JOURNAL OF THE AMERICAN WATER RESOURCES ASSOCIATION

AMERICAN WATER RESOURCES ASSOCIATION

Water Storage Decisions and Consumptive Use May Constrain Ecosystem Management under Severe Sustained Drought

Lindsey A. Bruckerhoff, Kevin Wheeler, Kimberly L. Dibble, Bryce A. Mihalevich, Bethany T. Neilson, Jian Wang, Charles B. Yackulic, and John C. Schmidt

Research Impact Statement: Limiting consumptive water use in the Colorado River basin will likely provide the most flexibility for ecosystem management under continued drought.

ABSTRACT: Drought has impacted the Colorado River basin for the past 20 years and is predicted to continue. In response, decisions about how much water should be stored in large reservoirs and how much water can be consumptively used will be necessary. These decisions have the potential to limit riverine ecosystem management options through the effect water-supply decisions have on reservoir elevations. We used projected hydrology and river temperatures to compare the outcome of combinations of water storage scenarios and consumptive use limits on metrics associated with ecosystem management of the Colorado River in Grand Canyon. Ecosystem management metrics included the ability to implement designer flows, temperature suitability for fishes, and fragmentation. We compared current water management operations to prioritizing storage in either Lake Mead or Lake Powell combined with three levels of consumptive use. Projected reservoir levels limited environmental flow delivery and increased fragmentation regardless of where water was stored if consumptive use was not limited. Warmer river temperatures associated with low reservoir levels are likely, creating suitable conditions for non-native species of concern, such as smallmouth bass. Water storage decisions provided variability and management flexibility, but water storage was less important when less water was available, highlighting the importance of keeping water in the system to provide flexibility for achieving ecosystem goals.

(KEYWORDS: river temperature; fish; flow regime; designer flows; reservoir management; climate change; fragmentation; Colorado River; water policy.)

INTRODUCTION

The Colorado River is one of the most extensively managed rivers in the world. The entire natural flow is consumed and the river does not reach the sea in most years. Lake Mead and Lake Powell are responsible for ~80% of the watershed's total reservoir capacity. These two reservoirs contribute almost equally to a combined capacity of 50 million acre-feet (maf) that is more than three times the river's annual natural flow, resulting in the largest degree of control of any major river system in North America (Hirsch et al. 1990). Decisions about water storage in Lake Mead and Lake Powell dominate discussion about how to manage the regional water supply, particularly in light of ongoing drought in the region. Water is consumptively used by irrigated agriculture, municipalities, and industry or is diverted

Paper No. JAWR-21-0061-P of the *Journal of the American Water Resources Association* (JAWR). Received March 31, 2021; accepted May 13, 2022. **Discussions are open until six months from issue publication**.

U.S. Geological Survey (Bruckerhoff), Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University Stillwater, Oklahoma, USA; Environmental Change Institute and Oxford Martin School (Wheeler), University of Oxford Oxford, UK; U.S. Geological Survey (Dibble, Yackulic), Southwest Biological Science Center, Grand Canyon Monitoring and Research Center Flagstaff, Arizona, USA; Utah Water Research Laboratory (Mihalevich, Neilson, Wang), Department of Civil and Environmental Engineering, Utah State University Logan, Utah, USA; and Department of Watershed Sciences (Schmidt), Utah State University Logan, Utah, USA (Correspondence to Bruckerhoff: lindsey.bruckerhoff@okstate.edu).

Citation: Bruckerhoff, L.A., K. Wheeler, K.L. Dibble, B.A. Mihalevich, B.T. Neilson, J. Wang, C.B. Yackulic, and J.C. Schmidt. 2022. "Water Storage Decisions and Consumptive Use May Constrain Ecosystem Management under Severe Sustained Drought." *JAWRA Journal of the American Water Resources Association* n/a–n/a. https://doi.org/10.1111/1752-1688.13020.

out of the watershed to surrounding metropolitan and agricultural areas.

The extensive storage capacity in the Colorado River basin was designed to allow water users to store watershed runoff during wet periods and withstand multiyear droughts, however, the ongoing drought and climate change are leading to declining average watershed runoff that will likely require renegotiation of agreements concerning existing uses. The natural flow of the Colorado River at Lees Ferry between 2000 and 2021 was 12.3 maf/year (Reclamation 2021a), a 14% decrease from the 21st Century average annual natural flow. This water supply was 17% less than the average annual consumptive use during this same period and this imbalance between use and runoff has drained the watershed's reservoirs from nearly full in 2000 to 30% of capacity in the spring of 2022. Recent declines in runoff have been linked to warmer air temperatures, increased evapotranspiration, and drier soils (Udall and Overpeck 2017; Xiao et al. 2018), trends that are expected to continue under global climate change. As a result, the natural flow of the Colorado River is projected to further decline by 30% (relative to mean flows from 1906 to 1999) by mid-21st Century (Reynolds et al. 2015; Udall and Overpeck 2017; Udall 2021). Preparing for a dry future may not only require reconsideration of how the water supply is allocated but is also likely to involve reconsideration of the rules concerning where water is stored and how water is released from reservoirs. The policies concerning how much, where, and when water is stored and consumptively used by Mexico, seven U.S. states, and many Native American tribes are described by an evolving array of interstate compacts, Supreme Court decisions, laws, administrative policies, and a bi-national treaty collectively called the *Law of the River* (MacDonnell et al. 1995; Verburg 2011). Renegotiation of one element of the *Law of the River*, the 2007 *Interim Guidelines for Lower Basin Shortages and Coordinated Operations of Lake Powell and Lake Mead* (hereafter, *Interim Guidelines*), is presently underway (Reclamation 2021b).

Declining runoff not only forces reconsideration of issues associated with water supply management but also provides a need and opportunity to reconsider how reservoir management might be used to mitigate or rehabilitate undesired riverine ecosystem conditions associated with the reservoirs. The physical existence of dams and reservoirs, the diversion of streamflow, and reservoir management disrupt many ecosystem processes (Petts 1987; Nilsson et al. 2005; Schmidt et al. in press). Some disruptions can be mitigated by reducing the magnitude of diversions or by changing the rules that concern water storage and reservoir releases (hereafter, reservoir operations). Here, we focus on how consumptive uses and water storage decisions affect a limited set of ecosystem metrics that are expected to be closely linked to these decisions. We focus on metrics linked to Lake Powell, Lake Mead, and the Grand Canyon segment of the Colorado River found between these two large reservoirs.

Specifically, we estimate how river temperature, temperature suitability for various native and nonnative fish species, the presence of putative fish barriers, and the ability to implement specific flow regimes will be affected by different policy alternatives concerning consumptive water use and reservoir operations. We evaluated river temperature, because temperature exerts a critical control on ecosystem processes that in turn affects native and non-native fish species and their interactions (Dibble et al. 2021). We also evaluated the effect of the alternatives on creating or maintaining barriers to fish movement at the inflows to Lake Powell and Lake Mead, because barriers affect native fish movement and interactions between native and non-native fish. Additionally, we evaluated whether low reservoir storage in Lake Powell might restrict the ability to implement *designer flows*, which are short-term reservoir releases that do not affect the total annual volume of reservoir releases. Designer flows are aimed at achieving specific ecological goals and include controlled floods (Webb et al. 1999; Melis 2011) and macroinvertebrate production flows (Kennedy et al. 2016; Poff and Schmidt 2016) released from Lake Powell to mitigate some undesirable ecosystem conditions in Grand Canyon.

We focused on the Colorado River ecosystem in the Grand Canyon, and we primarily considered the implications of reduced consumptive water use upstream from Lake Powell. We considered policies that address the challenge of matching consumptive water use to declining supply. Current reservoir operations result in storing water in approximately equal volumes between Lake Mead and Lake Powell. We assessed ecosystem changes assuming this current operation, as well as alternative management policies that prioritize water storage either in Lake Mead or Lake Powell. When developing alternative management paradigms, we focused on combinations of operational strategies that represent extreme endpoints of water supply options that could inform discussion among stakeholders (Bair et al. 2019; Wheeler et al. 2021). We did not estimate the likelihood of adoption of any of these policies. By quantifying relationships among consumptive use, water storage, and ecosystem drivers, we sought to inform conversations about how the Colorado River can be managed under sustained drought while serving ecosystem and human needs. Understanding how ecosystem drivers respond to changes in consumptive water use and reservoir operations may help guide future management of the Colorado River.

Study Area

Three ecosystem attributes are of great interest in the Lake Powell/Grand Canyon/Lake Mead segment of the Colorado River (Figure 1). First, federally listed fish species are of interest in both reservoirs and in the Grand Canyon. The Colorado River and its tributaries in Grand Canyon are home to the largest populations of the endemic humpback chub (*Gila cypha*), which was recently down-listed from federally endangered to threatened (USFWS 2021). Populations of other native fishes of conservation concern also use this segment of the basin, including endemic razorback suckers (*Xyrauchen texanus*) that move between reservoirs and the rivers that drain into them provided barriers are not present (Van Haverbeke et al. 2017; Kegerries et al. 2020). Bare sand bars are a second attribute of interest to managers in the Grand Canyon because they provide recreational value as campsites and as an integral part of the natural river landscape. Third, the tailwater ecosystem downstream from Lake Powell is home to a rainbow trout fishery of regional importance.

METHODS

Modeling Colorado River Reservoir Operations

The Colorado River Simulation System (CRSS; for full description see Alexander et al. 2013; Wheeler et al. 2019) is developed by the Bureau of Reclamation (hereafter Reclamation) and implemented in the RiverWare software (Zagona et al. 2001). It simulates

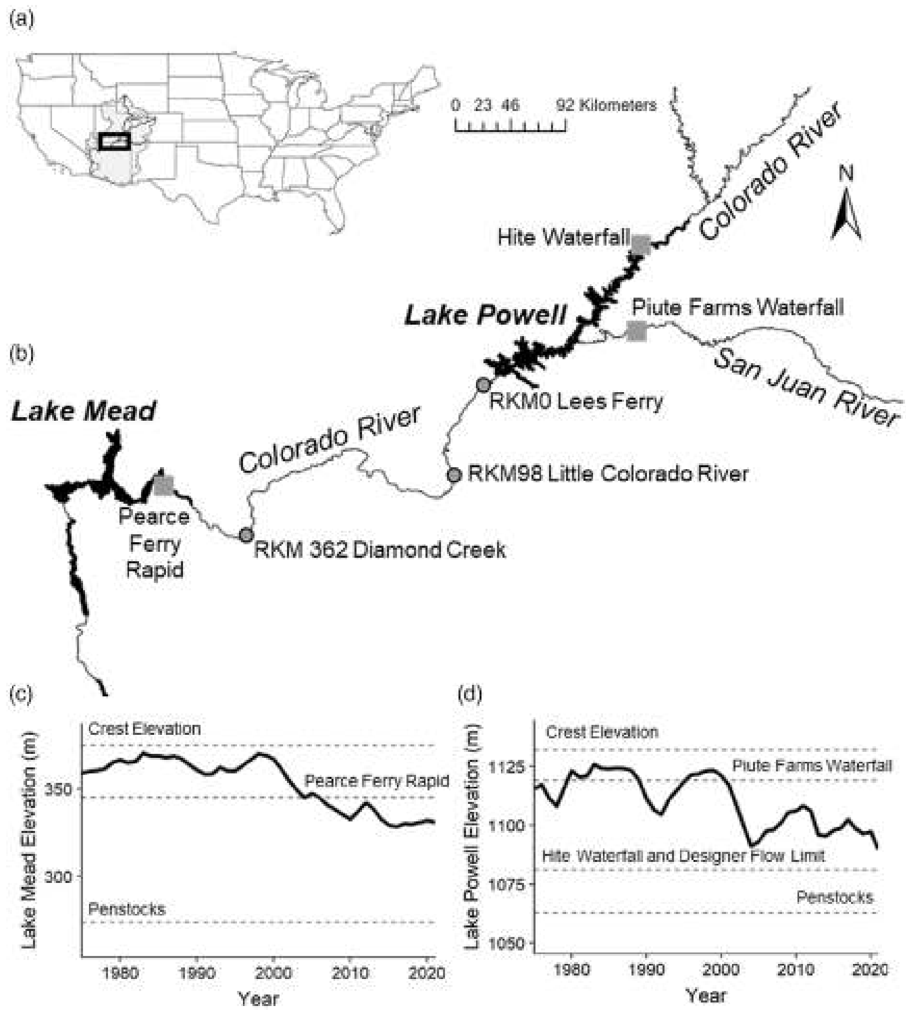

FIGURE 1. We quantified ecosystem responses to changes in storage decisions and consumptive use in the Colorado River Basin, USA (a). We focused on temperature of the Colorado River between Lake Powell and Lake Mead reservoirs at three locations (b, gray circles) and barriers upstream of Lake Mead and Lake Powell (b, gray squares). Elevations of Lake Mead (c) and Lake Powell (d) are important drivers of downstream river temperature, the presence of barriers upstream of reservoirs, and the ability to release designer flows.

how water is managed throughout the basin based on the *Law of the River*. Reclamation's implementation of the CRSS codifies current water management policies, and the model is used to inform policy and management decisions concerning water storage, reservoir releases, and water available for use in response to scenarios representing projections of future hydrologic conditions. We refer to the rules embedded in the April 2020 version of the CRSS model as the "baseline" operations. Rules and assumptions in this baseline configuration were modified to evaluate the implications of the alternative policies that we considered (Wheeler et al. 2018).

Current Management of the Colorado River: Baseline

The *Law of the River* ensures water is available for consumptive use in both the Upper Basin and the Lower Basin. Consumptive uses in the Upper Basin averaged 3.66 maf/year between 2001 and 2019 (Figure 2). During this period, losses due to evaporation from federal and state reservoirs in the Upper Basin were estimated by Reclamation to be 0.71 maf/year. Annual use in the Upper Basin has changed little since 1988 and varied between 81% and 113% of the post-2001 average (Reclamation 2020; Wang and Schmidt 2020; Wheeler et al. 2021). In contrast, consumptive water use in the Lower Basin averaged 7.39 and 1.55 maf/year was delivered to Mexico between 2001 and 2019. The Upper and Lower Basin states disagree about whether the *Law of the River* guarantees the right of the Upper Basin to increase its consumptive uses to approximately match that of the Lower Basin. The rate at which Upper Basin uses might increase in the future has been estimated by the Upper Colorado River Commission (UCRC) and incorporated into the CRSS model. For the baseline scenario, we used projections of increasing future use developed in 2007 (UCRC 2007). Revised estimates of future Upper Basin use (UCRC 2016) were recently incorporated into CRSS by Reclamation, but this update was not available at the time we conducted our modeling.

In addition to evaluating different patterns of consumptive use, we explored alternatives related to prioritizing storage in either Lake Mead or Lake Powell. Since 2008, coordinated operations of the two reservoirs have followed a policy described in the *Interim Guidelines* that generally seeks to balance storage between the two reservoirs by varying releases from Lake Powell based on the amount of water in the two reservoirs. Releases from Lake Powell are determined by the relative elevation of the water surface of each reservoir. The amount of water in Lake Mead is used to trigger reductions in water use in the Lower Basin; the reductions in water deliveries in the Lower Basin are called *shortages*. Lower Basin shortages were implemented for the first time during the 2022 water year (Reclamation 2021c).

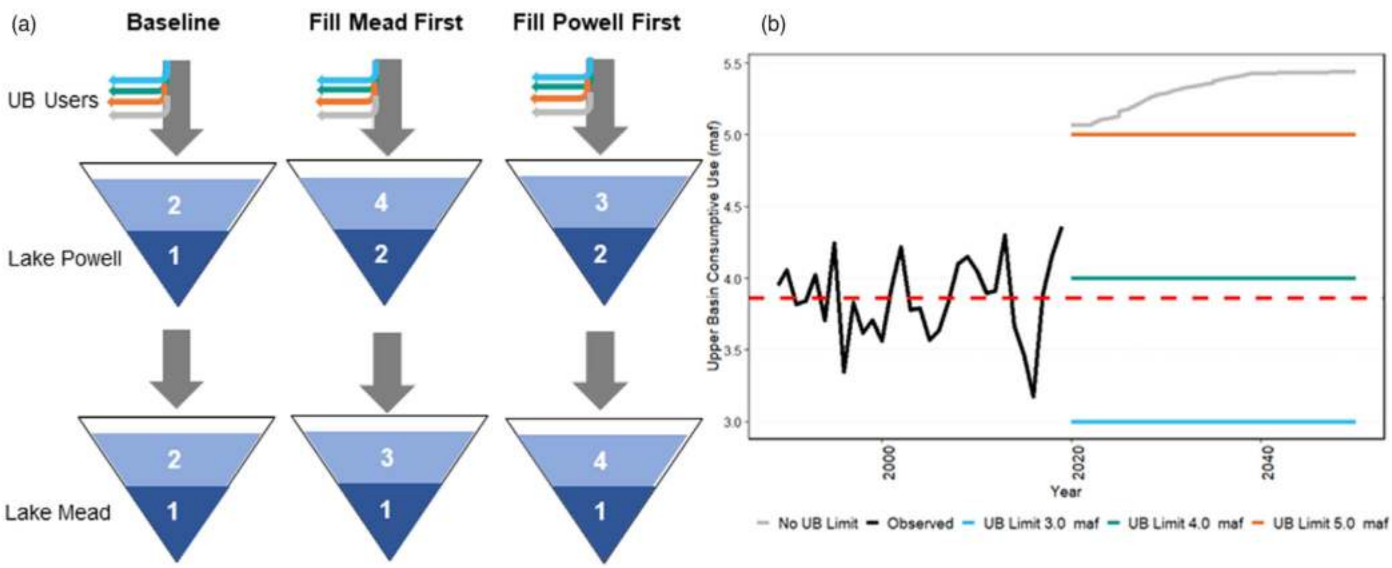

FIGURE 2. Alternative management paradigms included different combinations of Upper Basin (UB) demands and prioritizing storage in Lake Mead or Lake Powell reservoirs. Numbers in Lake Powell and Lake Mead reservoir diagrams represent priority zones and the order of reservoir filling (a). Historic annual UB demands (2001–2019) and long-term average (red dashed) provide context on use patterns. Future UB demands either followed the UCRC 2007 demand schedule (b, "No UB Limit", gray) or were capped at 3.0 (blue), 4.0 (green), or 5.0 (orange) million acre-feet per year (maf, b).

Alternative Management Paradigms

Here, we briefly describe the implementation, benefits, and risks of each policy or management alternative that we considered.

Limits on Present or Future Upper Basin Consumptive Use. The Upper Basin states use less water than the Lower Basin states, but the Upper Basin aspires to increase its future use. Proposed increases in use in the Upper Basin are controversial and would require reductions in use in the Lower Basin or in Mexico if total watershed use is to match the declining future supply. We considered three scenarios that included (1) a reduction in Upper Basin use to 3.0 maf/year, (2) a slight increase in use to 4.0 maf/year, and (3) a modest increase in Upper Basin use to 5.0 maf/year (Figure 2). We recognized that future water conservation efforts would likely include reduction of Lower Basin consumptive uses, but we did not simultaneously adjust those demands for simplicity of analysis. We did, however, apply the Lower Basin shortage tiers defined in the *Interim Guidelines* as part of the baseline (Figure 3).

Prioritize Water Storage in Lake Mead. This alternative was inspired by the Fill Mead First proposal (Kellett 2013) analyzed by Schmidt et al. (2016). This alternative (hereafter, Fill Mead First) to reservoir balancing would prioritize water storage in Lake Mead, and water storage in Lake Powell would only occur if Lake Mead were relatively full. To simulate this policy, we defined a reservoir operation policy wherein priority zones, or different reservoir elevations, were established for Lake Powell and Lake Mead (Figure 2a). Priority zone 1 (305 m above mean sea level, masl), would fill Lake Mead first and water would be stored in Lake Powell up to 1,067 masl if and when the elevation of Lake Mead was higher than priority Zone 1 (Figure 2a). Additional storage in Lake Powell would occur in priority Zone 4 only if priority Zone 3 in Lake Mead was filled (366 masl; Figure 2a). The priority zones were defined based on the minimum elevations needed to generate hydropower from both dams.

Potential advantages of this alternative include reducing the ratio of reservoir surface area to storage volume by concentrating storage in one reservoir, reducing the potential for seepage losses from Lake Powell, increasing riverine habitat in the upstream parts of Lake Powell, and exposing scenic geological features inundated by Lake Powell. Despite these potential benefits, there are significant uncertainties in quantifying the reduction in evaporative and seepage losses associated with this alternative (Schmidt et al. 2016). Additionally, implementation of this alternative is challenged by the potential loss of power generation from Glen Canyon Dam and infrastructure constraints on releasing water.

Prioritize Water Storage in Lake Powell. This alternative (hereafter Fill Powell First) was developed as the antithesis to the Fill Mead First alternative and was derived from a standard maxim of water-supply engineering—retain the maximum volume of water in upstream reservoirs and allow downstream reservoirs to fluctuate to meet immediate needs of downstream water users (Lund and Guzman 1999; Sheer 2014). In our implementation, Lake Powell would be filled to its maximum capacity, filling priority Zones 2 and 3 (Figure 2a) while Lake Mead would be maintained at an elevation of 305 masl to sustain power generation (priority Zone 1). Only when Lake Powell was full would additional water be stored in Lake Mead in priority Zone 4 (Figure 2a). Potential advantages of Fill Powell First include reduced evaporative loss by concentrating storage in one facility, increasing riverine habitat upstream of Lake Mead, providing increased flexibility in power generation through both reservoirs and maintaining conditions more similar to existing reservoir operating rules. Potential disadvantages include increased seepage into the permeable bedrock that surrounds Lake Powell (Schmidt et al. 2016) and continued inundation of geological features in Lake Powell of interest to some stakeholder groups.

Future Hydrologic Scenarios

We evaluated the policy and management alternatives under a future hydrologic scenario that assumed the ongoing Millennium Drought (Salehabadi et al. 2020) persists. This scenario assumed that magnitude of natural streamflow that has existed since 2000 continues, but the sequence in which the annual runoff occurred differs from what has occurred. This scenario was developed using randomized sequences of runoff based on the observed runoff between 2000 and 2018 (Salehabadi et al. 2020; Wheeler et al. 2021; Salehabadi et al., this issue) as input into the CRSS model. We randomly selected 50 (of 100) traces to use as input into the CRSS. This hydrologic scenario represents a plausible future under a warming atmosphere and declining runoff in the Colorado River watershed.

Ecosystem Metrics

We defined metrics relevant to management of Colorado River resources (Table 1), especially

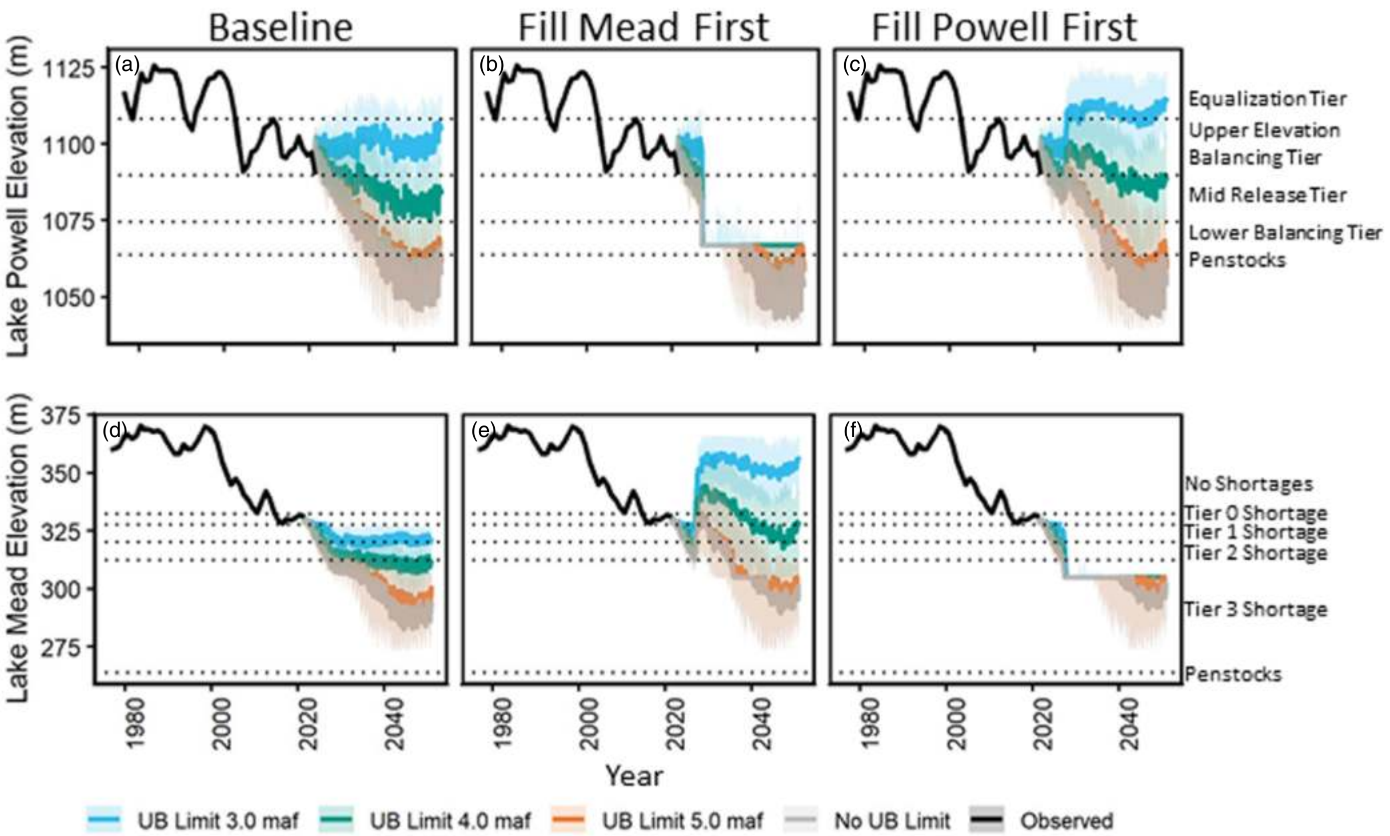

FIGURE 3. Lake Powell (top) and Lake Mead (bottom) historic (black) and projected elevations assuming that future inflows are the same as those of the Millennium Drought and future consumptive water use in the UB is 3.0 maf/year (blue), 4.0 maf/year (green), 5.0 maf/year (tan), or increases as projected by the UCRC (2007) (gray). Three reservoir operations policies are considered: baseline policy that seeks to equalize storage contents in the two reservoirs, Fill Mead First (FMF), and Fill Powell First (FPF). For reference, dotted lines in the upper panels, represent different thresholds for equalization releases from Lake Powell (top), shortage tiers for the Lower Basin defined by Lake Mead elevations (bottom) or the elevations of the penstocks in each reservoir.

management of native and non-native fishes (Reclamation and NPS 2016; USFWS 2018, 2020).

Index of Designer Flow Implementation. Designer flows are a category of reservoir releases whose intent is to achieve desired changes in downstream ecosystem conditions through changes to flow regimes at hourly to monthly time scales. Previously implemented designer flows include controlled floods (Webb et al. 1999; Melis 2011) and macroinvertebrate production flows wherein dam releases are steady on weekends from May through August (Kennedy et al. 2016; Poff and Schmidt 2016). Controlled floods mitigate the loss of sand bars caused by trapping of fine sediment in Lake Powell. Macroinvertebrate production flows are designed to enhance reproduction of macroinvertebates that serve as food for the Grand Canyon fish community.

In the Colorado River, designer flows do not disrupt the annual delivery of water from the Upper Basin to the Lower Basin (Melis et al. 2015; Yarnell et al. 2015) as the short periods of atypically high or low stream flow are balanced by low or high releases in other days or months. Nevertheless, designer flows were not implemented in 2021 when Lake Powell was at an elevation of 1,079 masl, because reservoir managers would not allow for a few months of lower elevations in Lake Powell and were concerned about losses to hydropower production. To predict whether future designer flows would occur, we assigned a threshold of 1,082 masl, which is ~1.5 m less than the lowest reservoir elevation in which designer flows have been implemented in the past. We recognize there are other factors in addition to elevation that also limit implementation of designer flows. We calculated the probability that Lake Powell elevations might drop below this threshold for each year in the simulation. Probabilities were calculated using the proportion of hydrologic traces in which predicted reservoir elevations fell below the threshold in April each year. We chose April because some designer flows focus on spring and summer flow releases.

TABLE 1. Responses of metrics related to flow regime, river temperature, and fragmentation (drivers) to water storage and consumptive use alternatives were assessed due to the ecological importance and management relevance of these metrics in the Colorado River.

Driver	Ecological importance	Metric	Management relevance
Flow regime	"Master variable" driving riverine processes[1] and community structure[2]	Designer flow flexibility	Incorporated into adaptive management programs, can implement new designer flows as new flow-ecology relationships determined
River temperature	Species have different thermal tolerances for survival, growth, and reproduction[3] Influences productivity and resource availability[4] Strongly influenced by reservoir elevations[5]	Temperature suitability for native and non-native fishes	First step at predicting how community structure might change in response to changes in temperature,[6] including the establishment of new warm-water non-native species
		Upper temperature threshold to maintain trout fishery	Trout fishery is economically and recreationally important[7] Non-native trout impact native fish populations[8]
Fragmentation	Barriers block reproductive migrations of some endangered large-bodied, mainstem Colorado River fishes[9] May block establishment of non-native species, potentially benefitting native species[10]	Probability of presence of known barriers	Aid in planning mitigation of impacts of barriers on native fish movement[10] Determine need to find other solutions to keeping non-native fish out of upstream river segments

[1]Poff and Ward (1989); Jowett and Duncan (1990); Poff et al. (1997); Sofi et al. (2020).
[2]Bunn and Arthington (2002); Poff and Zimmerman (2010).
[3]Robinson and Childs (2001); Bestgen (2008).
[4]Hall et al. (2015); Rüegg et al. (2021).
[5]Mihalevich et al. (2020); Dibble et al. (2021).
[6]Dibble et al. (2021).
[7]Reclamation and NPS (2016); Bair et al. (2019).
[8]Yard et al. (2011); Yackulic et al. (2018).
[9]Minckley and Deacon (1991); Irving and Modde (2000); Cathcart et al. (2019).
[10]Cathcart et al. (2018); Kegerries et al. (2020); Pennock et al. (2020).

Thermal Suitability for Fishes. Temperature is a fundamental driver determining what species can persist in different habitats because species have different thermal thresholds for survival, growth, and reproduction (Robinson and Childs 2001; Bestgen 2008). Modern river temperatures in much of the Colorado River system are closely linked to the temperatures of water released from reservoirs (Mihalevich et al. 2020; Dibble et al. 2021). The penstocks at Glen Canyon Dam are typically deep below the water surface when Lake Powell is full, so the water released downstream is cool when reservoir elevations are high. After Lake Powell reached full capacity, the temperatures at Lees Ferry averaged 10.3°C (range: 7.0°C to 16.5°C), much less than the pre-dam annual average water temperature of 14°C (range: 0°C to 27°C; Vernieu et al. 2005; Wright et al. 2009). The cooling of warmer summer river temperatures in the Grand Canyon contributed to the proliferation of cool-water non-native trout that are of recreational value in the tailwater below Lake Powell and declines in native fish abundance throughout the system (Clarkson and Childs 2000). However, over the last 20 years, releases from Glen Canyon Dam have warmed as Lake Powell levels have dropped (USGS 2021). This is because as reservoir levels drop, the water pulled through the penstocks is from warmer water higher in the water column, leading to warmer release temperatures. These warming water temperatures in Grand Canyon have contributed to dramatic increases in native fish species, including humpback chub (Van Haverbeke et al. 2017; Kegerries et al. 2020). If the thermal regime warms further, however, the Grand Canyon may become suitable for warm-water nonnatives, like smallmouth bass *Micropterus dolomieu*, that have likely contributed to the decline of native fish in other parts of the basin (Bestgen 2018; Bestgen et al. 2018).

We focused on thermal suitability for three native species (humpback chub, Colorado pikeminnow *Ptychocheilus lucius*, and razorback sucker) and three warm-water non-native species (red shiner *Cyprinella lutrensis*, channel catfish *Ictalurus punctatus*, and smallmouth bass). Humpback chub are currently common in the Grand Canyon, and razorback sucker are infrequently observed in the western Grand

Canyon and in Lake Mead (Van Haverbeke et al. 2017; Kegerries et al. 2020). Although Colorado pikeminnow was extirpated from Grand Canyon, their reintroduction has been considered by management agencies. The three non-native species are rare in the Grand Canyon (Dibble et al. 2021), but colonization of these species is of concern due to their presence in Lake Mead (Rosen et al. 2012) and in Lake Powell (Pennock and Gido 2021) and the high likelihood of negative interactions with native species (Johnson et al. 2008; Bestgen et al. 2018).

We simulated temperatures in Lake Powell and the Colorado River to predict future thermal suitability for the local fish species. Using CRSS to predict reservoir releases from Lake Powell, we predicted reservoir release temperatures using Reclamation's Lake Powell CE-QUAL-W2 model (Williams 2007) for each of the alternatives that we considered. Downstream river temperatures within the Grand Canyon were simulated using a process-based river temperature model (Mihalevich et al. 2020). The details about the reservoir and river temperature models, CRSS linkages to these models, and assumptions about future climate and water temperature inputs are described in the Supporting Information. The thermal suitability of river temperatures was analyzed using subdaily predictions at three locations in the Grand Canyon (Figure 1): at Lees Ferry (river kilometer, RKM 0), immediately upstream from the confluence of the Colorado River and the Little Colorado River (RKM 98), and upstream from the confluence with Diamond Creek (RKM 362). We chose these three locations, because they represent a gradient of temperature change from Glen Canyon Dam to Lake Mead and are ecologically significant for native and non-native fishes. For instance, the tailwater trout fishery is located between the dam and Lees Ferry, the Little Colorado River is an important tributary for humpback chub populations (Yackulic et al. 2014), and Diamond Creek is in western Grand Canyon where there have been recent increases in the abundance of native fishes (Van Haverbeke et al. 2017; Kegerries et al. 2020; Van Haverbeke et al. 2017).

We used the model developed by Dibble et al. (2021) to predict the probability that temperatures would be suitable for several native and non-native fishes under baseline and alternative scenarios. This model was developed based on laboratory-derived information about water temperatures that are suitable for growth, which was used to calculate the number of days in a year that is thermally suitable for different species. The number of thermally suitable days was then related to species abundance and distributional data to develop a predictive model of the probability a species is common in different parts of the watershed. See Supporting Information and Dibble et al. (2021) for a full description of the model; data associated with model development can be found at Dibble et al. (2020).

The temperature suitability model assumed temperature is the predominant limiting factor to the focal species, and our analysis did not consider the many other factors limiting species distributions, such as habitat, flow regime, biotic interactions, or dispersal limitation. This metric served as an index of whether temperature conditions in the Grand Canyon will be suitable for native and non-native fishes in the future, regardless of the current distribution and abundance of these species in Grand Canyon. We identified the median probabilities calculated from this model across 50 hydrologic traces.

Upper-Temperature Threshold to Maintain Trout Fishery. The tailwater rainbow trout fishery in Grand Canyon is an economic and recreational resource (Bair et al. 2019). The tailwater ecosystem in Grand Canyon is characterized by a depauperate food base and rainbow trout that live in it are especially vulnerable to increasing water temperature (Dodrill et al. 2016). In recent years, brown trout populations have increased in the tailwater—an increase that may have been facilitated by warming water temperature (Runge et al. 2018). While brown trout appear to be growing well under current conditions (J. Korman, personal communication, 2021) and may tolerate a slight increase in water temperature better than rainbow trout, they have similar physiologic limits to rainbow trout. Rainbow trout can survive acute (short-term) exposure of temperatures up to 29°C (Rodgers and Griffiths 1983; Currie et al. 1998), but chronic exposure to high temperatures have negative effects on survival and growth (Nelitz et al. 2007) and limits their distribution (Mandeville et al. 2019). Meta-analysis of standardized laboratory studies suggests the maximum weekly average temperature (MWAT) tolerated by rainbow and brown trout are 19.4°C and 19.3°C, respectively, (Walters et al. 2018; Mandeville et al. 2019) and survival of rainbow trout eggs decreases significantly when MWAT values are above 17°C (Nelitz et al. 2007).

We defined a threshold of average summer (June through September) river temperatures greater than 20°C as not suitable to maintain either a rainbow or brown trout fishery, based on reported MWATs. We suspect that as temperatures approach this threshold brown trout may persist longer but will eventually decline. We considered this a conservative threshold because we used mean monthly temperatures rather than weekly temperatures. This threshold represents a large deviation from observed mean summer temperatures at Lees Ferry since Lake Powell filled (max observed mean daily summer temperature = 13.7°C, median = 10.5°C). We calculated the probability that summer mean temperature exceeded 20°C. Probabilities represented the proportion of traces each year in which temperatures exceeded 20°C.

Probability of Presence of Known Barriers. Semi-natural barriers such as waterfalls or unnavigable rapids can form upstream from drawn-down reservoirs if inflowing rivers do not incise into the delta sediments in the same place as the pre-dam channel. These barriers form when reservoir levels drop and no longer inundate the river channel (Figure 1). These barriers have the potential to prevent desirable movement of native fish species between the reservoir and inflowing rivers (Cathcart et al. 2018; Pennock et al. 2020) or prevent undesirable movement of non-native warm-water fishes from reservoirs upstream into reaches inhabited by native fish (Clarkson and Marsh 2010). However, the tradeoffs between adverse impacts of fragmentation and the potential benefits of blocking non-native fish are not well understood (Fausch et al. 2009).

Several barriers impact the fishes of the Colorado River. On the San Juan arm of Lake Powell, Piute Falls now prevents the upstream movement of large numbers of native razorback sucker into the San Juan River (Cathcart et al. 2018; Pennock et al. 2020). In the Colorado River upstream from Lake Mead, the river flows over a bedrock ledge and forms Pearce Ferry Rapid that likely blocks the upstream movement of non-native warm-water reservoir fishes into the western Grand Canyon, potentially benefiting native fish (Kegerries et al. 2020). No feature like this currently exists in the Colorado River arm of Lake Powell, but a similar barrier (Hite waterfall) is predicted to develop if Lake Powell continues to drop (Returning Rapids of Cataract Canyon 2021). We tracked the presence of these three semi-natural barriers that presently exist or might exist based on reservoir elevations in which each barrier would no longer be inundated by the downstream reservoir (Figure 1). These inundation thresholds were 1,082 and 1,120 m at Lake Powell (Hite and Piute Farms waterfalls, respectively) and 456 m at Lake Mead (Pearce Ferry Rapid). We calculated the probability of each of these barriers would be present each year under the different alternatives using the proportion of traces in which the elevations were below the thresholds each year.

RESULTS

Results obtained from the CRSS model suggest the magnitude of consumptive water use is the most significant determinant of the amount of water stored in Lake Powell, assuming watershed runoff in the next 20 years is similar to that of the Millennium Drought. Reservoir operations, whether Fill Mead First or Fill Powell First, will play a secondary role. Assuming no change in Lower Basin consumptive use, Lake Powell elevation will continue to decline if Upper Basin consumptive use follows the 2007 UCRC demand schedule or if use is increased from 3.65 maf/year (on average) to 4.0 or 5.0 maf/year, regardless of how water storage is distributed between Lake Powell and Lake Mead (Figure 3a–3c). The elevation of Lake Powell is predicted to be above the penstocks (so hydropower generation can continue) only if Upper Basin consumptive use is limited to 3.0 or 4.0 maf/year and Lake Powell is filled first. Lake Mead elevations were predicted to fall below current shortage tier thresholds (i.e., defined in the *Interim Guidelines*, Figure 3d–3f) in most scenarios, even when water was preferentially stored in Lake Mead, highlighting the predominant role of basin-wide consumptive water use relative to water storage decisions in driving reservoir levels.

Flexibility in Implementing Designer Flows

Only when consumptive water use in the Upper Basin is less than 4.0 maf/year will there be sufficient reservoir water storage to allow the implementation of designer flows in the future. Water storage will be greatest in Lake Powell if Upper Basin consumptive use is limited to less than 4.0 maf/year and if the current rules of equalizing water storage in Lake Mead and Lake Powell remain or if Lake Powell is identified as the primary water storage facility. Implementation of the Fill Mead First strategy of emphasizing water storage in Lake Mead would also greatly limit the ability to implement designer flows. The probability that water storage in Lake Powell will be too low to implement designer flows is more than 75% in each year after 2030 if the Fill Mead First alternative were implemented, even if Upper Basin consumptive water use is 3.0 maf/year (Figure 4b; Table 2). After 2040, it is unlikely designer flows could be implemented under any water storage management alternative if Upper Basin consumptive use is 5.0 maf/year or follows the 2007 UCRC demand schedule (Figure 4). However, if Upper Basin consumptive use is 3.0 maf/year and reservoir storage is managed under the baseline policy or implementation of the Fill Powell First alternative, there is an increased likelihood that designer flows could still be implemented (Table 2), because the probability that Lake Powell elevations drop below the threshold was less than 25% in our model runs (Figure 4). Under the

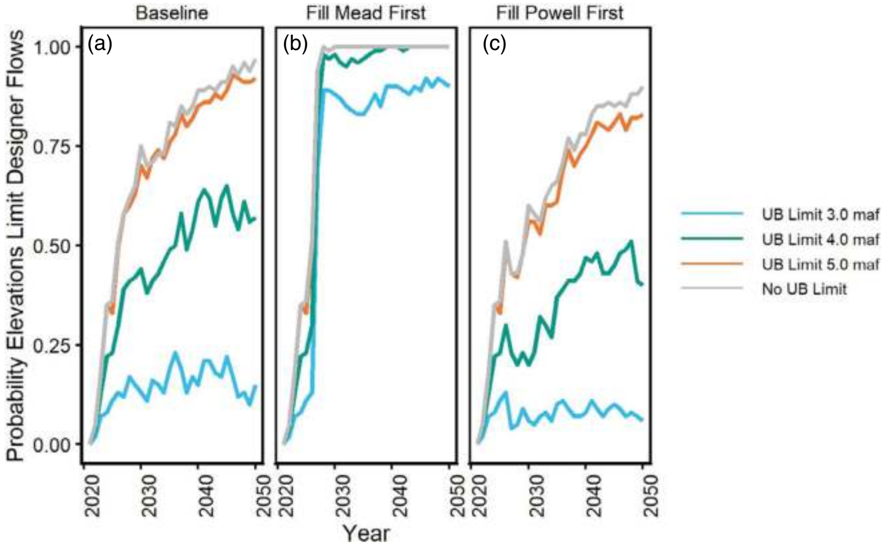

FIGURE 4. The probability that Lake Powell reservoir elevations will fall below 1,082 m, a threshold in which designer flows would likely cease to be implemented, varied across storage and use alternatives. Probabilities were calculated as the number of hydrologic traces in which reservoir elevations fell below the threshold out of all 50 traces and were calculated across combinations of baseline conditions (a), the FMF (b), and the FPF (c) alternatives crossed with different UB limit scenarios.

TABLE 2. Combinations of storage and consumptive use alternatives that provided the best and worst outcomes for different management goals.

Management goal	Top alternatives	Worst alternatives
Designer flow flexibility	Baseline, 3.0 maf UB Limit FPF, 3.0 maf UB Limit	FMF, No UB Limit FMF, 5.0 maf UB Limit
Increase native fish temperature suitability	FMF, all use limits	FPF, 3.0 maf UB Limit
Decrease non-native fish temperature suitability	FPF, 3.0 maf UB Limit Baseline, 3.0 maf UB Limit	FMF, all use limits
Maintain trout fishery	Baseline, 3.0 maf UB Limit FPF, 3.0 maf UB Limit	FMF, all use limits
Support movement of native fish above Lake Powell	Baseline, 3.0 maf UB Limit FPF, 3.0 maf UB Limit	FMF, all use limits
Block upstream movement of non-native fish from Lake Mead	Baseline, all use limits	FMF, 3.0 UB Limit FMF, 4.0 UB Limit

Fill Powell First alternative and if Upper Basin consumptive use is capped at 4.0 maf/year, there is at least a 50% probability of being able to implement designer flows each year from 2020 to 2050.

Thermal Suitability for Fishes

Because warmer water is released when Lake Powell is relatively empty, any policy regarding consumptive water use or reservoir operations that leads to less water in Lake Powell will yield river temperatures more suitable for growth of native fish. These policies include larger Upper Basin consumptive uses or reservoir operations that shift storage to Lake Mead (Figure 5). Less desirable conditions for native fish growth will occur if the Fill Powell First alternative is implemented or if Upper Basin water use is greatly reduced (Figure 5; Table 2). Temperature suitability was greater than 75% for all native species for all storage scenarios if there is no limit to Upper Basin water development, or if Upper Basin use is capped at 5.0 maf/year limit (Figure 5), but was less than 25% for all species in the upstream reaches of Grand Canyon if 3.0 maf/year limits were paired with the baseline or Fill Powell First policies (Figure 5a–5f).

However, suitable river temperatures for native fish come at a price, because warm-water non-native fishes would also benefit from warmer river temperatures associated with low Lake Powell levels. Under the Fill Powell First and baseline alternatives with 3.0 and 4.0 maf/year limits, predicted river temperatures were less suitable for non-native, warm-water species relative to native species in river segments closer to Glen Canyon Dam (Figure 6). For example, 4.0 maf limits on Upper Basin consumptive use combined with Fill Powell First and baseline alternatives produced river temperatures that were less suitable

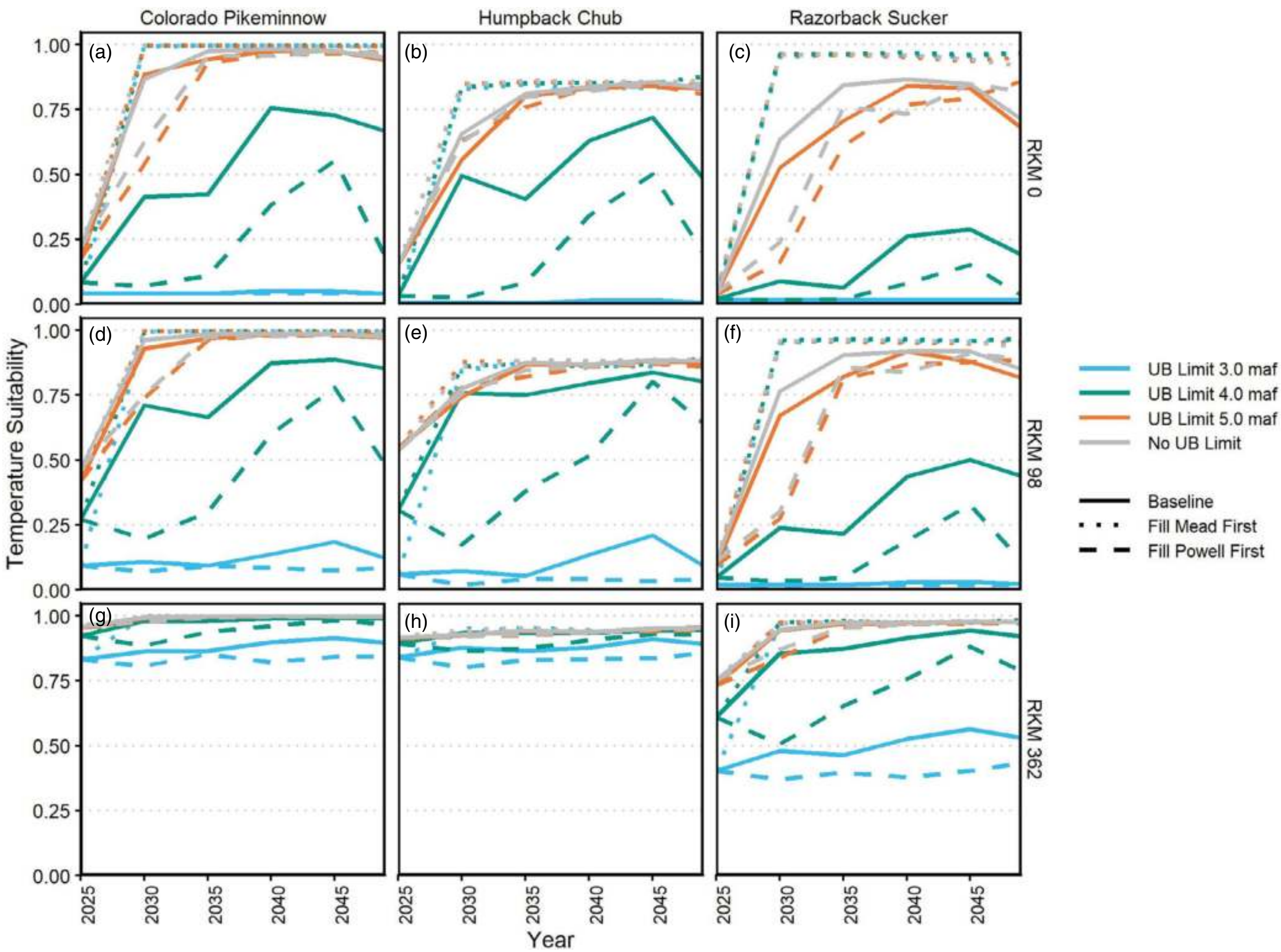

FIGURE 5. Temperature suitability for several native (Colorado pikeminnow, humpback chub, and razorback sucker) fish was measured using the model developed by Dibble et al. 2021 predicting the probability of these species would be common or rare as a function of river temperature. Probabilities were calculated using predicted river temperatures at three locations along the Colorado River, including Lees Ferry (river kilometer, RKM 0), at the confluence with the Little Colorado River (RKM 98), and at the confluence with Diamond Creek (RKM 362). Future management alternatives included combinations of baseline conditions, FMF, and FPF crossed with different UB limit scenarios. Lines represent medians of predicted probabilities of each species being common across hydrologic traces.

(approximately 25% or less) for all three non-native species (Figure 6a–6c), while suitability for humpback chub and Colorado pikeminnow was greater than 25% by 2040 (Figure 5a, 5b) at RKM0. Under all Fill Mead First and consumptive use alternatives, all locations in Grand Canyon will be thermally suitable for all warm-water non-native species by 2030 (Figure 6a–6i).

Reservoir releases warmer than 20°C threaten the non-native recreational trout (brown trout and rainbow trout), and these species would benefit from policies that keep Lake Powell levels higher (Table 2). The probability of mean summer river temperatures (June through September) will exceed 20°C increased over time for most alternatives (Figure 7). The Fill Mead First alternative had the highest annual probabilities (>50%) of temperatures being greater than 20°C across all river locations, even at Lees Ferry (RKM 0). Probabilities of river temperatures exceeding 20°C remained less than 25% for the baseline scenario for all locations and Fill Powell First alternative at RKM 0 and RKM 98 with Upper Basin limits of 3.0 maf and below 50% for the baseline and Fill Powell first alternatives at all locations with 4.0 maf Upper Basin use limits. No Upper Basin limits or a 5.0 maf/year cap under baseline and Fill Powell First alternatives led to an increasing probability (75%) of exceeding the thermal tolerance for trout near RKM 362 (Figure 7g, 7i).

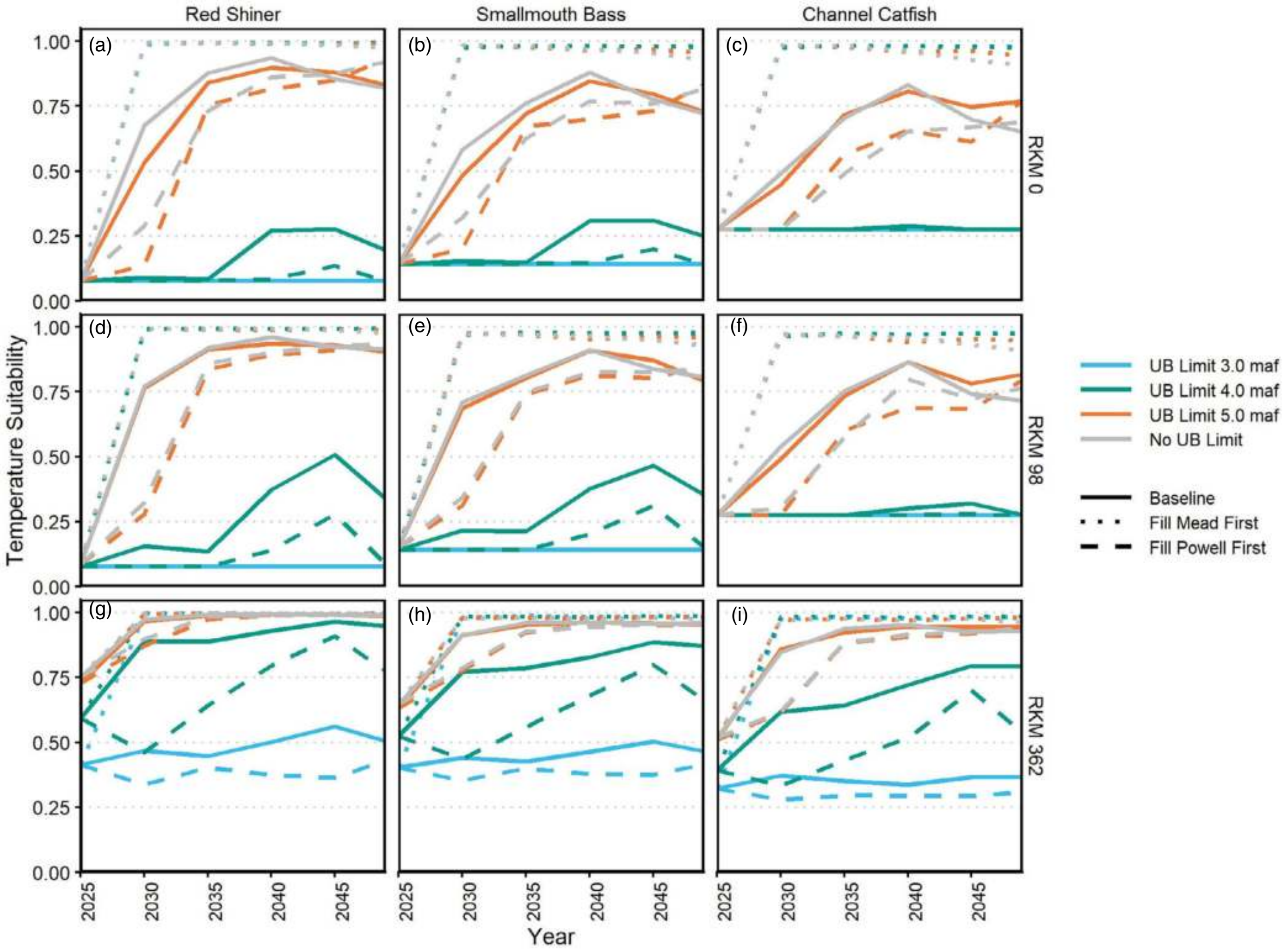

FIGURE 6. Temperature suitability for several non-native (red shiner, smallmouth bass, and channel catfish) fish was measured using the model developed by Dibble et al. (2021) predicting the probability of these species would be common or rare as a function of river temperature. Probabilities were calculated using predicted river temperatures at three locations along the Colorado River, including Lees Ferry (RKM 0), at the confluence with the Little Colorado River (RKM 98), and at the confluence with Diamond Creek (RKM 362). Future management alternatives included combinations of baseline conditions, FMF, and FPF crossed with different UB limit scenarios. Lines represent medians of predicted probabilities of each species being common across hydrologic traces.

Probability of Emergence and Persistence of Barriers

Low reservoir elevation in Lake Powell causes the emergence and persistence of barriers at the inflow points as has already occurred in the San Juan arm at Piute Falls and is likely to occur in the Colorado River arm near Hite. Low reservoir elevation in Lake Mead has led to the formation of a barrier at the inflow of the Colorado River at Pearce Ferry Rapids. Thus, the existence of these barriers in Lake Powell is most probable if the Fill Mead First alternative (Figure 8b, 8e; Table 2) were implemented. Piute Farms waterfall had more than a 75% annual probability of being present across all combinations of alternatives except Fill Powell First combined with 3.0 maf/year limits on Upper Basin use (Figure 8f). The probability of the Hite waterfall on the Colorado River arm of Lake Powell would be present was highly variable across limits on consumptive use, especially in the baseline and Fill Powell First storage alternatives (Figure 8a, 8c). Pearce Ferry Rapid also had more than a 75% annual probability of being present across all combinations of baseline and Fill Powell First alternatives (Figure 8g, 8i; Table 2). Annual probabilities of the presence of Pearce Ferry Rapid declined between 2025 and 2030 across all consumption scenarios, but then increased when water levels are predicted to decline, especially with no limits on Upper Basin use or only 5.0 maf limits (Figure 8h). The probability that Pearce Ferry Rapid

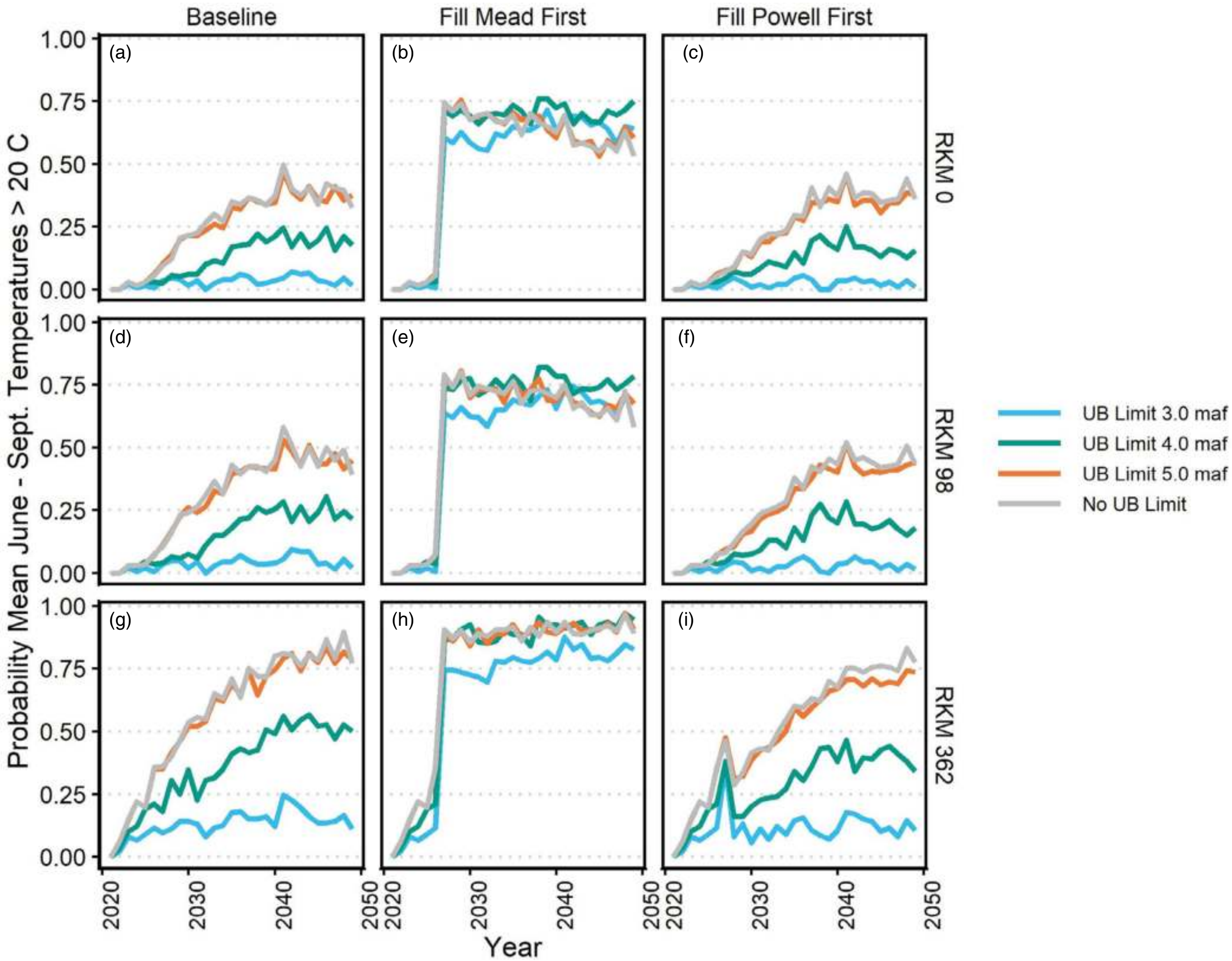

FIGURE 7. The probability of mean summer (June through September) temperatures would exceed 20°C, the predicted sustained upper tolerance for brown and rainbow trout, increased over time at three locations along the Colorado River downstream from Glen Canyon Dam. Probabilities were calculated as the number of hydrologic traces in which reservoir elevations fell below the threshold out of all 50 traces and were calculated across combinations baseline conditions, the FMF policy, and the FPF policy crossed with different UB limit scenarios.

remains a barrier in western Grand Canyon was lowest in the Fill Mead First and 3.0 maf/year consumptive use alternative (Figure 8h).

DISCUSSION

If watershed runoff during the next 20 years maintains a similar statistical distribution as watershed runoff between 2000 and 2020 *and* if Upper Basin consumptive water use increases to 5 maf/year or more *and* if Lower Basin consumptive water use continues at its current level, there is a very high likelihood that Lake Powell and Lake Mead will be very low most of the time. It is unlikely designer flows can be implemented under such conditions of sustained low reservoir levels. Unless the facilities by which reservoir water is released are reengineered, releases from Lake Powell will be consistently warm in summer, and there may be significant shifts in the Colorado River fish community in the Grand Canyon. Lake Powell and Lake Mead will be fragmented from the inflowing Colorado River by waterfalls and unnavigable rapids unless the inflow rivers are relocated to their predam channels. The only way these expected environmental changes can be avoided is by significantly reducing consumptive water use in the entire basin

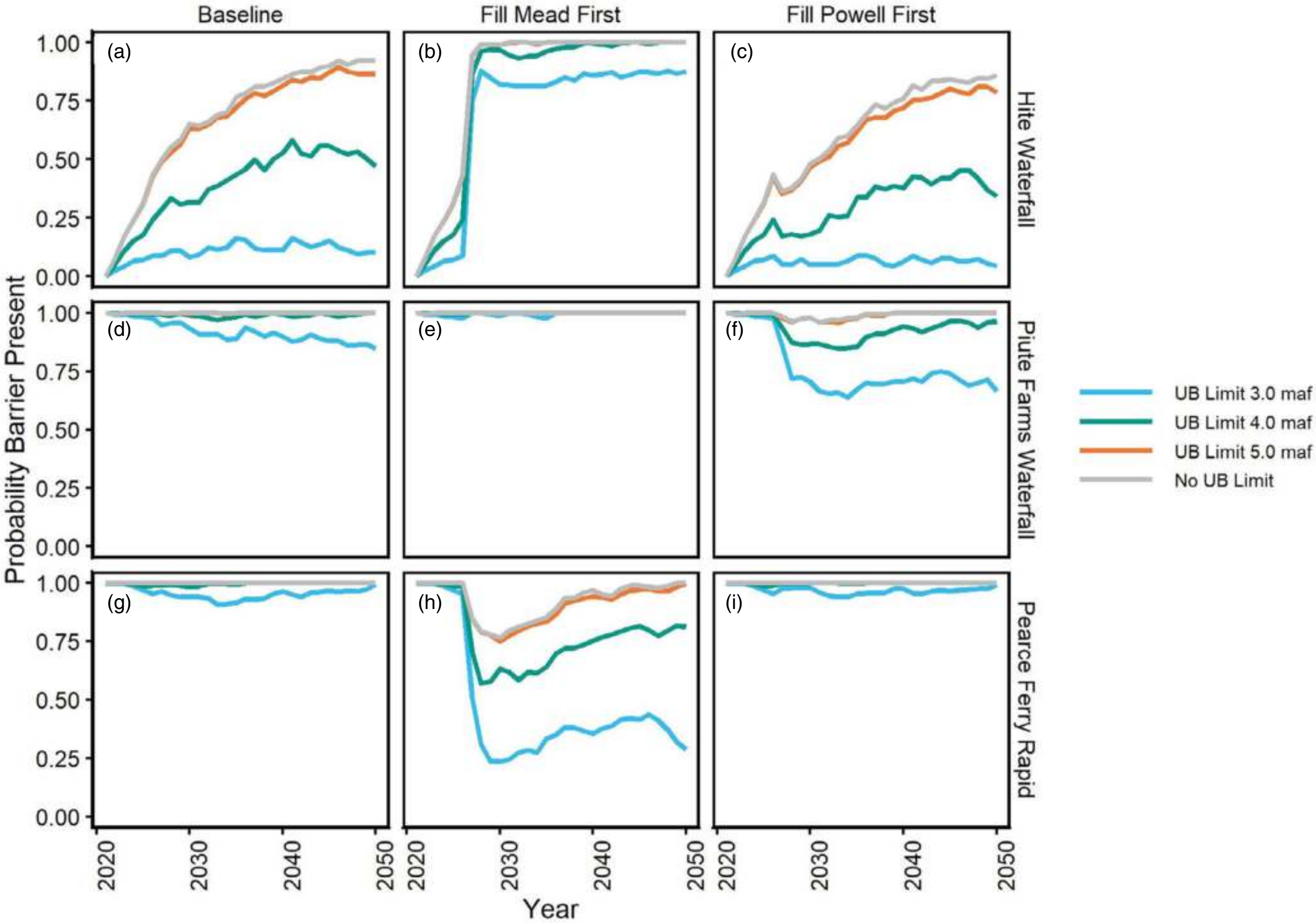

FIGURE 8. The probability of three barriers, including the Hite waterfall on the Colorado River arm of Lake Powell, Piute Farms waterfall on the San Juan River arm of Lake Powell, and Pearce Ferry Rapid on the Colorado River upstream from Lake Mead will be present under future management alternatives. Probabilities were calculated as the number of hydrologic traces in which reservoir elevations fell below the elevation of each barrier out of all 50 traces and were calculated across combinations of baseline conditions, FMF, and FPF alternatives crossed with different UB limit scenarios.

so that there is more water stored in Lake Powell and Lake Mead.

The outcomes of decisions about how to manage consumptive water use and where to store water in reservoirs does not represent a tradeoff in optimizing between water supply and ecosystem outcomes. Instead, the different outcomes represent choices in what kind of a future river ecosystem is desired (Schmidt et al. 1998). Whether the ecosystem changes in Grand Canyon associated with persistently lower reservoir levels are viewed as good or bad depends on the goals established for the system (Table 2). For example, if maintaining relative cool reservoir releases to avoid the establishment of warm-water non-native fish is a priority, limiting consumptive use may be the only water-supply management strategy available to achieve this goal if the Millennium Drought persists because the Fill Powell First alternative alone would not maintain Lake Powell reservoir levels. We believe the analysis provided here should be expanded and might provide an important perspective to natural resource managers as they define future ecosystem goals and consult with water supply managers about how to meet the societal challenge of sustained drought.

The future assemblage of fish in the Grand Canyon will probably be very different than it is today due to continued increases in river temperatures associated with lower Lake Powell reservoir levels. Two of the warm-water non-native species we modeled, channel catfish and red shiner, are already present in the Colorado River or its tributaries and would be expected to expand their distribution and abundance. A third species we modeled, smallmouth bass, is present in both reservoirs, but is currently relatively rare in the Colorado River system. All three of these species, as well as the many other warm-water non-natives that have similar temperature preferences and are present within the basin, are capable of negatively impacting native fish. In the absence of these species, native fish would be expected to benefit from warming water temperatures, but other work in this system suggests non-native species may have an advantage over natives within shared habitats as river temperatures warm (Dibble et al. 2021). The Green and Yampa Rivers in the upper portion of the Colorado Basin have thermal regimes like the warmer conditions we predict and were once seen as strongholds for many native, endemic fish species that thrived under these conditions. However, the invasion and expansion of smallmouth bass populations has likely contributed to dramatic declines in these native fish species in the 21st Century (Bestgen et al. 2018). In response, managers are experimenting with flows designed specifically to disadvantage smallmouth bass reproduction (Bestgen 2018). Our results suggest such flows would be difficult to replicate in the Grand Canyon if elevations in Lake Powell are not kept relatively high as they require designer flow flexibility and releases of cooler water from deeper in the reservoir.

Economically important trout fisheries may also be impacted by warmer river temperatures, especially under the Fill Mead First alternative. In fact, a decision may need to be made concerning whether maintenance of tailwater trout populations is viable if natural inflows to Lake Powell decline, consumptive water use upstream from Lake Powell continues to increase, or if releases to the Lower Basin are reduced. The probability of mean summer temperatures will be greater than 20°C near Lees Ferry, where the highest densities of rainbow trout are found (Korman et al. 2016), was between 50% and 75% under the Fill Mead First policy across all consumptive use alternatives. This temperature is a potential chronic threshold for rainbow and brown trout populations. Only limits on Upper Basin consumptive use (3.0/4.0 maf/year) under the baseline and Fill Powell First alternatives maintained relatively low probabilities (less than 25%) of summer temperatures becoming chronically warm in Lees Ferry. Chronically warm temperatures may have important implications for the blue-ribbon trout fishery between Glen Canyon Dam and Lees Ferry. Even if temperatures remain within tolerance limits, increased temperature may limit trout densities, growth, and size through increased resource demand (Brown et al. 2004; Marquet et al. 2004) and food limitation (Dodrill et al. 2016; Korman et al. 2020). However, these potential changes in trout populations could positively impact native fish populations. Because rainbow and brown trout can compete with and prey on young native fish (Yard et al. 2011), lowering survival of humpback chub juveniles (Yackulic et al. 2018), warmer temperatures restricting trout population to the Lees Ferry segment could be beneficial for native fish downstream.

Our analysis of future Lake Powell water storage suggested the magnitude of consumptive water use will likely limit the ability to implement designer flows in Grand Canyon. This will be the case even if the Fill Powell First storage alternative is pursued. In the case of macroinvertebrates, there may be little need for designer flows if the elevation of Lake Powell declines below the penstocks as the stressor represented by hydropeaking will also disappear. Controlled floods are generally viewed as an effective tool in maintaining sandbars in Grand Canyon and the need for this maintenance would be expected to persist at lower lake elevations. At especially low elevations in Lake Powell, managers would become even more limited in their flexibility to implement designer flows because constant year-round flows would be the only option to meet annual water targets for the Lower Basin. The effects of such constant flows on geomorphic processes and sandbar retention may be dramatic.

Regardless of water storage or limits on use, reservoir levels in both Lake Mead and Lake Powell will likely remain low enough that Piute Farms waterfall and Pearce Ferry Rapid continue to fragment the system. This has important implications for the management of fish movement between these reservoirs and their upstream riverine habitats. For example, with increased temperature suitability for warm-water non-native fishes previously discussed, Pearce Ferry Rapid could be particularly important for keeping non-native fish out of the Colorado River in Grand Canyon (Kegerries et al. 2020). However, the structural integrity and longevity of this barrier remain unknown, and some observers have noticed signs of erosion. While Pearce Ferry Rapid may provide a benefit to native fish, the Piute Farms waterfall on the San Juan arm of Lake Powell may block upstream movement of native fish (Cathcart et al. 2018; Pennock et al. 2020). The continued persistence of the Piute Farms waterfall may require ongoing management actions, such as selectively moving native fish above this barrier. The only barrier that displayed large variation in response to alternatives was the potential Hite barrier on the Colorado River arm of Lake Powell. Should a barrier form in this location, extreme efforts to remove the barrier (such as by dynamite or by heavy construction) or active management and movement of native fish similar to that at Piute Farms may be necessary.

There are many combinations of future management alternatives and levels of consumptive use, and it is impossible to predict future watershed runoff with any precision. Nevertheless, the climate continues to warm and the linkage between a warming climate and declining runoff is well established. Because it is impossible to predict the future hydrology of the Colorado River, our results only present the management implications of one future hydrologic scenario—persistence of the Millennium Drought. We believe this is a conservative planning approach. We also recognize that predicting future consumptive use is difficult, because there are many political and socioeconomic drivers of water demand. Although our use of the UCRC (2007) demand schedule does not reflect future patterns of demands and use, comparing this demand schedule to limits on consumptive use allowed us to explore ecological outcomes of a wide range of potential future use scenarios. Water conservation under sustained drought will fall to all users of the Colorado River, but it is impossible for us to predict how negotiations of future use will be resolved.

Despite uncertainties associated with future hydrology and consumptive use, we believe our analysis of alternative management paradigms using conditions of the Millennium Drought provides insight into the relative importance of water storage decisions versus consumptive use. Our analysis indicates a wide range of outcomes across storage and consumptive use limit alternatives. Reservoir levels of both Lake Powell and Lake Mead will likely continue to decline regardless of where water is stored unless consumptive use is limited (Figure 3), so limiting consumptive use may provide the most flexibility in managing ecosystem drivers. Understanding how storage decisions and water availability constrain management could provide the opportunity for ecosystem management to be considered in future water supply and management agreements.

DATA AVAILABILITY STATEMENT

All data used in this paper are publicly available from various repositories and websites cited within the paper.

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: Methods for predicting future water temperature in Lake Powell and Grand Canyon and for predicting future thermal suitability of fish populations.

ACKNOWLEDGMENTS

Funding was provided by the U. S. Geological Survey Southwest Climate Adaptation Science Center, Catena Foundation, the Walton Family Foundation, My Good Fund, and David Bonderman. L. Bruckerhoff was supported by the Center for Colorado River Studies at Utah State University when initiating this work. We acknowledge members of the Future of the Colorado River Project team that developed hydrologic scenarios and ideas for management alternatives including Eric Kuhn, Brad Udall, Sara Goeking, Alan Kasprak, David Rosenberg, Homa Salehabadi, David Tarboton, and Lael Gilbert. We thank Theodore Kennedy and three anonymous reviewers for providing suggestions to improve this paper.

AUTHOR CONTRIBUTIONS

Lindsey A. Bruckerhoff: Formal analysis; investigation; methodology; writing – original draft. Kevin Wheeler: Conceptualization; formal analysis; investigation; methodology; writing – review and editing. Kimberly L. Dibble: Formal analysis; investigation; methodology; writing – review and editing. Bryce A. Mihalevich: Formal analysis; investigation; methodology; writing – review and editing. Bethany T. Neilson: Formal analysis; investigation; methodology; writing – review and editing. Jian Wang: Formal analysis; investigation; methodology; writing – review and editing. Charles B. Yackulic: Formal analysis; funding acquisition; investigation; methodology; writing – review and editing. John C. Schmidt: Conceptualization; funding acquisition; project administration; writing – review and editing.

LITERATURE CITED

Alexander, C.A.D., E. Olson, and J. Carron, 2013. "Integrated Water Management in the Colorado River Basin: Evaluation of Decision Support Platforms and Tools." Final Report, Prepared by ESSA Technologies Ltd. and Hydros Consulting for the Colorado River Program of the Natural Conservancy, Boulder, CO.

Bair, L.S., C.B. Yackulic, J.C. Schmidt, D.M. Perry, C.J. Kirchhoff, K. Chief, and B.J. Colombi. 2019. "Incorporating Social-Ecological Considerations into Basin-Wide Responses to Climate Change in the Colorado River Basin." *Current Opinion in Environmental Sustainability* 37: 14–19. https://doi.org/10.1016/j.cosust.2019.04.002.

Bestgen, K. 2008. "Effects of Water Temperature on Growth of Razorback Sucker Larvae." *Western North American Naturalist* 68 (10): 15–20. https://doi.org/10.3398/1527-0904(2008)68[15:EOWTOG]2.0.CO;2.

Bestgen, K., 2018. "Evaluate Effects of Flow Spikes to Disrupt Reproduction of Smallmouth Bass in the Green River Downstream of Flaming Gorge Dam." Final Report to the Upper Colorado River Endangered Fish Recovery Program, Denver, CO.

Bestgen, K.R., C.D. Walford, G.C. White, J.A. Hawkins, M.T. Jones, P.A. Webber, M. Breen, et al. 2018. "Population Status and Trends of Colorado Pikeminnow in the Green River Sub-Basin, Utah and Colorado, 2000–2013." Final Report, Contribution, Colorado State University, Larval Fish Laboratory to Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado. Larval Fish Laboratory Contribution 200.

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85 (7): 1771–89. https://doi.org/10.1890/03-9000.

Bunn, S.E., and A.H. Arthington. 2002. "Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity." *Environmental Management* 4 (30): 492–507.

Cathcart, C.N., K.B. Gido, and W.H. Brandenburg. 2019. "Spawning Locations within and among Tributaries Influence Flannelmouth Sucker Offspring Experience." *Transactions of the American Fisheries Society* 148: 963–77. https://doi.org/10.1002/tafs.10191.

Cathcart, C.N., C.A. Pennock, C.A. Cheek, M.C. McKinstry, P.D. MacKinnon, M.M. Conner, and K.B. Gido. 2018. "Waterfall Formation at a Desert River–Reservoir Delta Isolates Endangered Fishes." *River Research and Applications* 34 (8): 948–56. https://doi.org/10.1002/rra.3341.

Clarkson, R.W., and M.R. Childs. 2000. "Temperature Effects of Hypolimnial-Release Dams on Early Life Stages of Colorado River Basin Big-River Fishes." *Copeia* 2000 (2): 402–12.

Clarkson, R.W., and P.C. Marsh. 2010. "Effectiveness of the Barrier-and-Renovate Approach to Recovery of Warmwater Native Fishes in the Gila River Basin." *Proceedings of the Colorado River Basin Science and Resource Management Symposium*. Scientific Investigations Report, 2010-5135: 211–17.

Currie, R.J., W.A. Bennett, and T.L. Beitinger. 1998. "Critical Thermal Minima and Maxima of Three Freshwater Game-Fish Species Acclimated to Constant Temperatures." *Environmental Biology of Fishes* 51 (2): 187–200. https://doi.org/10.1023/a:1007447417546.

Dibble, K.L., C.B. Yackulic, and K.R. Bestgen. 2020. "Water Temperature Models, Data and Code for the Colorado, Colorado, Green, San Juan, Yampa, and White Rivers in the Colorado River Basin." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9HFKV7Q.

Dibble, K.L., C.B. Yackulic, T.A. Kennedy, K.R. Bestgen, and J.C. Schmidt. 2021. "Water Storage Decisions Will Determine the Distribution and Persistence of Imperiled River Fishes." *Ecological Applications*. https://doi.org/10.1002/eap.2279.

Dodrill, M.J., C.B. Yackulic, T.A. Kennedy, and J.W. Hayes. 2016. "Prey Size and Availability Limits Maximum Size of Rainbow Trout in a Large Tailwater: Insights from a Drift-Foraging Bioenergetics Model." *Canadian Journal of Fisheries and Aquatic Sciences* 73 (5): 759–72. https://doi.org/10.1139/cjfas-2015-0268.

Fausch, K.D., B.E. Rieman, J.B. Dunham, M.K. Young, and D.P. Peterson. 2009. "Invasion Versus Isolation: Trade-Offs in Managing Native Salmonids with Barriers to Upstream Movement." *Conservation Biology* 23 (4): 859–70. https://doi.org/10.1111/j.1523-1739.2008.01159.x.

Hall, R.O., C.B. Yackulic, T.A. Kennedy, M.D. Yard, E.J. Rosi-Marshall, N. Voichick, and K.E. Behn. "Turbidty, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon." *Limnology and Oceanography* 60 (2): 512–26. https://doi.org/10.1002/lno.10031.

Hirsch, R.M., J.F. Walker, J.C. Day, and R. Kallio. 1990. "The Influence of Man on Hydrologic Systems." In Surface Water Hydrology. Geological Society of America, Boulder, CO, 329–59.

Irving, D.B., and T. Modde. 2000. "Home-Range Fidelity and Use of Historic Habitat by Adult Colorado Pikeminnow (*Ptychocheilus lucius*) in the White River, Colorado and Utah." *Western North American Naturalist* 60 (1): 16–25.

Johnson, B.M., P.J. Martinez, J.A. Hawkins, and K.R. Bestgen. 2008. "Ranking Predatory Threats by Nonnative Fishes in the Yampa River, Colorado, Via Bioenergetics Modeling." *North American Journal of Fisheries Management* 28: 1941–53. https://doi.org/10.1577/M07-199.1.

Jowett, I.G., and M.J. Duncan. 1990. "Flow Variability in New Zealand Rivers and its Relationship to In-Stream Habitat and Biota." *New Zealand Journal of Marine and Freshwater Research* 24 (3): 305–17. https://doi.org/10.1080/00288330.1990.9516427.

Kegerries, R.B., B. Albrecht, M.C. McKinstry, R.J. Rogers, R.A. Valdez, A.L. Barkalow, E.I. Gilbert, H.E. Mohn, B. Healy, and E.O. Smith. 2020. "Small-Bodied Fish Surveys Demonstrate Native Fish Dominance over 300 Kilometers of the Colorado River through Grand Canyon Arizona." *Western North American Naturalist* 80 (2): 146. https://doi.org/10.3398/064.080.0202.

Kellett, M. 2013. "Fill Mead First: a Plan for Saving Colorado River Water & Beginning the Restoration of Glen and Grand Canyons, Hidden Passage." *Journal of Glen Canyon Institute* XIX: 4–6. https://www.glencanyon.org/system/pdfs/7/original/Hidden_Passage_XIX.pdf?13845418.

Kennedy, T.A., J.D. Muehlbauer, C.B. Yackulic, D.A. Lytle, S.W. Miller, K.L. Dibble, E.W. Kortenhoeven, A.N. Metcalfe, and C.V. Baxter. 2016. "Flow Management for Hydropower Extirpates Aquatic Insects Undermining River Food Webs." *Bioscience* 66 (7): 561–75. https://doi.org/10.1093/biosci/biw059.

Korman, J., M.D. Yard, M.C. Dzul, C.B. Yackulic, M.J. Dodrill, B.R. Deemer, and T.A. Kennedy. 2020. "Changes in Prey Turbidity, and Competition Reduce Somatic Growth and Cause the Collapse of a Fish Population." *Ecological Monographs* 91 (1). https://doi.org/10.1002/ecm.1427.

Korman, J., M.D. Yard, and C.B. Yackulic. 2016. "Factors Controlling the Abundance of Rainbow Trout in the Colorado River in Grand Canyon in a Reach Utilized by Endangered Humpback Chub." *Canadian Journal of Fisheries and Aquatic Sciences* 73 (1): 105–24. https://doi.org/10.1139/cjfas-2015-0101.

Lund, J.R., and J. Guzman. 1999. "Derived Operating Rules for Reservoirs in Series or in Parallel." *Journal of Water Resources Planning and Management* 125 (3): 143–53. https://doi.org/10.1061/(asce)0733-9496(1999)125:3(143).

MacDonnell, L.J., D.H. Getches, and W.C. Hugenberg. 1995. "The Law of the Colorado River: Coping with Severe Sustained Drought." *Journal of the American Water Resources Association* 31 (5): 825–36. https://doi.org/10.1111/j.1752-1688.1995.tb03404.x.

Mandeville, C.P., F.J. Rahel, L.S. Patterson, and A.W. Walters. 2019. "Integrating Fish Assemblage Data Modeled Stream Temperatures, and Thermal Tolerance Metrics to Develop Thermal Guilds for Water Temperature Regulation: Wyoming Case Study." *Transactions of the American Fisheries Society* 148 (4): 739–54. https://doi.org/10.1002/tafs.10169.

Marquet, P.A., F.A. Labra, and B.A. Maurer. 2004. "Metabolic Ecology: Linking Individuals to Ecosystems." *Ecology* 85 (7): 1794–96. https://doi.org/10.1890/03-0694.

Melis, T.S. 2011. "Effects of Three High-Flow Experiments on the Colorado River Ecosystem Downstream from Glen Canyon Dam, Arizona (No. 1366)." US Geological Survey.

Melis, T.S., C.J. Walters, and J. Korman. 2015. "Surprise and Opportunity for Learning in Grand Canyon: The Glen Canyon Dam Adaptive Management Program." *Ecology and Society* 20 (3): 22. https://doi.org/10.5751/ES-07621-200322.

Mihalevich, B.A., B.T. Neilson, C.A. Buahin, C.B. Yackulic, and J.C. Schmidt. 2020. "Water Temperature Controls for Regulated Canyon-Bound Rivers." *Water Resources Research* 56 (12). https://doi.org/10.1029/2020wr027566.

Minckley, W.L., and J.E. Deacon. 1991. *Battle against Extinction: Native Fish Management in the American West*. Tucson: University of Arizona Press.

Nelitz, M.A., E.A. MacIsaac, and R.M. Peterman. 2007. "A Science-Based Approach for Identifying Temperature-Sensitive Streams for Rainbow Trout." *North American Journal of Fisheries Management* 27 (2): 405–24. https://doi.org/10.1577/m05-146.1.

Nilsson, C., C.A. Reidy, M. Dynesius, and C. Revenga. 2005. "Fragmentation and Flow Regulation of the world's Large River Systems." *Science* 308 (5720): 405–08.

Pennock, C.A., and K.B. Gido. 2021. "Spatial and Temporal Dynamics of Fish Assemblages in a Desert Reservoir over 38 Years." *Hydrobiologia* 848: 1231–48. https://doi.org/10.1007/s10750-021-04514-z.

Pennock, C.A., M.C. McKinstry, C.N. Cathcart, K.B. Gido, T.A. Francis, B.A. Hines, P.D. MacKinnon, et al. 2020. "Movement Ecology of Imperiled Fish in a Novel Ecosystem: River-Reservoir Movements by Razorback Sucker and Translocations to Aid Conservation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 1540–51. https://doi.org/10.1002/aqc.3399.

Petts, G.E. 1987. "Time-Scales for Ecological Change in Regulated Rivers. " In *Regulated Streams*, edited by Craig, J.F. and Kemper, J.B., 257–66. Boston, MA: Springer.

Poff, N.L., and J.C. Schmidt. 2016. "How Dams Can Go with the Flow." *Science* 353 (6304): 1099–100. https://doi.org/10.1126/science.aah4926.

Poff, N.L.R., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. "The Natural Flow Regime." *Bioscience* 47 (11): 769–84.

Poff, N.L.R., and J.V. Ward. 1989. "Implications of Streamflow Variability and Predictability for Lotic Community Structure: A Regional Analysis of Streamflow Patterns." *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1805–18. https://doi.org/10.1139/f89-228.

Poff, N.L.R., and J.K.H. Zimmerman. 2010. "Ecological Responses to Altered Flow Regimes: A Literature Review to Inform the Science and Management of Environmental Flows." *Freshwater Biology* 55 (1): 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x.

Reclamation. 2020. "Consumptive Uses and Losses Reports." https://www.usbr.gov/uc/envdocs/plans.html.

Reclamation. 2021a. "Natural Flow Data 1906–2019, Updated April 2021, and Provisional Natural Flow Data." Updated August 2021. https://www.usbr.gov/lc/region/g4000/NaturalFlow/.

Reclamation. 2021b. "Reclamation/Colorado River Basin/Current Focus." Updated 12/18/2020. https://www.usbr.gov/ColoradoRiverBasin/.

Reclamation. 2021c. "Colorado River Basin August 2021, 24-Month Study." Updated 08/16/2021. https://www.usbr.gov/uc/water/crsp/studies/24Month_08.pdf.

Reclamation & NPS (Reclamation and National Park Service). 2016. "Glen Canyon Dam Long-Term Experimental and Management Plan Environmental Impact Statement."

Returning Rapids of Cataract Canyon. 2021. "Lake Powell's Effect on Cataract Canyon." https://www.returningrapids.com/.

Reynolds, L.V., P.B. Shafroth, and N.L.R. Poff. 2015. "Modeled Intermittency Risk for Small Streams in the Upper Colorado River Basin under Climate Change." *Journal of Hydrology* 523: 768–80. https://doi.org/10.1016/j.jhydrol.2015.02.025.

Robinson, A.T., and M.R. Childs. 2001. "Juvenile Growth of Native Fishes in the Little Colorado River and in a Thermally Modified Portion of the Colorado River." *North American Journal of Fisheries Management* 21: 809–15. https://doi.org/10.1577/1548-8675(2001)021<0809:JGONFI>2.0.CO;2.

Rodgers, D.W., and J.S. Griffiths. 1983. "Effects of Elevated Thermal Regimes on Survival of Rainbow Trout (Salmo Gairdneri) Alevins." *Journal of Great Lakes Research* 9 (3): 421–24. https://doi.org/10.1016/s0380-1330(83)71913-1.

Rosen, M.R., K. Turner, S.L. Goodbred, and J.M. Miller. 2012. "A Synthesis of Aquatic Science for Management of Lakes Mead and Mohave." U.S. Geological Survey Circular 1381.

Rüegg, J., C.C. Conn, E.P. Anderson, T.J. Battin, E.S. Bernhardt, M. Boix Canadell, S.M. Bonjour, J.D. Hosen, N.S. Marzolf, and C.B. Yackulic. 2021. "Thinking like a Consumer: Linking Aquatic Basal Metabolism and Consumer Dynamics." *Limnology and Oceanography Letters* 6 (1): 1–17. https://doi.org/10.1002/lol2.10172.

Runge, M.C., C.B. Yackulic, L.S. Bair, T.A. Kennedy, R.A. Valdez, C. Ellsworth, J.L. Kershner, R.S. Rogers, M.A. Trammell, and K.L. Young. 2018. "Brown Trout in the Lees Ferry Reach of the Colorado River — Evaluation of Causal Hypotheses and Potential Interventions (No. 2018-1069)." US Geological Survey.

Salehabadi, H., D. Tarboton, E. Kuhn, B. Udall, K. Wheeler, D. Rosenberg, S. Goeking, and J.C. Schmidt. 2020. "The Future Hydrology of the Colorado River Basin." Center for Colorado River Studies, Quinney College of Natural Resources, Utah State University White Paper No. 4. https://qcnr.usu.edu/coloradoriver/files/WhitePaper4.pdfere.

Schmidt, J.C., L.A. Bruckerhoff, J. Wang, and C.B. Yackulic. in press. "The Colorado River-The Science-Policy Interface." In Cornerstone: A Century of the Colorado River Compact.

Schmidt, J.C., M. Kraft, D. Tuzlak, and A. Walker. 2016. "Fill Mead First: a technical assessment." Center for Colorado River Studies, Quinney College of Natural Resources, Utah State University White Paper No. 1. https://qcnr.usu.edu/coloradoriver/files/WhitePaper4.pdfere.

Schmidt, J.C., R.H. Webb, R.A. Valdez, G.R. Marzolf, and L.E. Stevens. 1998. "Science and Values in River Restoration in the Grand Canyon: There Is no Restoration or Rehabilitation Strategy that Will Improve the Status of every Riverine Resource." *Bioscience* 48: 735–47. https://doi.org/10.2307/1313336.

Sheer, D.P. 2014. *Reservoir Operations Development Guide: The Theory and Practice of Developing Reservoir Operating Rules for Managing Multiple Objectives*. Denver: Water Research Foundation.

Sofi, M.S., S.U. Bhat, I. Rashid, and J.C. Kuniyal. 2020. "The Natural Flow Regime: A Master Variable for Maintaining River Ecosystem Health." *Ecohydrology* 13 (3). https://doi.org/10.1002/eco.2247.

UCRC. 2007. "Upper Colorado River Division States Schedule A Current and Future Depletion Demand Schedule." http://www.ucrcommission.com/RepDoc/DepSchedules/Dep_Schedules_2007.pdf.

UCRC. 2016. "Upper Colorado River Division States, Current and Future Depletion Demand Schedule." http://www.ucrcommission.com/RepDoc/DepSchedules/CurFutDemandSchedule.pdf.

Udall, B. 2021. "Running on Empty: Southwestern Water Supplies and Climate Change." In *Standing between Life and Extinction*, edited by D. Probst, J.E. Williams, K.R. Bestgen, and C.W. Hoagstrom, 109–23. Chicago: The University of Chicago Press.

Udall, B., and J. Overpeck. 2017. "The Twenty-First Century Colorado River Hot Drought and Implications for the Future." *Water Resources Research* 53 (3): 2404–18. https://doi.org/10.1002/2016wr019638.

USFWS (U.S. Fish and Wildlife Service). 2018. "San Juan River Basin Recovery Implementation Program Final Program Document." https://www.fws.gov/southwest/sjrip/pdf/DOC_Final_Program_Document_SJRIP_2018.pdf.

USFWS (U.S. Fish and Wildlife Service). 2020. "Upper Colorado River Endangered Fish Recovery Program. Recovery Implementation Program Recovery Action Plan." https://

coloradoriverrecovery.org/documents-publications/foundational-documents/RIPRAP/2020%20RIPRAP.pdf

USFWS (U.S. Fish and Wildlife Service). 2021. "Endangered and Threatened Wildlife and Plants; Reclassification of the Humpback Chub from Endangered to Threatened With a Section 4(d) Rule." Federal Register 86: 57588:5761017 November 2021.

USGS (U.S. Geological Survey). 2021. "Release Temperature Data for Glen Canyon Dam near Page, AZ." https://www.gcmrc.gov/discharge_qw_sediment/station/GCDAMP/09379901.

Van Haverbeke, D.R., D.M. Stone, M.J. Dodrill, K.L. Young, and M.J. Pillow. 2017. "Population Expansion of Humpback Chub in Western Grand Canyon and Hypothesized Mechanisms." *The Southwestern Naturalist* 62 (4): 285–92. https://doi.org/10.1894/0038-4909-62.4.285.

Verburg, K.O. 2011. *The Colorado River Documents, 2008*. Washington D.C.: Government Printing Office.

Vernieu, W.S., S.J. Hueftle, and S.P. Gloss. 2005. "Water Quality in the Lake Powell and the Colorado River." *U. S. Geological Survey Circular* 1282: 69–85.

Walters, A.W., C.P. Mandeville, and F.J. Rahel. 2018. "The Interaction of Exposure and Warming Tolerance Determines Fish Species Vulnerability to Warming Stream Temperatures." *Biology Letters* 14 (9): 20180342. https://doi.org/10.1098/rsbl.2018.0342.

Wang, J., and J.C. Schmidt. 2020. Stream Flow and Losses of the Colorado River in the Southern Colorado Plateau." Center for Colorado River Studies, Quinney College of Natural Resources, Utah State University White Paper No. 5. https://qcnr.usu.edu/coloradoriver/files/WhitePaper5.pdf.

Webb, R.H., J.C. Schmidt, G.R. Marzolf, and R.A. Valdez. 1999. "The Controlled Flood in Grand Canyon." American Geophysical Union Geophysical Monograph 110, Washington, D.C.

Wheeler, K., E. Kuhn, L. Bruckerhoff, B. Udall, J. Wang, L. Gilbert, S. Goeking, A. Kasprak, B. Mihalevich, B. Neilson, D. Rosenberg, H. Salehabadi, and J.C. Schmidt. 2021. "Alternative Management Paradigms for the Future of the Colorado and Green Rivers." Center for Colorado River Studies, Quinney College of Natural Resources, Utah State University White Paper, No. 6. https://qcnr.usu.edu/coloradoriver/files/WhitePaper6.pdf.

Wheeler, K.G., C.J. Robinson, and R.H. Bark. 2018. "Modelling to Bridge Many Boundaries: The Colorado and Murray-Darling River Basins." *Regional Environmental Change* 18 (6): 1607–19. https://doi.org/10.1007/s10113-018-1304-z.

Wheeler, K.G., D.E. Rosenberg, and J.C. Schmidt. 2019. "Water Resource Modeling of the Colorado River: Present and Future Strategies." Future of the Colorado River Project, Center for Colorado River Studies, Utah State University White Paper 2. https://qcnr.usu.edu/coloradoriver/files/WhitePaper2.pdfre.

Williams, N.T. 2007. *Modeling Dissolved Oxygen in Lake Powell Using CE-QUAL-W2*. Provo: Brigham Young University.

Wright, S.A., C.R. Anderson, and N. Voichick. 2009. "A Simplified Water Temperature Model for the Colorado River Below Glen Canyon Dam." *River Research and Applications* 25 (6): 675–86.

Xiao, M., B. Udall, and D.P. Lettenmaier. 2018. "On the Causes of Declining Colorado River Streamflows." *Water Resources Research* 54: 6739–56. https://doi.org/10.1029/2018wr023153.

Yackulic, C.B., J. Korman, M.D. Yard, and M. Dzul. 2018. "Inferring Species Interactions through Joint Mark-Recapture Analysis." *Ecology* 99 (4): 812–21. https://doi.org/10.1002/ecy.2166.

Yackulic, C.B., M.D. Yard, J. Korman, and D.V. Van Haverbeke. 2014. "A Quantitative Life History of Endangered Humpback Chub that Spawn in the Little Colorado River: Variation in Movement, Growth, and Survival." *Ecology and Evolution* 4 (7): 1006–18. https://doi.org/10.1002/ece3.990.

Yard, M.D., L.G. Coggins, C.V. Baxter, G.E. Bennett, and J. Korman. 2011. "Trout Piscivory in the Colorado River Grand Canyon: Effects of Turbidity, Temperature, and Fish Prey Availability." *Transactions of the American Fisheries Society* 140 (3): 471–86. https://doi.org/10.1890/12-1727.1.

Yarnell, S.M., G.E. Petts, J.C. Schmidt, A.A. Whipple, E.E. Beller, C.N. Dahm, P. Goodwin, and J.H. Viers. 2015. "Functional Flows in Modified Riverscapes: Hydrographs Habitats and Opportunities." *Bioscience* 65 (10): 963–72. https://doi.org/10.1093/biosci/biv102.

Zagona, E.A., T.J. Fulp, R. Shane, T. Magee, and H.M. Goranflo. 2001. "Riverware: A Generalized Tool for Complex Reservoir System Modeling." *Journal of the American Water Resources Association* 37: 913–29. https://doi.org/10.1111/j.1752-1688.2001.tb05522.x.