grained substrate

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behind. In the post-dam era only ~25% of debris fans are reworked during floods, such that sand is a component of the debris fan matrix (Webb et al. 2000) that increases substrate embeddedness. As such, the strength of the monsoon season, delivery of new substrate, and reworking of that substrate with normal operational flows or HFEs will affect the quality and quantity of spawning habitats available.

The majority of the river is canyon-bound and the channel has undergone some simplification since Glen Canyon Dam was constructed. In the 'classic' sense, backwaters are the only nursery areas available in Grand Canyon. The total number of backwaters available varies annually and seasonally based on geomorphology and dam operations, since flow fluctuations reduce the area of and persistence of backwaters (Grams et al. 2010). The total number of backwaters available for use by fish from Lees Ferry to Diamond Creek ranges from <100 sites (0.2 sites/km) to >300 sites (0.6 sites/km, rkm 25-389; M. Dodrill, USGS, unpub. data). The stability and size of backwaters is also influenced by daily fluctuations in release, such that they are formed and potentially drained on a 24-hour cycle (Vernieu and Anderson 2013). However, similar to the San Juan River, the Grand Canyon hosts an array of other low velocity nursery habitats that include the inside bends of the river, microhabitats behind debris piles, shallow shorelines downstream from debris fans, and flooded tributary mouths.

Suitability of complex, redundant habitat to support Colorado Pikeminnow in Grand Canyon. Spawning substrate embeddedness and a lack of persistent nursery habitats may pose a challenge for fish recruitment. Cobble bars in Grand Canyon differ from the upper basin because they are smaller in areal extent and the substrate is highly embedded with gravel and fine-grained sediment, which may hinder egg attachment and adequate development. Flow experiments in the LTEMP EIS such as spring and fall HFEs may remove fine sediment from cobble bars, but it is unclear the extent to which these bars are re-worked during an HFE since much of the mobilized sand to build

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sandbars is lying on the bed. During monsoon season, stochastic tributary flooding events introduce new coarse material into the system that could augment spawning habitat in the mainstem river. The products of tributary floods are usually poorly sorted, so it is unclear how long newly deposited coarse material from monsoonal events will remain un-embedded and useful as sufficiently loose and well-oxygenated spawning substrate. Nonetheless, there are good sources of cobble in Grand Canyon, and there is potentially adequate-sized spawning habitat at tributary junctions like Spencer Creek and Surprise Canyon. This potential spawning habitat provides optimism for success, since it is loose, aerated, and adds complexity to areas that could be used by Colorado Pikeminnow, which do not need large areas of river habitat to successfully spawn.

Backwaters in Grand Canyon are highly dynamic, easily eroded in the months after an HFE, can be overtopped at maximum daily flow, and are less stable due to fluctuations in temperature and flow (M. Dodrill, USGS, unpub. data; Grams et al. 2010). As with other native species, Colorado Pikeminnow would need to move out of backwaters at different flow regimes into the main channel, which is colder (USGS 2013; Vernieu and Anderson 2013) and could present difficulties in finding prey resources. However, young fish display diel movements across river channels and backwaters in the upper basin (Tyus and Haines 1991), so these fish do not necessarily need to remain in backwaters to successfully grow. While backwaters are essential areas for larval Colorado Pikeminnow, they could adapt to the regulated nature of the Grand Canyon ecosystem as Humpback Chub, Flannelmouth Sucker, Bluehead Sucker, and Speckled Dace have, using other habitats like debris fans, talus, coves and embayments, flooded tributary mouths, and tributaries to support their mainstem populations (Converse et al. 1998; Dodrill et al. 2015). In addition, river-inflow habitat in Lake Mead may provide the level of complexity needed for growth and survival, if they can avoid predation by nonnative fish. Razorback Sucker use the Lake Mead inflow as well as other inflow areas for this purpose (Kegerries et al. 2017) and may be somewhat protected from sight-feeding

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predators by turbidity. Colorado Pikeminnow exhibit the same behavior around the San Juan River inflow area to Lake Powell (e.g., Cathcart et al. 2018).

Forage base

Colorado Pikeminnow require an abundant forage base, and low predation and competition from nonnative species during all life stages (Table 2). Early larvae feed off their yolk sac, but once larvae emerge from cobble bars and drift to shallow, warmwater nursery habitats they consume diatoms, algae, early instars of chironomids, and other small invertebrates (Vanicek 1967; Vanicek and Kramer 1969; Muth and Snyder 1995; Snyder et al. 2016). Age-0 fish (up to 50 mm TL) consume algae and aquatic invertebrates including cladocerans, copepods, and chironomid larvae (Vanicek 1967; Vanicek and Kramer 1969; Muth and Snyder 1995). Age-1 fish remain in low-velocity nursery habitats in spring but may start moving between backwaters and the main channel to forage or seek preferred thermal regimes (Tyus and Haines 1991). Juvenile fish begin the transition to piscivory at age-1, consuming both aquatic invertebrates and soft-rayed fish (Vanicek and Kramer 1969). By age-2 the majority of their diet is fish (Vanicek and Kramer 1969), but up to 25% of their diet may still include invertebrate taxa (Franssen et al. 2019).

Colorado Pikeminnow was, for millions of years, the sole large-bodied predator at the top of the food web in the basin (Tyus 1991). Its population persistence depended on abundant soft-rayed fishes including native Flannelmouth Sucker, Bluehead Sucker, Roundtail Chub *Gila robusta*, Speckled Dace, and now-threatened and endangered species Humpback Chub, Razorback Sucker, and Bonytail *Gila elegans*. At the present time Colorado Pikeminnow also consume nonnative fishes including Sand Shiner *Notropis stramineus*, Red Shiner, and Fathead Minnow (Vanicek and Kramer 1969; Osmundson 1999). Colorado Pikeminnow can consume fish up to 40% of their body length (Osmundson et al. 1998; Ryden and Smith 2002; Gilbert et al. 2018), but anatomical changes

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in head morphology with age may limit the size of suitable prey (Gilbert et al. 2018). Colorado Pikeminnow vertical gape is proportionally smaller relative to other non-native species that have invaded the basin, including Northern Pike, Channel Catfish, Flathead Catfish *Pylodictis olivaris*, Striped Bass, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass, Brown Trout *Salmo trutta*, and Rainbow Trout (*Oncorhynchus mykiss*; D. Ward, pers. comm). For example, an adult Colorado Pikeminnow measuring 600 mm has a vertical gape of ~38 mm, whereas nonnative species range from 52-75 mm at the same body length (D. Ward, USGS, unpub. data). Collectively, these studies indicate this top predator has anatomical features that limit predation to smaller-bodied fishes relative to their body length.

Forage base in Grand Canyon. In Grand Canyon, the aquatic invertebrate food base is unstable and exhibits low diversity, such that fish persisting primarily on aquatic invertebrates to adulthood are food-limited (Kennedy et al. 2013). In backwaters, Behn et al. (2010) found the biomass and abundance of four common invertebrates after the spring 2008 HFE was highest in Marble Canyon and lowest in western Grand Canyon. Since there are unknowns regarding the historical and current state of plankton and invertebrates in backwaters in western Grand Canyon under normal operations and during bug flows (samples have not been processed yet), it is unclear whether food resource conditions for larval and age-0 fish are improving relative to limited data collected more than a decade ago. Furthermore, many of the river reaches that could be used by Colorado Pikeminnow were lake habitat 5-20 years ago. Nonetheless, Humpback Chub and Flannelmouth Sucker have expanded into and increased in abundance at these same locations (Van Haverbeke et al. 2017), and both species primarily consume aquatic invertebrates.

The composition and abundance of the fish community downstream from Lees Ferry has shifted dramatically since 2000 (Van Haverbeke et al. 2017; Boyer and Rogowski 2020). In the late 1990s and early 2000s nonnative fish were abundant throughout the river but transitioned to a mix

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of nonnative and native species by ~2009, and the lower river community is now primarily native fish (Boyer and Rogowski 2020; Kegerries et al. 2020; Van Haverbeke et al. 2020). While the cause for this shift in community composition is unknown, hypotheses include warming temperatures in western Grand Canyon combined with the emergence of Pearce Ferry Rapid and a lack of nonnative fish predators. Trends in catch indicate system-wide declines in nonnative Common Carp and Brown Trout (except between Glen Canyon Dam and Lees Ferry) that coincided with increases in native Flannelmouth Sucker, Bluehead Sucker, and Speckled Dace (Boyer and Rogowski 2020; Kegerries et al. 2020). Flannelmouth Sucker, an important prey source, represents the largest proportion of native fish biomass and are larger in eastern Grand Canyon but smaller and more numerous in western Grand Canyon (Van Haverbeke et al. 2020).

Nonnative species in Grand Canyon have declined in abundance and distribution over the past two decades and captures of Walleye, Northern Pike, and Smallmouth Bass throughout the system remain extremely rare. Red Shiner is captured via electrofishing and seining in western Grand Canyon but overall catch rates are low relative to native species (Boyer and Rogowski 2020; Kegerries et al. 2020). From 2014-2018, four native species (Bluehead Sucker, Flannelmouth Sucker, Humpback Chub, Speckled Dace) comprised 80.5-98.2% of the larval fish catch while eight nonnative species (Brown Trout, Rainbow Trout, Common Carp, Fathead Minnow, Plains Killifish *Fundulus zebrinus*, Green Sunfish *Lepomis cyanellus*, Western Mosquitofish *Gambusia affinis*, Red Shiner) comprised 1.8-19.5% of the larval catch (Kegerries et al. 2020; Gilbert et al. 2022). Green Sunfish, Plains Killifish, Channel Catfish, and Red Shiner may prey on juvenile stages of Colorado Pikeminnow (e.g., Ward and Vaage 2018; Hedden et al. 2020) but they are consistently <1% of the fish community (Boyer and Rogowski 2020; Kegerries et al. 2020). Annual backwater seining data from 2000-2018 indicate Fathead Minnow are more abundant than Red Shiner in Grand Canyon backwaters (Table S2); however, Fathead Minnows tend not to be piscivorous in the wild and may

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provide a good food source for juvenile fish (M. McKinstry, pers. comm). In the upper Colorado River, a significant positive relationship has been detected between Colorado Pikeminnow condition factor and Fathead Minnow abundance (D. Osmundson, USFWS, unpub. data).

With the abrupt decline in Lake Powell elevations from 2021-2022, the thermal regime of the Colorado River in Grand Canyon shifted quickly toward one conducive to warmwater fish growth. In the past five years, peak annual temperatures in Lees Ferry reached 13.5°C (2017), 12.9°C (2018), 15.4°C (2019), 12.8°C (2020), and 16.7°C (2021). Temperatures in September 2022 reached 21.4°C and are anticipated to continue to warm. This warming has increased the suitability of this reach for nonnative predators, such that there is now concern this reach may not remain in low abundance of predatory nonnative fish, creating additional pressure on native fish populations. State and Federal agencies are currently planning management actions to slow or prevent a potential invasion of nonnative predatory fishes into Grand Canyon.

Suitability of forage base to support Colorado Pikeminnow in Grand Canyon. Western Grand Canyon exhibits low algal and invertebrate productivity and low production of small-bodied fishes to support the mixed diet of juvenile Colorado Pikeminnow, but there are no forage base concerns for sub-adult and adult fish once they switch to full piscivory. The aquatic food web in Grand Canyon exhibits poor diversity relative to other basin rivers (Kennedy et al. 2013; Kennedy et al. 2016), even in western Grand Canyon (Behn et al. 2010; Kennedy et al. 2013). However, multiple life history stages of Humpback Chub are abundant in a seemingly food-limited area of the canyon and consume macroinvertebrates including early instars of chironomids that support larval fish. Bug flows, which were tested from 2018-2020, increased gross primary production and improved aquatic insect diversity and abundance for higher trophic levels, including fishes (T. Kennedy, USGS, unpub. data; Deemer et al. 2022).

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Sub-adult and adult Colorado Pikeminnow could be supported by native fishes such as Flannelmouth Sucker, which are more abundant than Humpback Chub in western Grand Canyon, in addition to small-bodied nonnative fishes such as Fathead Minnow and Red Shiner. We recognize that reintroducing a top predator into a river segment with Humpback Chub is not without risk. However, Humpback Chub overlap with Colorado Pikeminnow in three upper basin reaches (Westwater Canyon and Black Rocks in the middle Colorado River, and Desolation/Gray Canyon on the Green River) that have not exhibited population level impacts—instead, Humpback Chub are affected more by flows and predatory nonnative fish (USFWS 2018). There are bioenergetic differences between native predators such as Colorado Pikeminnow and high-risk nonnative predators such as Smallmouth Bass, Northern Pike, and Channel Catfish (Johnson et al. 2008; Zelasko et al. 2016; Bestgen et al. 2018). On an individual basis, Colorado Pikeminnow consume fewer fish prey and also maintain lower densities when their populations are stable (e.g., McGarvey et al. 2010). As such, Colorado Pikeminnow and nonnative predators should not be viewed as interchangeable relative to their impact on Humpback Chub. In addition, Colorado Pikeminnow and Humpback Chub co-evolved over three million years (Mueller and Marsh 2002) and the latter has developed morphological and behavioral adaptations that may afford the latter with some protection from predation (Gilbert et al. 2018; Ward and Ward 2020). For these reasons, it is unlikely that Colorado Pikeminnow will impact Grand Canyon Humpback Chub at a population level.

Science Panel Recommendation and Next Steps

Myriad factors contribute to the successful reproduction, growth, and viability of fish populations. However, there are key habitat attributes and demographic factors that are essential for the successful reintroduction of a species like Colorado Pikeminnow into an ecosystem. During the first phase of this project, Science Panel experts reviewed information from Grand Canyon and

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conducted a habitat suitability assessment based on expert opinion, combined with an on-the-ground assessment of the Colorado River in Grand Canyon. The Panel also took into consideration the current status of populations in the upper basin, their recovery trajectory, and threats that could decrease future resiliency and the redundancy of Colorado Pikeminnow basin-wide. Based on this collective information, the Panel offers their unanimous recommendation with supporting evidence, below.

The Science Panel concluded that habitat attributes currently available in Grand Canyon could satisfy some, but perhaps not all, of the life history requirements of Colorado Pikeminnow. The Panel was in agreement that the Grand Canyon has the potential to provide habitat to support adult and sub-adult growth, foraging, migrations, and spawning, but the potential for low survival of early life history stages may create a recruitment bottleneck that reduces the species' recovery potential in Grand Canyon. As opportunists, adult fish are likely to find suitable spawning substrate that provides loose, oxygenated substrate for egg deposition and embryo and larval development. However, at the present time there is uncertainty on whether the Colorado River in Grand Canyon could provide redundant, stable nursery habitats for dispersed larvae and other young life stages. Backwaters in Grand Canyon erode and fill in quickly and are not persistent or stable when subject to daily flow fluctuations. While warm water temperatures are likely to facilitate larval and juvenile growth, redundant sources of complex, low-velocity areas to support foraging are fewer in number than in the upper basin. Further, there is concern over the productivity of western Grand Canyon and whether food resources could support larval and juvenile fish prior to their transition to full piscivory.

Regardless, the Science Panel recognized that native populations of Humpback Chub and Flannelmouth Sucker have expanded in western Grand Canyon, even though habitat quality for native fishes there may be lower relative to some other upper basin reaches that have more diverse

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nursery habitats combined with more natural flow and temperature regimes. Humpback Chub populations in western Grand Canyon have increased substantially in the last few years, exhibit a high condition factor, and reside in areas that support multiple life stages. Flannelmouth Sucker are more numerically abundant than Humpback Chub in western Grand Canyon. Combined with a lack of problematic warmwater nonnative predators, the Grand Canyon is providing conditions that faciliate native, endemic fish population success, and that may facilitate establishment of Colorado Pikeminnow.

Colorado Pikeminnow populations in the Green and upper Colorado rivers have declined precipitously in the presence of warmwater predators, and the San Juan River population persists mainly via augmentation with age-0 and age-1 fish, although there is some recent evidence of recruitment. At this rate, currently self-sustaining populations in the Green and upper Colorado rivers may need augmentation in the next decade to persist. As such, there is interest in finding river reaches that may support a self-sustaining population, or at least a population of fish that persists through stocking and would provide a natural refuge. The Panel believes that Grand Canyon may provide the best option in the species' currently unoccupied range because:

1. The thermal regime has warmed and is expected to continue to warm.
2. There are large self-sustaining populations of native species in the river.
3. Nonnative piscivorous fishes are considerably less abundant than in other rivers.
4. There is a reliable water supply that is unfragmented and not affected by river withdrawals.
5. The Colorado River in Grand Canyon represents a historically occupied river reach.
6. There is a robust multi-level monitoring and research program in place to assist with research, and if warranted, reintroduction/augmentation efforts and recovery evaluation.

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7. If all life history requirements cannot be met, there is potential to provide an additional genetic refuge with only the adult life stage present. From a recovery planning perspective, this could contribute to population redundancy, even if it is not self-sustaining.
8. There is tribal and river community support for a potential reintroduction. Tribal members from the Navajo and Hualapai tribes are supportive of this work, since there is a cultural significance of reestablishing a native species into the Colorado River ecosystem. The Hualapai Tribe is open to providing logistical support on the river and offered to provide a nearby tribal hatchery to species propagation. There is also river community support, which include boatmen that run commercial and recreational trips in the canyon.
9. Reintroduction of extirpated species is consistent with the National Park Service mission in Grand Canyon and is supported by state fish and game departments.

Science Panel recommendation

The Colorado Pikeminnow Science Panel recommends that wildlife resource managers pursue the next phase of this process, which focuses on experimentation to assess reintroduction feasibility. Experimentation will help resolve critical uncertainties to determine whether the Grand Canyon could support all life history stages of Colorado Pikeminnow in the future. To meet this goal, the Science Panel developed a preliminary list of research questions to consider during the experimentation phase (Text S2). While not exhaustive, this list provides discussion points for future research priorities that may better inform a decision on reintroduction into Grand Canyon, which would entail recovery plan inclusion, implementation of translocations and stocking, and population monitoring. The panel recognizes that many regulatory and administrative steps would need to be completed prior to experimentation, however a review and numeration of those steps is beyond the scope of this document.

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This recommendation, with its supporting information, is in agreement with the recent release of the Species Status Assessment for Colorado Pikeminnow by the U.S. Fish and Wildlife Service, which evaluated habitat and demographic features in reaches where the species was historically present. The SSA states: *"The Grand Canyon reach of the Colorado River ranked moderate for habitat factors. While peak flows and base flows are not managed in consideration of Colorado Pikeminnow needs, recent warming of water temperatures and large increases in native fish abundance, particularly in the western Grand Canyon, have improved the suitability of this river reach. This segment of river is also relatively long, and has some tributary habitat, but the upstream extent is likely cold for most life stages of Colorado Pikeminnow, and it is not clear to what extent spawning and nursery habitats might be available."*(USFWS 2020b). As such, the Science Panel recommends by consensus that Grand Canyon resource management agencies move to the experimentation phase, as guided by unresolved research questions outlined in Text S2.

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Supplemental Material

Text S1. Final version of the Colorado Pikeminnow life history survey that was distributed to Science Panel members prior to the workshop and Colorado River trip in September 2019. Results were used to reach consensus on life stage requirements related to flow, temperature, nursery habitat, and prey using information from remaining populations in the upper basin.

Text S2. Colorado Pikeminnow Science Panel members developed a list of research questions that could be addressed if natural resource managers decide to pursue experimentation within Grand Canyon. Note: This is not an exhaustive list of all of the research questions that can or should be addressed. It merely represents a list of questions the Science Panel thought would provide fodder for future discussion.

Table S1. Population estimates for adult Colorado Pikeminnow *Ptychocheilus lucius* (≥ 450 mm TL) in the Green, upper Colorado, and San Juan rivers based on mark-recapture data for the years 1992-2018. Numbers in parentheses indicate 95% confidence intervals, where available. Green River estimates are from Bestgen et al. (2018) and additional data published in Dibble et al. (2020; 2021) and include populations in the Middle and Lower Green, Yampa, and White rivers. Upper Colorado River estimates are from Osmundson and White (2014) and Elverud and Ryden (2018). The San Juan River estimate for 1995 is from Ryden (2000), while 2011-2016 estimates are from Diver and Wilson (2018) and indicate mean adult census estimates (N_c) from genetics.

Table S2. Fish monitoring data collected by the U.S. Geological Survey, Grand Canyon Monitoring and Research Center for the total number of Red Shiner *Cyprinella lutrensis* and Fathead Minnow *Pimephales promelas* captured during backwater seine hauls in the Colorado River in Grand Canyon, AZ from 2000-2018. Backwaters were sampled canyon-wide from the Lees Ferry to Diamond Creek segment of river.

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Figure S1. Plots showing the total number of Annual Thermal Units (ATUs) in the Colorado River at sites located throughout Grand Canyon using data from 1988-2020. Annual Thermal Units are a metric of cumulative thermal heating of the river, and were calculated using mean daily water temperature and model predictions from Dibble et al. (2020) following the methods of Osmundson (2011).

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Tables

Table 1. Members of the Science Panel (subject matter experts), Steering Committee (representatives from resource management agencies), and staff from the U.S. Geological Survey that were involved in the Colorado Pikeminnow Reintroduction Feasibility Study.

Science Panel	**Affiliation**	**Role**
Kevin Bestgen	Colorado State University	Colorado Pikeminnow expert; provided scientific review of habitat suitability in Grand Canyon and provided recommendation on experimentation phase
Keith Gido	Kansas State University	
Tildon Jones	U.S. Fish and Wildlife Service	
Mark McKinstry	U.S. Bureau of Reclamation	
Doug Osmundson	U.S. Fish and Wildlife Service (*Emeritus*)	
Dale Ryden	U.S. Fish and Wildlife Service	
Robert (Bob) Schelly	National Park Service	

Steering Committee	**Affiliation**	**Role**
Winkie Crook	Hualapai Tribe	Resource management agency representative who guided this process; selected Science Panel members; participated in workshop and river trip; developed list of questions to be addressed by panel; reviewed recommendation from panel
Mark Grover	Arizona Game and Fish Department (*replaced by Skyler Hedden, 2021*)	
Brian Healy	U.S. National Park Service	
Emily Omana Smith	U.S. Bureau of Reclamation	
Brandon Senger	Nevada Department of Wildlife	
Kim Yazzie	Navajo Nation	
Kirk Young	U.S. Fish and Wildlife Service	

USGS Staff	**Role**	**Role**
Kimberly Dibble	Fish Biologist, Facilitator of Project	Facilitator and lead author; synthesized information and recommendation from panel
David Ward	Research Fish Biologist	Grand Canyon native fish expert; participated in workshop and river trip
Charles Yackulic	Research Statistician	Second author and co-lead; participated in workshop and river trip

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Table 2. Summarized results from a structured Life History Survey completed by Science Panel members prior to the workshop. The 'original' metric (see Text S1) contains information on specific environmental features associated with each life history stage compiled using existing literature. The 'revised' metric (this table) reflects suggested edits to the original metric by Panel members. Each Panel member ranked the 'importance' of each metric for completing each life history stage, and then ranked their 'certainty' on this score (i.e., how certain they were of their answer to the 'importance' question). Numbers presented reflect the average score across seven panelists. Low scores indicate higher importance and certainty by panel members. The importance scale was: 1=essential, 2=preferred, 3=not essential, 4=unsure. For certainty, the scale was: 1=highly certain, 2=certain, 3=neutral, 4=uncertain, 5=highly uncertain.

Life Stage	**Flows (Peak, Base)**	**Water Temperature**	**Refuge/Nursery Habitat**	**Migration, Habitat Connectivity**	**Substrate**	**Forage Base**
Spawning Adult	Spring snowmelt runoff leading to a peak spring flow that stimulates spawning; flows sufficient to clean/ maintain spawning substrate; peak flow followed by declining summer base flows	>16°C (and increasing) in late spring to late summer	River reaches with a gradient sufficient to provide spawning riffles with cobble clean of accumulated sediments that are located upstream from low-velocity nursery habitats	Habitat connectivity sufficient to provide passage between home range and spawning bars in spring/summer	Cobble and gravel recently cleaned by spring flows	Abundant soft-rayed fishes to support energetic needs
Importance	1.7	1.3	2.0	1.8	1.3	1.5
Certainty	2.4	1.9	2.2	3.0	2.3	2.2
Egg	Riffle habitats with sufficient flow to oxygenate interstitial spaces in substrate; peak flow followed by higher base flows to facilitate hatching success	18-26°C in late spring to late summer	River reaches with a gradient sufficient to provide spawning riffles with cobble clean of accumulated sediments that are located upstream from low-velocity nursery habitats	NA	Cobble and gravel recently cleaned by spring flows	NA
Importance	1.0	1.5	2.2	NA	1.3	NA
Certainty	1.8	2.2	1.8	NA	2.0	NA
Embryo/ Larvae (substrate)	Riffle habitats with sufficient flow to oxygenate interstitial spaces in substrate; moderate peak and base flows	18-26°C to support embryo incubation, hatch, and larval survival	River reaches with a gradient sufficient to provide spawning riffles with cobble clean of accumulated sediments that are located upstream	NA	Cobble and gravel recently cleaned by spring flows	Sufficient energy reserves available via yolk sac to sustain protolarval and flexion mesolarval stages, as long as they are upstream from

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			from low-velocity nursery habitats			suitable nursery habitats
Importance	1.1	1.6	2.3	NA	1.3	1.5
Certainty	2.0	2.0	2.0	NA	2.0	1.5
Larvae (dispersed)	Low to zero velocity backwater habitats; summer flows sufficient to provide complete inundation of nursery habitats and transport larvae to them	18-30+°C to support larval growth; lack of 'cold shock' conditions (e.g., <5°C difference between tributary and mainstem)	Low elevation gradients with low-velocity channel habitats	Long stretches of habitat that allow for larval entrainment in backwater areas as they somewhat passively drift downstream	Low-velocity areas with high levels of shoreline complexity	Abundant diatoms, algae, and first instars of aquatic invertebrates such as chironomids
Importance	1.3	1.6	2.3	2.1	2.3	1.1
Certainty	2.0	2.3	2.4	2.4	2.9	1.6
Juvenile (age-0)	Low-velocity areas with steady, moderate flows that inundate nursery areas but do not overtop them; peak flows to maintain/create these habitats and maintain channel complexity; peak flows to reduce reproduction by non-native predators; steady mainstem flows	18-30°C to support juvenile growth and maximize energy reservoirs prior to winter	Low elevation gradients with low-velocity channel habitats	Mosaic of connected or closely located nursery habitats to allow for dispersion and use of multiple backwater habitats	Low-velocity areas with high levels of shoreline complexity	Larger aquatic invertebrates and algae available, including cladocerans, copepods, and chironomid larvae
Importance	1.9	2.0	2.3	2.0	2.1	1.3
Certainty	2.3	1.9	2.6	2.0	2.3	1.7
Juvenile (age 1-2)	Low-velocity areas with steady, moderate flows that inundate nursery areas but do not overtop them; peak flows to reduce reproduction by non-native predators	18-30°C to support juvenile growth	Low elevation gradients with low-velocity channel habitats	Mosaic of connected or closely located nursery habitats to allow for dispersion and use of multiple backwater habitats	Low-velocity areas with high levels of shoreline complexity	Large aquatic invertebrates and small soft-rayed fishes to support mixed diet
Importance	2.6	1.9	2.3	2.3	2.4	1.4
Certainty	2.4	2.4	2.7	2.5	2.7	1.6
Sub-adult and Adult	Variable and high peak spring flows to redistribute substrate, flush fine sediment, and prevent vegetation encroachment and channel narrowing	18-30°C to support sub-adult and adult growth, or Annual Thermal Units >47-50	Access to deep pools, runs, and eddies for foraging and refuge	Sufficient habitat available to forage and spawn that supports an adult population	Cobble, gravel, and sandy substrate	Abundant soft-rayed fishes to support fully piscivorous adult diet
Importance	1.9	1.7	1.7	1.6	2.4	1.1
Certainty	2.4	2.6	2.3	2.1	2.9	1.4

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Figure Legends

Figure 1. Map of the Colorado River Basin in western North America, delineated into six geographic subbasins where Colorado Pikeminnow populations currently (in red) or historically (in blue) existed. The three remaining populations of Colorado Pikeminnow (shaded blue) are located in the Green, Colorado, and San Juan river subbasins. The species is extirated from the Lower Colorado River Mainstem and Gila River subbasins (shaded gray). Colorado Pikeminnow are also extirpated from the focal area of this study, the Colorado River in Grand Canyon (shaded yellow). Inset map shows Colorado River basin states in western North America (Wyoming, Colorado, Utah, New Mexico, Arizona, Nevada, California).

Figure 2. Map of the Colorado River in Grand Canyon and its major tributaries, with boundaries for Glen Canyon National Recreation Area, Grand Canyon National Park, Lake Mead National Recreation Area, and Havasupai, Hualapai, and Navajo Nation lands. Inset map shows study area states of Arizona, Utah, and Nevada (red box).

Figure 3. Colorado River flows in the pre-dam period (1950-1955), during construction (1956-1963), and post-dam (1963-2020) downstream from Glen Canyon Dam, Arizona. This includes the pre- Environmental Impact Statement (EIS) time period (1963-1995), the time period governed by the 1996 EIS and Record of Decision (ROD; 1995-2015), and current operations under the Long-Term Experimental and Management Plan EIS and ROD (2017-present).

Figure 4. a) Daily representative thermal profiles at depth in Lake Powell, Arizona in July during low, intermediate, and high storage conditions leading to warm, cool, and cold releases. The horizontal gray line at 75 meters deep is penstock depth relative to the dam crest (i.e., “0”). b) Pre- and post-dam release temperatures from Lake Powell in July. In the pre-dam era (1949-1956), mean July river temperatures were consistently warm (25.3 ± 1.6°C SD), whereas in the post-dam era (1965-2015), mean July release temperatures were highly influenced by reservoir storage.

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Figure 5. Predicted mean monthly water temperatures from Glen Canyon Dam to Pearce Ferry, Arizona, from May-October using conditions present from 2010-2020 and the water temperature model developed by Dibble et al. (2021). Colors are associated with water temperatures from 8-20°C, with temperatures nearest the dam cool in May and warming to peak temperatures in October, whereas water temperatures reach their peak in mid-summer and decline in fall.

Figure 6. Calculated number of Annual Thermal Units (ATU) in the Colorado River from 1988-2020 for four locations in western Grand Canyon, Arizona (National Canyon, rkm 293; at Diamond Creek, rkm 388; at Spencer Creek, rkm 422; modeled at Pearce Ferry, rkm 476). The horizontal line at 50 ATU represents the estimated threshold above which the thermal regime is suitable for adult growth. Eastern Grand Canyon locations are shown in Figure S1.

Figure 7. Maximum daily water temperature and flow in Havasu and Kanab creeks (tributaries to the Colorado River in Grand Canyon, Arizona) from 1990-2021. Warm water temperatures provide a thermal regime conducive to Colorado Pikeminnow growth, while flash floods are stochastic events that bring new sources of gravel and cobble to the river as potential spawning habitat.

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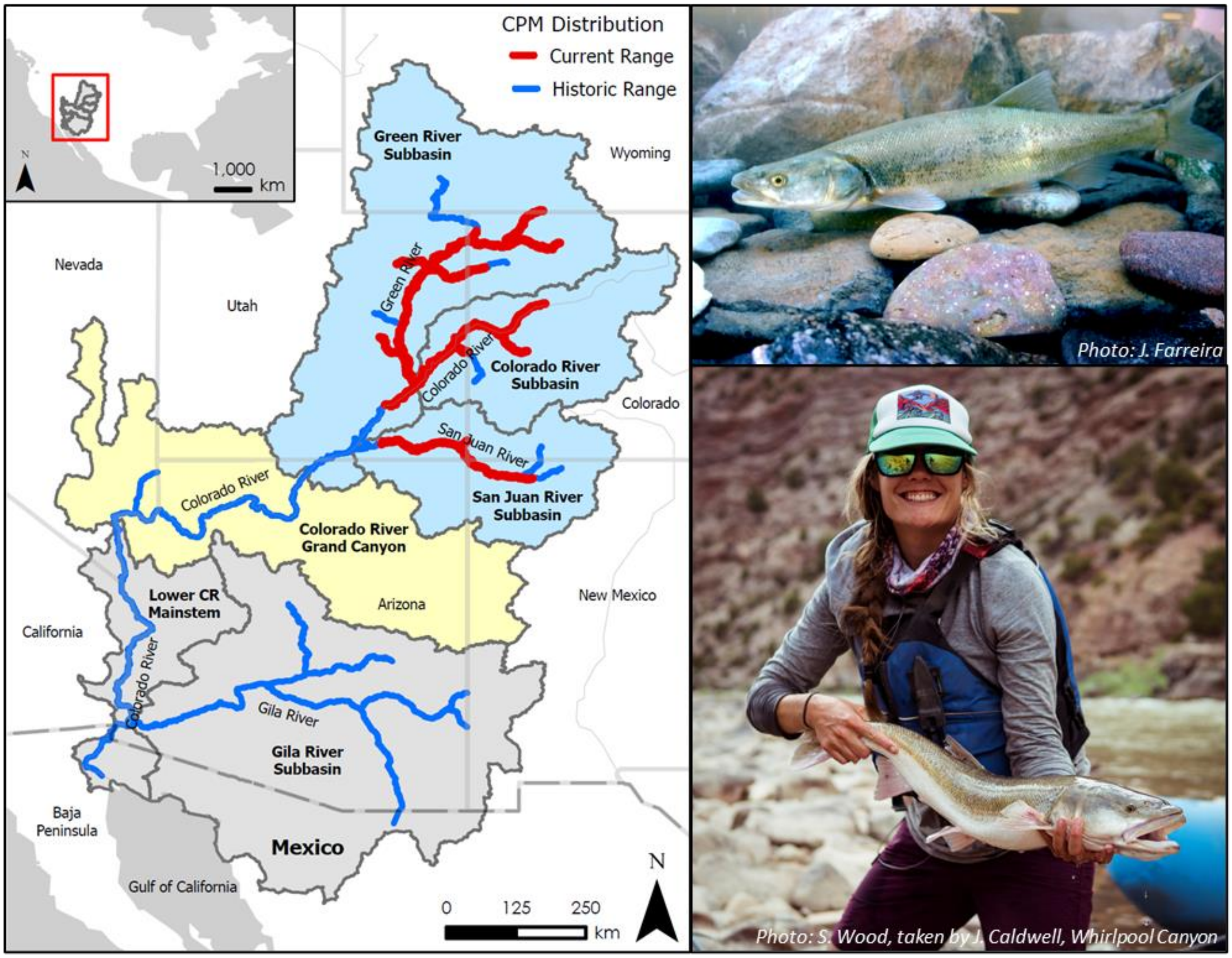
Figure 1



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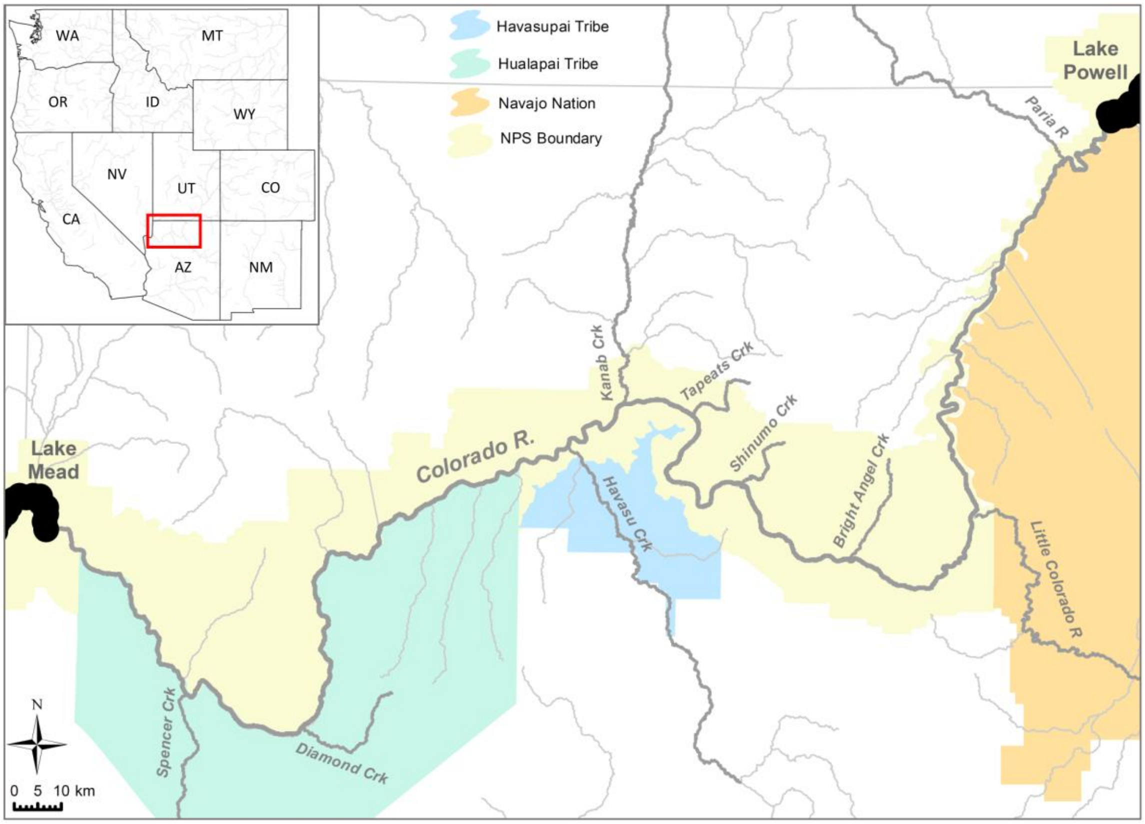

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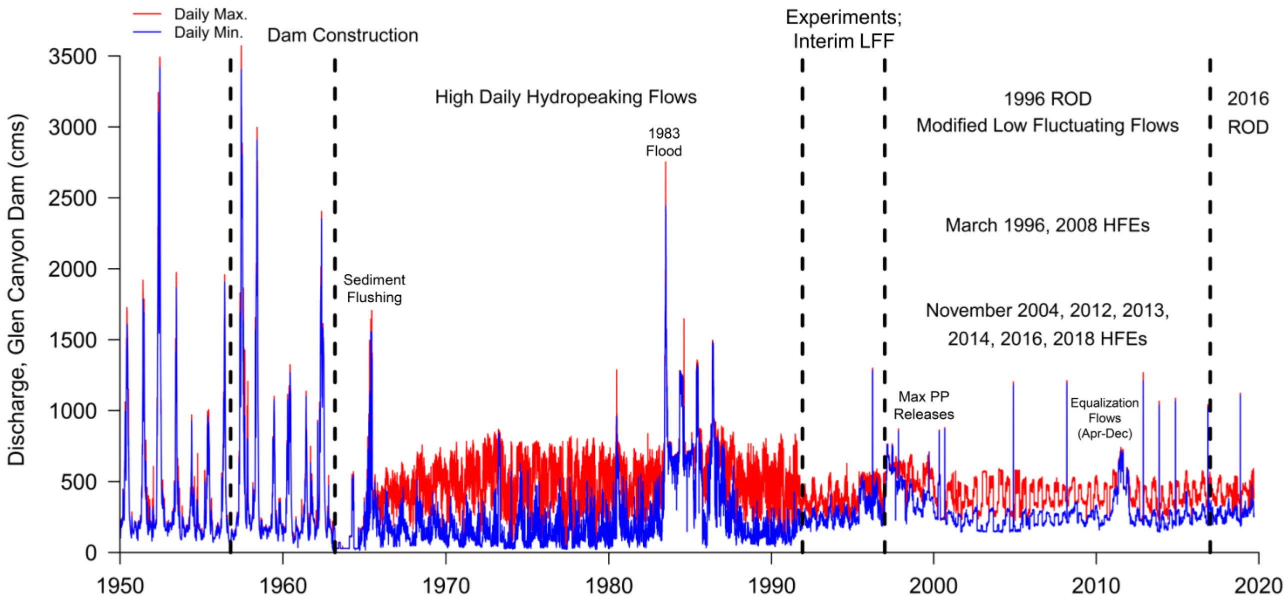

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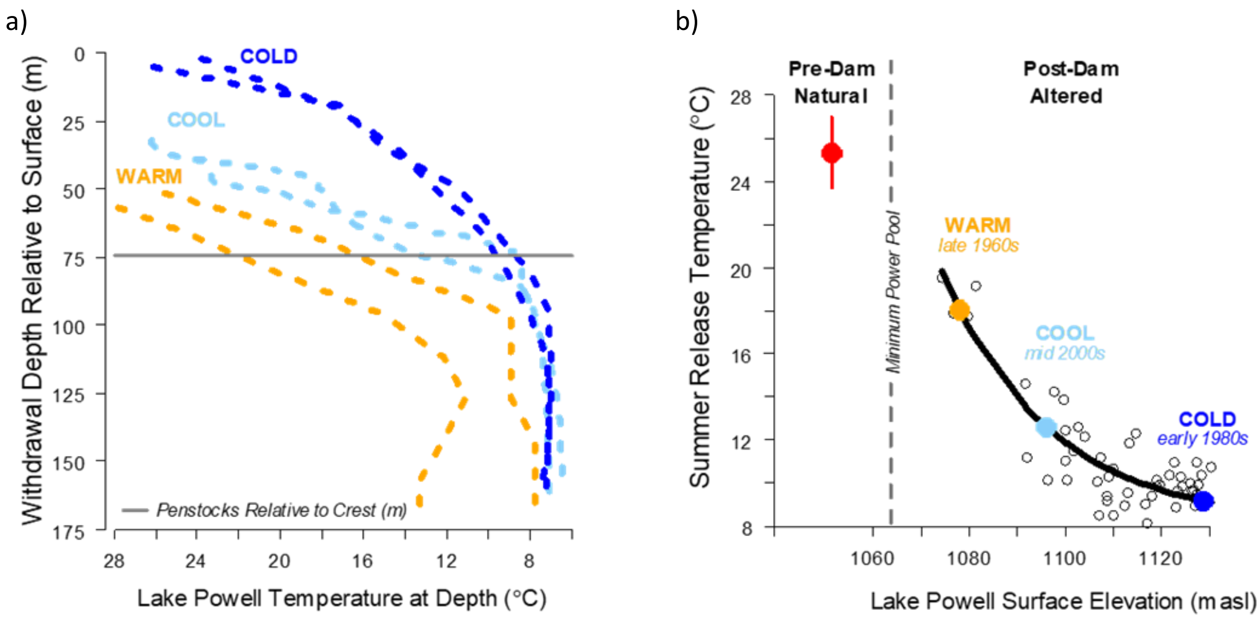

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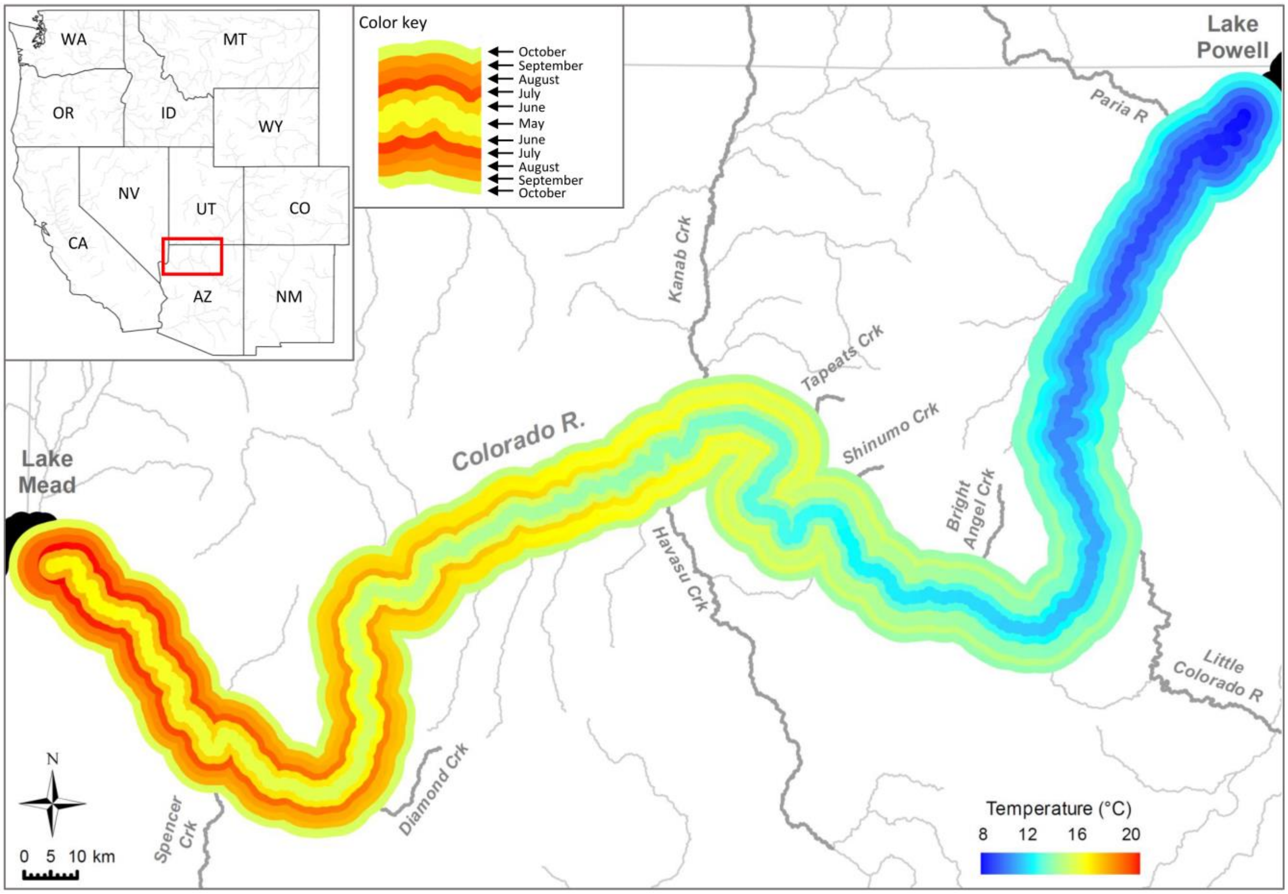

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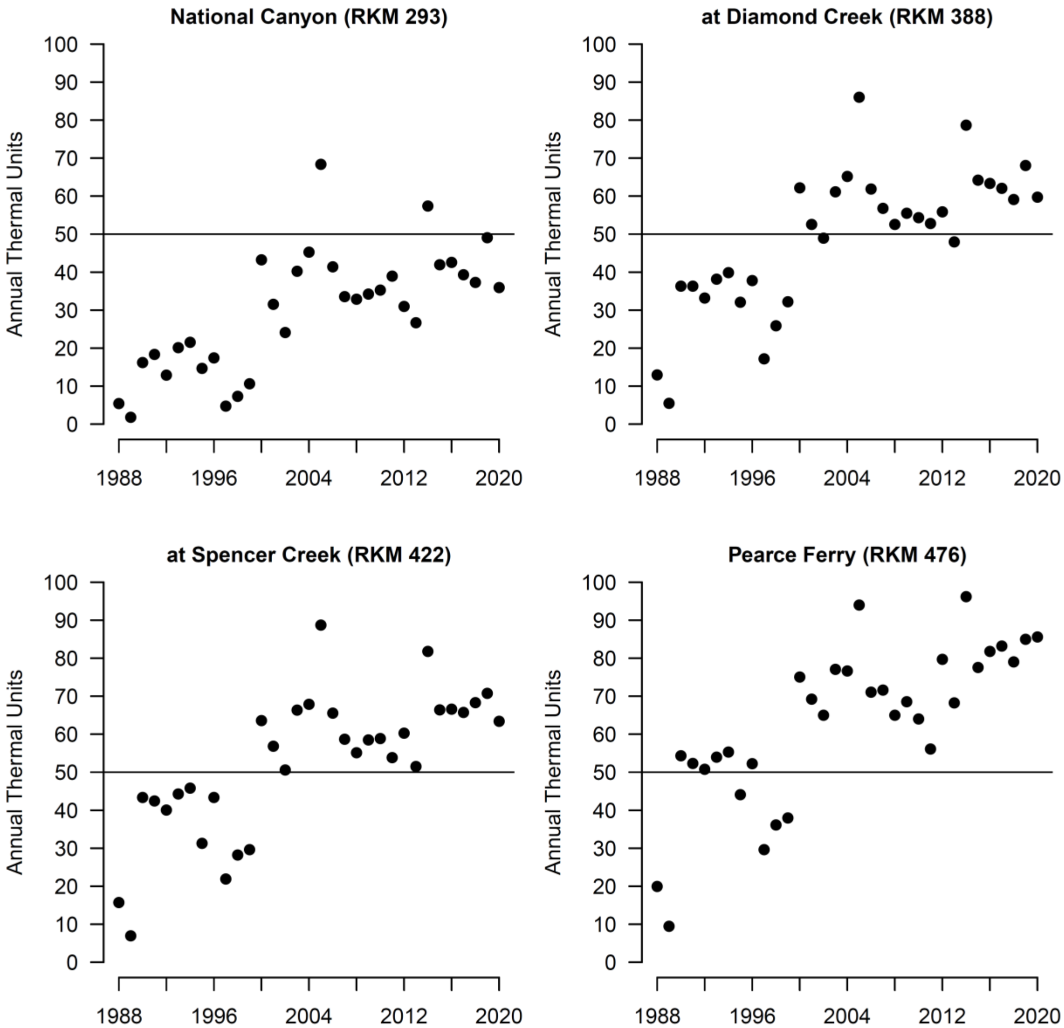

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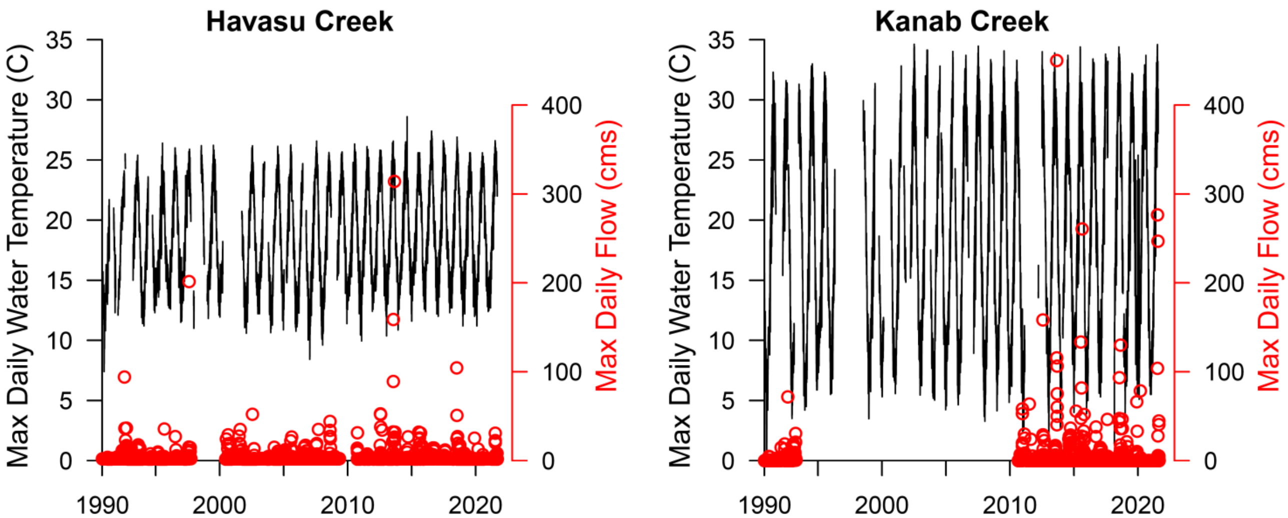

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