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

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ABSTRACT: Drought has impacted the Colorado River basin for the past 20 years and is predicted to continue. In response to ongoing drought, 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, including 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, but the outcome of interactions among warm-water native and non-native species is uncertain. 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, and total reservoir storage is the largest in comparison to the river's mean annual flow of any large river in North America (Hirsch *et al.*, 1990). The two largest reservoirs – Lake Mead and Lake Powell – each has a storage capacity of at least 25 million acre-feet (maf), and their combined capacity is more than three times the estimated annual natural flow. Decisions about water storage in Lake Mead and Lake Powell dominate discussion about how to manage the Colorado River for water supply, even though the combined storage of reservoirs upstream of Lake Powell is greater than 7.1 maf and combined storage below Lake Mead is 2.4 maf. The watershed's natural runoff is entirely consumed, and no water reaches the Gulf of California in most years. Consumptive uses within the watershed are for irrigated agriculture, municipalities, industry, trans-basin diversions that supply water to metropolitan and agricultural areas beyond the watershed. The policies concerning how much, where, and when water is stored and consumptively used by two countries, seven US 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* (Verburg, 2011).

Persistent decline in watershed runoff may require renegotiation of agreements concerning existing uses, especially because the river's flow was completely consumed prior to the recent decline in runoff. Natural flow of the Colorado River at Lees Ferry between 2000 and 2019 was 12.7 maf/yr (Reclamation, 2021a), 17% less than the average annual natural flow between 1906 and 1999 (15.2 maf/yr). There is increasing evidence this decrease is partly due to warmer air temperatures, increased evapotranspiration, and drier soils (Udall and Overpeck, 2017; Xiao *et al.*, 2018). Natural flow of the Colorado River is projected to further decline by as much as 30% by mid-century (Reynolds *et al.*, 2015; Udall and Overpeck, 2017; Udall 2021). Inflow to Lake Powell in 2021 was only 3.23 maf and was the second lowest since Glen Canyon Dam was completed in 1963 (Reclamation, 2021a). Preparing for a dry future may require new reservoir management practices to meet stakeholder needs under drier conditions. 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 and may provide an opportunity for such new management practices (Reclamation, 2021b).

Declining runoff not only forces reconsideration of how to allocate the water supply for human use, but also provides a need and opportunity to reconsider how streamflow might be managed to mitigate adverse ecosystem impacts of water development and achieve desirable ecosystem outcomes. The diversion of streamflow, the physical existence of dams, and the operation of reservoirs disrupt many ecosystem processes (Williams and Wolman 1984; 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 releases from reservoirs (hereafter, reservoir operations). These options are explored in this paper, but other disruptions can only be mitigated by removal of dams.

Impacts of diversions and reservoir operations on ecosystems is wide ranging. Diversions have resulted in severe dewatering, particularly in the Colorado River Delta (Glenn *et al.*, 1996) as well as in some tributaries in the Upper Basin. Large reservoirs thermally stratify, so how much water is stored in each reservoir and where in the water column the water is drawn influences the temperature of released water, which impacts downstream river temperature (Caissie, 2006; Mihalevich *et al.*, 2020; Dibble *et al.*, 2021). Cold water releases from relatively full reservoirs have historically limited growth and reproduction of native fishes in many portions of this basin, likely contributing to population declines (Clarkson and Childs, 2000; Dibble *et al.,* 2021). The flow regime of reservoir releases is typically highly altered from natural conditions and may include reduction in flood magnitude, increase in base flows, hydropeaking, and shifts in the timing of high and low flow (Steven *et al.* 1995; Grams and Schmidt 2005; Gido and Propst 2012). Cold water non-native fishes have been introduced in the tailwaters of many dams, warm water species have been introduced to many reservoirs, and non-native trees and shrubs have been introduced to many riparian ecosystems (Merritt and Poff, 2010), so that most of the Colorado River's riverine ecosystems are novel mixes of native and non-native species. The flow regimes, sediment supply, and non-native riparian vegetation expansion have also caused changes in channel form (Grams and Schmidt, 2005; Grams *et al.*, 2007; Walker *et al.*, 2020) and reduced connectivity with the floodplain (Mueller and Marsh, 2002). Collectively, these changes contributed to population declines of native fishes (Bezzerides and Bestgen, 2002; Budy *et al.*, 2015), loss of macroinvertebrate diversity (Kennedy *et al.*, 2016), and the listing of four mainstem, large-bodied fish species as endangered (Stanford *et al.*, 1986; Carlson and Muth, 1989).

Water storage and allocation decisions can exacerbate negative ecosystem impacts of water development. We refer to the abiotic factors that are influenced by water storage decisions, such as temperature, fragmentation, and hydrology, as ecosystem drivers. In this paper, we considered ecosystem drivers that are influenced by policy decisions about how much water to divert from different parts of the watershed and rules that guide reservoir operations. Understanding how these ecosystem drivers respond to changes in consumptive water use and reservoir operations may help guide future management of the Colorado River.

We assessed the response of ecosystem drivers to alternative paradigms for managing the diversions and reservoirs of the watershed. We considered alternatives that would constitute substantive policy changes that might address the present challenge of managing a declining water supply, but we did not estimate the likelihood that any of these administrative changes might be adopted. Furthermore, we did not consider changes to those ecosystem drivers that are affected by the existence of high dams, such as reducing the adverse effects of fragmentation or sediment trapping by removing those structures.

We focused our attention on alternatives related to the management of Lake Powell and Lake Mead and the effects of those alternatives on the river ecosystem of the Grand Canyon (Fig. 1). The major operational changes we considered concerned rules that prioritize water storage in one reservoir over the other. We also evaluated the effects of reducing consumptive water use upstream from Lake Powell. The primary ecosystem driver we evaluated was river temperature, because temperature exerts a critical control on ecosystem processes that in turn affect native and non-native fish species and their interactions. 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 would restrict the ability to implement *designer flows,* which are reservoir releases aimed at achieving ecological goals that are currently used to mitigate some undesirable ecosystem conditions in Grand Canyon. By quantifying relationships among water storage, consumptive use, and ecosystem drivers, we seek to inform conversations about how the Colorado River can be managed under sustained drought to best serve ecosystem and human needs.

Study Area

We focused on the Lake Powell/Grand Canyon/Lake Mead segment because most of the watershed's reservoir storage is here, and the intervening river segment is of administrative and ecological significance. Lee Ferry, 27 km downstream from Glen Canyon Dam, is the demarcation point between the Upper Basin (Colorado, New Mexico, Utah, Wyoming, and a small part of Arizona) and the Lower Basin (California, Nevada, and most of Arizona). Releases from Lake Powell are considered a transfer of water from the Upper Basin to the Lower Basin and comprise more than 90% of all the streamflow through Grand Canyon (Wang and Schmidt, 2021), the rest mainly coming from tributary inputs and springs. Thus, most of the streamflow that drives the Colorado River ecosystem in Grand Canyon is an administrative release that must be consistent with the *Law of the River*. The Colorado River and its tributaries in Grand Canyon are home to the largest populations of humpback chub (*Gila cypha*), which is federally listed as endangered (USFWS, 1974), as well as populations of other native fishes of conservation concern (Van Haverbeke *et al.,* 2017; Keggeries *et al.* 2020).

METHODS

Modeling Colorado River Reservoir Operations

The Colorado River Simulation System, (CRSS; for full description see Alexander *et al.*, 2013; Wheeler *et al.*, 2019) developed by the Bureau of Reclamation and implemented in RiverWare software (Fulp *et al.*, 1999, Zagona *et al.*, 2001), simulates how water is managed throughout the basin based on the *Law of the River.* Bureau of Reclamation's implementation of CRSS codifies current water management policies to estimate future water storage, reservoir elevation and releases, and the volume of water flowing in major river segments in response to hydrologic conditions, water use and operating rules. We refer to the rules embedded in the version of the CRSS model distributed by Reclamation as the "baseline" operations. Rules and assumptions in this baseline configuration can be modified to evaluate the implications of a wide variety of alternative operational policies (Wheeler *et al.*, 2018).

Current management of the Colorado River: Baseline

The current water policy ensures both basins can consumptively use some of the watershed's runoff, which is an essential aspect of the baseline scenario. Consumptive uses are lower in the Upper Basin and averaged 3.86 maf/yr between 2001 and 2018 (Figure 2). Annual use has changed little since 1988 and varied between 81 and 113% of the post-2001 average (Wang and Schmidt, 2020; Reclamation, 2020; Wheeler *et al.*, 2021). In contrast, an annual average of 7.43 maf/yr was used in the Lower Basin and 1.56 maf/yr was delivered to Mexico between 2001 and 2019. Current interpretation of the *Law of the River* suggests the Upper Basin has the right to increase its consumptive uses to approximately match that of the Lower Basin. The rate at which those uses might increase in the future has been estimated by the Upper Colorado River Commission (UCRC) and incorporated into the CRSS model by Reclamation. For the baseline scenario, we used projections of increasing future use developed in 2007 (UCRC, 2007). Revised depletion estimates (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 levels of consumptive use, we explored alternatives related to prioritizing storage between Lake Powell and Lake Mead. Since 2008, coordinated operations of the two reservoirs have followed a policy described in the *Interim Guidelines* that seeks to balance storage volumes between Lake Mead and Lake Powell by varying releases from Lake Powell based on relative storage in Lake Powell and Lake Mead. The requirement to balance the storage volumes is defined by the elevation of the water surface in both reservoirs (Figure 3 a-c). At times, the releases are limited to a specified range and Reclamation labels these as ‘balancing’ releases, and the releases are fixed values at other times. The amount of water in Lake Mead is also used to trigger reductions in water use (*i.e.* shortages) in the Lower Basin during times of low watershed runoff (Figure 3d-f). Lower Basin shortages (Tier 1, Figure 3) were implemented for the first time during the 2022 water year (Reclamation, 2021c). For more complete summaries of the history and implementation of baseline conditions as defined by the current implementation of the *Law of the River*, see MacDonnell *et al.* (1995) and MacDonnell *et al.* (this issue).

Alternative Management Paradigms

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 focused on reservoir operations that define where to store water and how much water to release each year. Here, we briefly describe the implementation, benefits, and risks of each alternative.

Limits on 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 compensating reductions in use elsewhere if the total supply remains low or declines further. We considered three scenarios that include 1) a reduction in Upper Basin use (3.0 maf/yr), 2) a slight increase in use relative to the long-term average (4.0 maf/yr), and 3) a modest increase in Upper Basin use (5.0 maf/yr) (Figure 2). We recognized future water conservation would likely include efforts to reduce consumptives uses within the Lower Basin, but we did not simultaneously adjust those demands for simplicity of analysis. We do include projected reservoir levels across our alternatives in relation to Lower Basin shortage tiers defined in the *Interim Guidelines* for reference (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 prioritizes main-stem water storage in Lake Mead and accumulates water in Lake Powell secondarily. To simulate this policy, we defined a reservoir operation policy wherein priority zones, or different storage elevations, were established for Lake Powell and Lake Mead (Figure 2a). Priority zone 1 (305 meters above mean sea level, masl), would fill Lake Mead first and water would be stored in Lake Powell up to 1067 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.

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 the reservoir. 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 is 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 maintains an elevation of 305 masl to maintain power generation (priority zone 1). Only when Lake Powell is 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, 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 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 alternatives under a future hydrologic scenario that assumed that the on-going Millennium Drought persists. This scenario assumes the average natural runoff since 2000 continues, but the sequence in which the annual runoff occurs differs from what has previously 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. Observed runoff was obtained from the Bureau of Reclamation's Natural Flow Database (available at https://www.usbr.gov/lc/region/g4000/NaturalFlow/documentation.html). We randomly selected 50 (of 100) traces to use as input into CRSS that provided ranges of predicted variability. This hydrologic scenario represents a plausible future under warming climate conditions.

Ecosystem Metrics

We estimated how the alternatives affect some abiotic drivers that influence the structure and function of river ecosystems, including flow regime, river temperature, and fragmentation (Table 1). For each of these drivers, we defined metrics relevant to management of Colorado River resources (Table 1), especially management of native and non-native fishes (BOR and NPS, 2016; USFWS 2018, 2020).

Index of Designer Flow Implementation.

Designer flows are an informally named category of reservoir releases whose intent is to achieve desired changes in downstream ecosystem conditions while not significantly changing the annual operating plans of reservoirs. Designer flows in the Colorado River seek to achieve desirable resource outcomes while not disrupting the annual delivery of water from the Upper Basin to the Lower Basin (Melis *et al.*, 2015; Yarnell *et al.*, 2015) and have become an important part of managing the Colorado River ecosystem. Previously implemented designer flows include controlled floods that last 2-7 days and macroinvertebrate production flows wherein dam releases are steady on summer weekends (Kennedy *et al.*, 2016; Poff and Schmidt, 2016). Elsewhere in the watershed, designer flows have been implemented at Flaming Gorge Dam to promote razorback sucker recruitment (LaGory *et al*., 2012) and disrupt smallmouth bass nursery activity (Bestgen, 2018). Although none of these designer flows simulate the pre-dam flow regime, this strategy is part of modern environmental management of the Colorado River (Acreman *et al.*, 2014; Poff and Schmidt, 2016), and these flows can be implemented without changing operations consistent with the *Law of the River*.

We defined an index of designer flow flexibility as the minimum Lake Powell reservoir elevation at which implementation of designer flows might be restricted. We assigned a threshold of 1082 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, such as hydropower generation or the lack of knowledge about flow ecology relationships, 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 many designer flows focus on spring and summer flow releases, and decisions to implement designer flows would likely be made at that time.

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 the Colorado River system are closely linked with the amount of water stored in reservoirs (Mihalevich *et al.*, 2020, Dibble *et al.*, 2021). The penstocks are deep below the water surface, so when Lake Powell is full, the water released through Glen Canyon Dam is cool. Since Lake Powell reached full capacity, the temperatures at Lees Ferry have averaged 10.3 °C (range: 7.0 to 16.5 °C), which is dramatically less than the pre-dam yearly average water temperature of 14 °C (range: 0 to 27 °C; Vernieu *et al.*, 2005; Wright *et al.*, 2009). This shift from warmer river temperatures likely contributed to the proliferation of cool-water non-native species (Lowney, 2000; Olden and Naiman, 2010), declines in native fish abundance (Clarkson and Childs, 2000) and extirpation of some native species, such as Colorado pikeminnow (*Ptychocheilus Lucius;* Holden, 1979).

In order to assess the thermal suitability for native and non-native fishes within Grand Canyon, we simulated temperatures in Lake Powell and the Colorado River. With predicted flow information from CRSS for each of the described alternatives, we predicted reservoir release temperatures using the Bureau of Reclamation's Lake Powell CE-QUAL-W2 model (Williams, 2007). Downstream river temperatures within Grand Canyon were then simulated with CE-QUAL-W2 and CRSS predictions using the process-based river temperature model developed by Mihalevich *et al.* (2020). The details about the reservoir and river temperature models, CRSS linkages to these models, and assumptions about future weather and water temperature inputs can be found in the Supporting Information. The thermal suitability of river temperatures was analyzed using sub-daily predictions at three locations along the Colorado River (Figure 1): at Lees Ferry (RKM 0), upstream from the confluence with 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 relative abundance of native fishes (Van Haverbeke *et al.*, 2017; Van Haverbeke *et al.*, 2020; Keggeries *et al.* 2020).

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 future scenarios. This model was developed based on laboratory-derived information about water temperatures that are suitable for fish growth, which were used to calculate the number of days in a year that are thermally suitable for different species. This temperature index was related to species relative abundance and distributional data to develop a predictive model of the probability a species is common in different parts of the watershed, based on thermal regime. See Supporting Information and (Dibble *et al.*, 2021) for a full description of the model and data associated with model development can be found at Dibble *et al.* (2020).

We assessed thermal suitability for six species (native: humpback chub, Colorado pikeminnow, and razorback sucker *Xyrauchen texanus*; non-native: red shiner *Cyprinella lutrensis*, channel catfish *Ictalurus punctatus*, and smallmouth bass *Micropterus dolomieu*). Humpback chub are currently common in Grand Canyon, and razorback sucker are infrequently observed in western Grand Canyon near Lake Mead. Although Colorado pikeminnow were extirpated from Grand Canyon, their reintroduction has been considered by management agencies. The three non-native species are rare in 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 Lake Powell (Pennock and Gido, 2021) and potential for negative interactions with native species (Johnson *et al.* 2008, Bestgen *et al.,* 2018).

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

Upper temperature threshold to maintain trout fishery. The tailwater trout fishery in Grand Canyon is an economic and recreational resource valued by some stakeholders. Although trout recruitment may benefit from increased temperatures up to a certain point (Dibble *et al.*, 2018), the trout fishery in Grand Canyon may suffer declines if average monthly temperatures increase significantly. 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 has negative effects on survival and growth of different life stages (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 and 19.3 °C, respectively (Walters *et al.*, 2018; Mandeville *et al.*, 2019) and survival of rainbow trout eggs drops off 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 no longer suitable to maintain the trout fishery, based on reported MWATs. We considered this a conservative threshold since 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 rapids can form in drawn-down reservoirs when rivers excavate their delta sediments in a different location than the pre-dam channel. These barriers have the potential to prevent desirable movement of native fish species (Cathcart *et al.*, 2018; Pennock *et al.*, 2020), prevent undesirable movement of non-native warm-water fishes from reservoirs into upstream river reaches inhabited by native fish (Clarkson and Marsh, 2010), and may be impossible to navigate by recreational boaters. For example, in 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 arm of Lake Mead, the Colorado River now flows over a bedrock ledge and forms Pearce Ferry Rapid that likely blocks the upstream movement of non-native warm-water reservoir fishes into 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 it is predicted a similar barrier would develop if Lake Powell elevations continue to drop (Returning Rapids of Cataract Canyon, 2021). The tradeoffs between adverse impacts of fragmentation and the potential benefits of blocking non-native fish are not well understood (Faush *et al.* 2009).

We tracked the presence of three semi-natural barriers that presently exist or might exist in Lake Powell and Lake Mead, based on the reservoir elevations:

- The potential Hite waterfall on the Colorado River arm of Lake Powell, predicted to be present when Lake Powell elevations are below 1,082 m.
- Piute Farms waterfall on the San Juan, present when Lake Powell elevations are below 1,120 m.
- Pearce Ferry Rapid on the Colorado River, present when Lake Mead elevations are below 456 m.

We calculated the probability that each of these barriers would be present each year under the different alternatives. Probabilities were calculated using the proportion of traces in which the elevations were below the thresholds each year.

RESULTS

Our models 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/yr (on average) to 4.0 or 5.0 maf/yr, regardless of how water storage is distributed between Lake Powell and Lake Mead (Figure 3 a-c). The elevation of Lake Powell is predicted to be above the penstocks only if Upper Basin consumptive use is limited to 3.0 or 4.0 maf/yr 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 3 d-f) 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.

Designer Flow Flexibility

The most significant factor influencing the flexibility of operations and the use of designer flows was the magnitude of upstream use, but implementation of the Fill Mead First strategy would also greatly limit the flexibility of Powell operations. 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/yr (Figure 4b, Table 2). After 2040, it is unlikely that designer flows could be implemented under any water storage management alternative if Upper Basin consumptive use is 5.0 maf/yr or follows the 2007 UCRC demand schedule (Figure 4). However, if Upper Basin consumptive use is 3.0 maf/yr 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 can 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 Fill Powell First alternative and if Upper Basin consumptive use is capped at 4.0 maf/yr, there is at least a 50% probability of being able to implement designer flows each year from 2020-2050.

Thermal Suitability for Fishes

Warmer river temperatures are desirable for native fish, and such conditions are facilitated by warm Lake Powell releases that occur when the reservoir level is low. Thus, larger UB consumptive uses and operations that shift storage to Mead create warmer river temperatures in Grand Canyon that are more suitable for native fish (Figure 5). The suitability of river temperature for native fish in Grand Canyon, even in the westernmost part, is least desirable if the baseline management policy remains in place or if the Fill Powell First alternative is implemented and paired with limits on use (Figure 5, Table 2). Temperature suitability was above 75% for all native species for all storage scenarios if no Upper Basin limit, or only a 5.0 maf/yr limit was included (Figure 5) but was less than 25% for all species in the upstream reaches of Grand Canyon if 3.0 maf/yr limits were paired with the baseline or Fill Powell First policies (Figure 5a-f).

Unsurprising, warm-water non-native fishes, including red shiners, smallmouth bass, and channel catfish, would also benefit from warmer river temperatures associated with low Lake Powell levels, while cold-water non-native fishes (brown trout and rainbow trout) would benefit from policies that keep Lake Powell levels higher (Table 2). Under the Fill Powell First and baseline alternatives with 3.0 and 4.0 maf/yr limits, predicted river temperatures were less suitable for non-native species relative to native species in river reaches 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 (around 25% or lower) for all three non-native species (Figure 6a-c), while suitability for humpback chub and Colorado pikeminnow were greater than 25% by 2040 (Figure 5a-b) at RKM0. Under all Fill Mead First and consumptive use alternatives, thermal suitability reached 100% for all warm-water non-native species evaluated at all locations in Grand Canyon by 2030 (Figure 6a-i).

The probability 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/yr 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,i).

Probability of presence of known barriers

Barriers at the inflows to Lake Powell (Piute Farms and Hite Waterfalls) had the highest annual probabilities of being present under the Fill Mead First alternative (Figure 8b,e; Table 2). 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/yr limits on Upper Basin use (Figure 8f). The probability 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,c). 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,i; Table 2). Annual probabilities of presence of Pearce Ferry Rapid declined between 2025 and 2030 across all consumption scenarios, but then increased as water levels declined over time, especially with no limits on Upper Basin use or only 5.0 maf limits (Figure 8h). The probability that Pearce Ferry Rapid remains a barrier in western Grand Canyon was lowest in the Fill Mead First and 3.0 maf/yr consumptive use alternative (Figure 8h).

DISCUSSION

If watershed runoff conditions typical of the 21st century persist, i.e., if the Millennium Drought continues, changes in water-supply management may necessitate changes in reservoir operations that will influence the amount and distribution of water in storage. Some reservoirs may be identified as sites to prioritize storage, and storage in other reservoirs may be considered secondary repositories. Reservoirs that remain relatively full will continue to produce hydroelectricity and release relatively cool water while those with lower water levels may not be able to consistently produce hydroelectricity and will release relatively warm water. If water storage in Lake Powell is not prioritized, the ability to implement designer flows may decrease, potentially limiting benefits to native fishes and the ability to disadvantage warm-water non-natives as river temperatures increase. Reservoirs that are relatively empty are likely to be fragmented from the inflowing riverine segments immediately upstream from each reservoir, thereby affecting the interactions between non-native, warm-water reservoir species and native, warm-water riverine fish. It may be difficult to maintain non-native, cool-water tailwater trout populations where reservoirs are relatively empty and consistently release warm water.

Identification of an optimal solution that responds to society's need for consumptive water use and yields desirable ecosystem outcomes partly depends on the ecosystem management goals defined for any part of the Colorado River system (Table 2). For example, if maintaining significant storage in Lake Powell is a priority to produce hydroelectricity, maintain relatively cool reservoir releases downstream, and maintain the opportunity to implement designer flows, limiting consumptive use may be the only water-supply management strategy available if the Millennium Drought persists. In this study, we focus on limits to Upper Basin use for simplicity, however, reductions are likely to be realized basin-wide (*e.g.,* lower basin shortages in 2022, Reclamation 2021c). Conversely, continuing the baseline policy of balancing reservoir storage in Lake Powell and Lake Mead or adopting a policy that prioritizes storage in Lake Mead is likely to yield completely different environmental outcomes. The different outcomes of decisions about how to manage consumptive water use and where to store water in reservoirs do 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). We believe the analysis provided here could be expanded and might provide important perspective to natural resource managers as they consult with water supply managers about how to meet the societal challenge of sustained drought.

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. Linking specific flow patterns to ecological responses is difficult (Davies et al, 2014), and benefits of designer flow releases have been uncertain (Korman et al, 2011, 2012; Finch et al, 2016) and sometimes have had unintended consequences (Korman *et al.* 2011). Despite these uncertainties, designer flows provide management flexibility. This flexibility may be more or less important under future conditions, such as warming river temperatures. Our understanding of the efficacy of designer flows has been focused on mitigating the effect of the baseline management policy, but it is likely that a completely different approach to designer flows may be necessary in the future.

Colorado River temperatures will likely increase in Grand Canyon (Mihalevich *et al.* 2020, Dibble *et al.* 2021) and predicting ecological responses to increased water temperature will be challenging. Our results suggested Colorado River temperatures in Grand Canyon will likely be warmer and more suitable for several native and non-native fishes if the Millennium Drought continues, even if water storage in Lake Powell is prioritized. While previous research has highlighted the importance of water storage decisions in determining future river temperatures downstream of Glen Canyon Dam (Dibble *et al.*, 2021), our results suggested the impact of water storage decisions is likely to be limited by how much overall water is available in the basin. Under continued drought conditions, only by maintaining or limiting consumptive use were reservoir levels in Lake Powell projected to be high enough to maintain relatively cool temperatures in Grand Canyon. Otherwise, the thermal regime of the Colorado River is likely to change greatly. The magnitude of temperature change in Grand Canyon will likely have significant impacts on both native fish and economically important tailwater fisheries, but there is immense uncertainty in those predictions. In the past decade, relatively low Lake Powell reservoir levels associated with increased river temperatures coincided with a shift in relative abundance of fishes in western Grand Canyon to be dominated by native fish instead of non-native fish (Van Haverbeke *et al.* 2017, Rogowski *et al.* 2018, Keggeries *et al.* 2020), but the role of temperature in this shift is unknown because Pearce Ferry Rapid (a potential barrier to non-native fish movement upstream from Lake Mead) developed around the same time. Despite this positive trend, it is difficult to predict how fish communities will respond to further increases in temperature. In the Upper Basin where some river segments retain more natural flow and temperature regimes, interactions with non-native species are hypothesized to limit native fish populations (Bestgen *et al.*, 2018; Bestgen, 2018), and 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). In addition to uncertain interactions between native and non-native fish, the importance of food limitation in a more metabolically demanding warmer river is also unknown, and some evidence suggests food limitation may already be an issue in Grand Canyon (Kelly *et al.*, 2013; Cross *et al.*, 2013; Dzul *et al.*, 2017; Korman *et al.*, 2020). Models considering the role of temperature in driving population dynamics, food limitation, and temperature-dependent interactions among native and non-native fish are necessary to obtain more specific predictions of native fish responses to increased river temperature.

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 consumptive water use continues to increase. The probability mean summer temperatures were above 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/yr) 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 in this economically important segment through increased resource demand (Marquet *et al.*, 2004; Brown *et al.*, 2004) and food limitation (Dodrill *et al.*, 2016; Korman *et al.*, 2020). These potential changes in trout populations could impact native fish populations. If warmer temperatures restricted trout populations to the Lees Ferry segment, this could potentially have positive outcomes for native fish in lower reaches where rainbow and brown trout can compete and prey on young native fish (Yard *et al.*, 2011), lowering survival of humpback chub juveniles (Yackulic *et al.*, 2018).

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 is 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). 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 Hite waterfall on the Colorado River arm of

Lake Powell. Should a barrier form in this location, 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. Since 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 that 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 to 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 2), 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.

SUPPORTING INFORMATION

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

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Table 1. Responses of metrics related to flow regime, river temperature, and fragmentation (drivers) to water storage and consumptive use alternatives was 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[5] Strongly influenced by reservoir elevations[6]	Temperature suitability for native and non-native fishes	First step at predicting how community structure might change in response to changes in temperature[4], 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, Power *et al.*, 1995; 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] Dibble *et al.*, 2021
[5] Hall *et al.,* 2015; Rüegg *et al.,* 2021
[6] Mihalevich *et al.*, 2020; Dibble *et al.*, 2021
[7] BOR and NPS, 2016
[8] Yard *et al.*, 2011; Korman *et al.*, 2016
[9] Hamman 1985; Tyus 1991; Minckley and Deacon, 1991; Irving and Modde 2000; Moyle, 1995; Cathcart *et al.* 2019
[10] Cathcart *et al.*, 2018; Kegerries *et al.*, 2020; Pennock *et al.*, 2020

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 Fill Powell First, 3.0 maf UB Limit	Fill Mead First, No UB Limit Fill Mead First, 5.0 maf UB Limit
Increase Native Fish Temperature Suitability	Fill Mead First, all use limits	Fill Powell First, 3.0 maf UB Limit Baseline, 3.0 maf UB Limit
Decrease Non-Native Fish Temperature Suitability	Fill Powell First, 3.0 maf UB Limit Baseline, 3.0 maf UB Limit	Fill Mead First, all use limits
Maintain Trout Fishery	Baseline, 3.0 maf UB Limit Fill Powell First, 3.0 maf UB Limit	Fill Mead First, all use limits
Support Movement of Native Fish above Lake Powell	Baseline, 3.0 maf UB Limit Fill Powell First, 3.0 maf UB Limit	Fill Mead First, all use limits
Block Upstream Movement of Non-native Fish from Lake Mead	Baseline, all use limits	Fill Mead First, 3.0 UB Limit Fill Mead First, 4.0 UB Limit

Figures

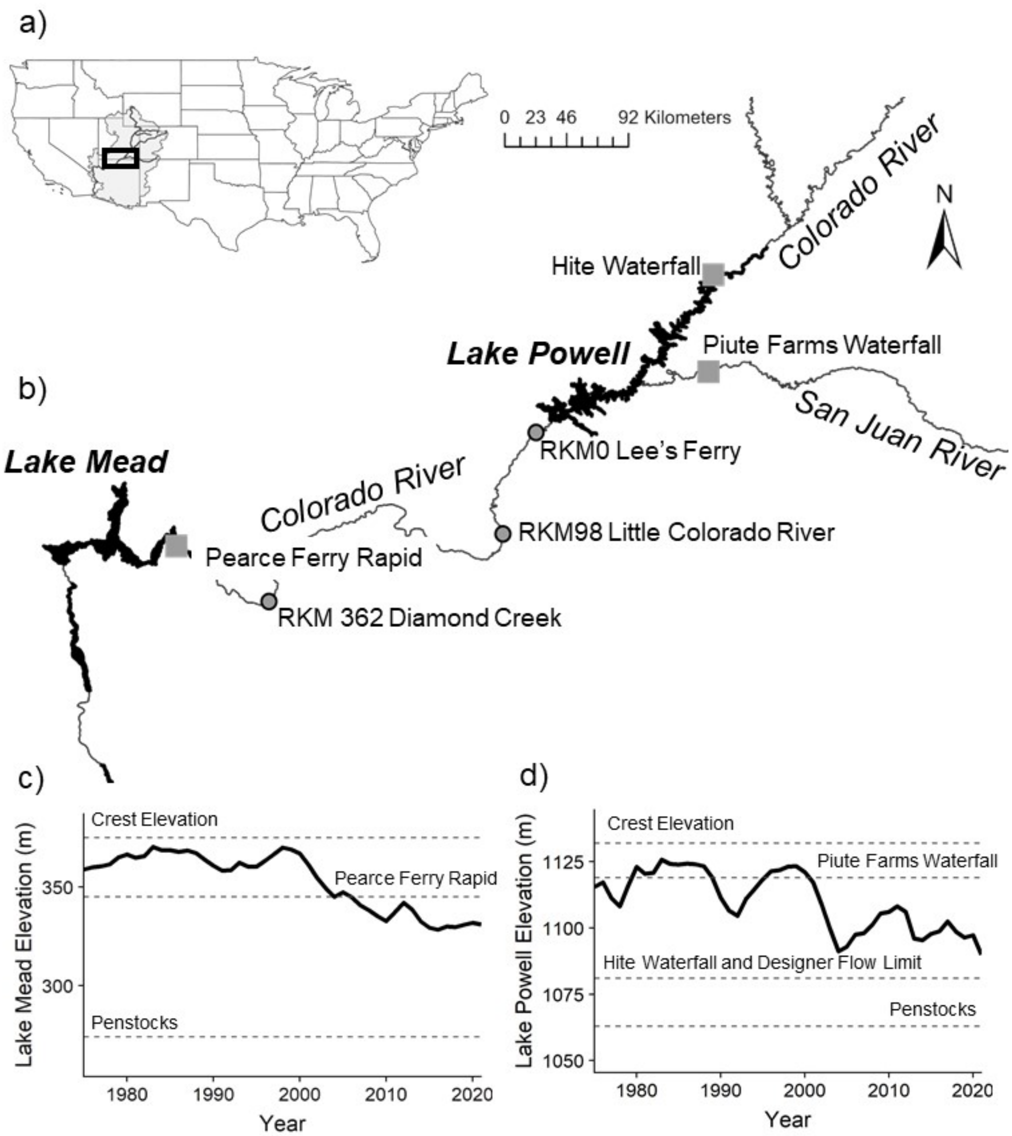

Figure 1. We quantified ecosystem responses to changes in storage decisions and consumptive use in the Colorado River basin, USA (a). We focused on temperature of the Colorado River between Lake Powell and Lake Mead reservoirs at three locations (b, grey circles) and barriers upstream of Lake Mead and Lake Powell (b, grey 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.

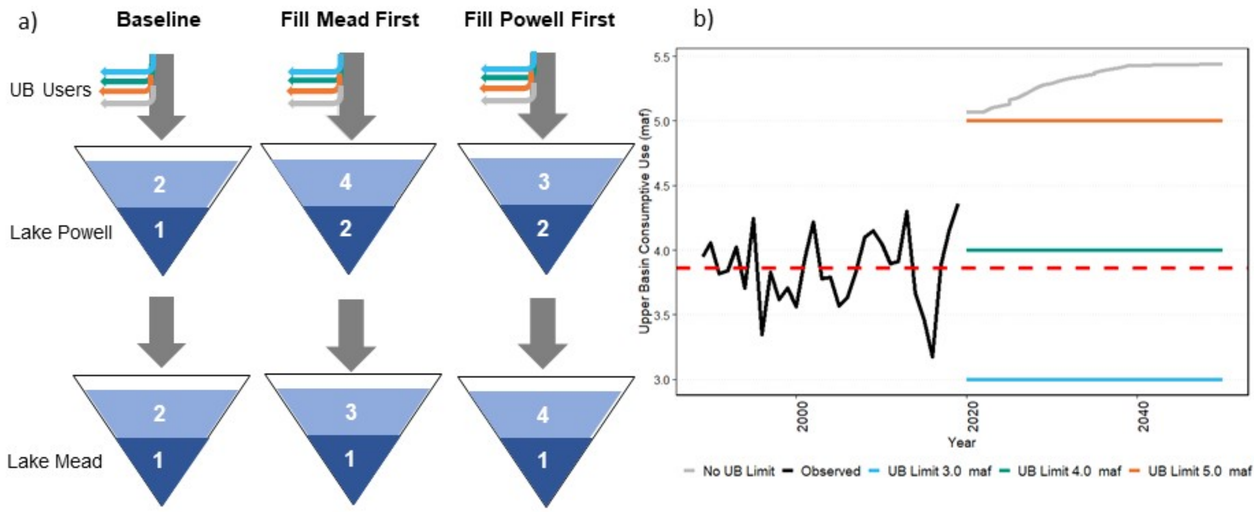

Figure 2. Alternative management paradigms included different combinations of Upper Basin (UB) demands and prioritizing storage in Lake Mead or Lake Powell reservoirs (a). Upper Basin demands either followed the URCRC 2007 demand schedule (b, "No UB Limit", grey) or were capped at 3.0 (blue), 4.0 (green), or 5.0 (orange) million acre-feet per year (maf, b). Numbers in Lake Powell and Lake Mead reservoir diagrams (a) represent priority zones and the order of reservoir filling.

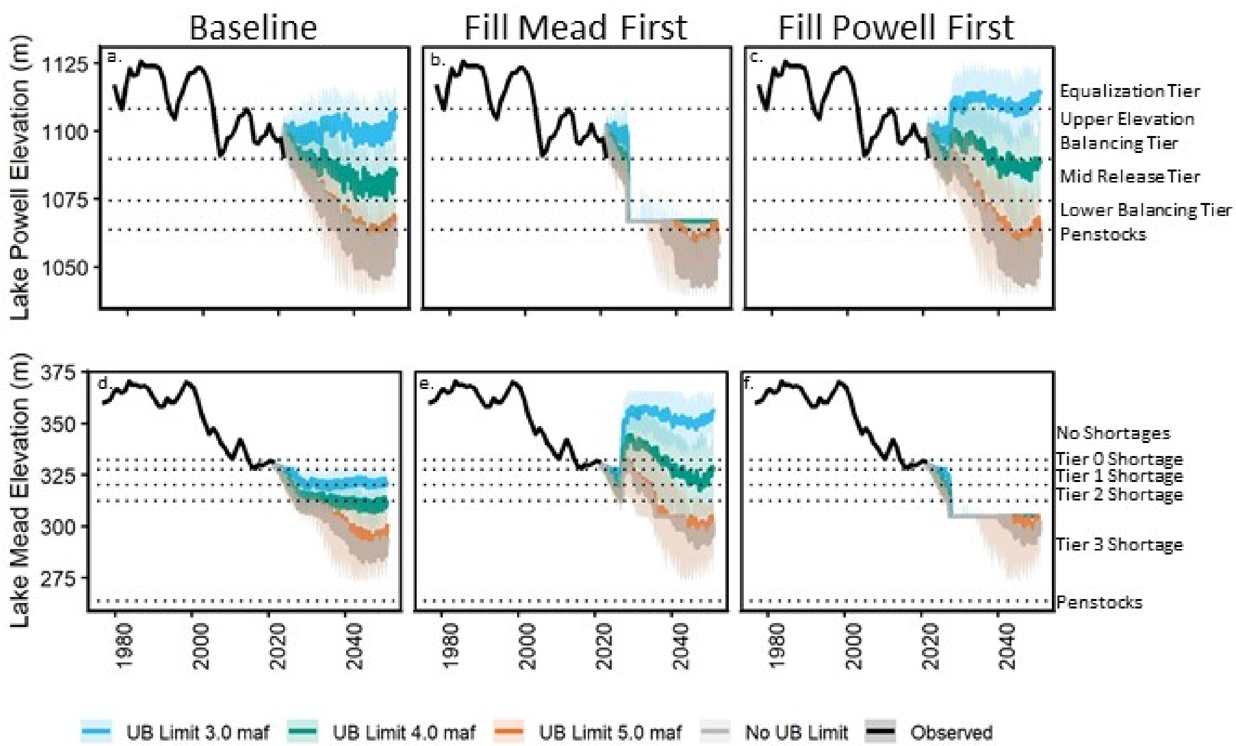

Figure 3. Lake Powell (top) and Lake Mead (bottom) historic (black) and projected elevations under combinations of the baseline, Fill Mead First, and Fill Powell First alternatives mixed with various Upper Basin (UB) limits on consumptive use. Dotted lines represent different thresholds for equalization releases from Lake Powell (top), shortages (in thousand acre-feet, kaf) to the Lower Basin defined by Lake Mead elevations (bottom) or the elevations of the penstocks in each reservoir.

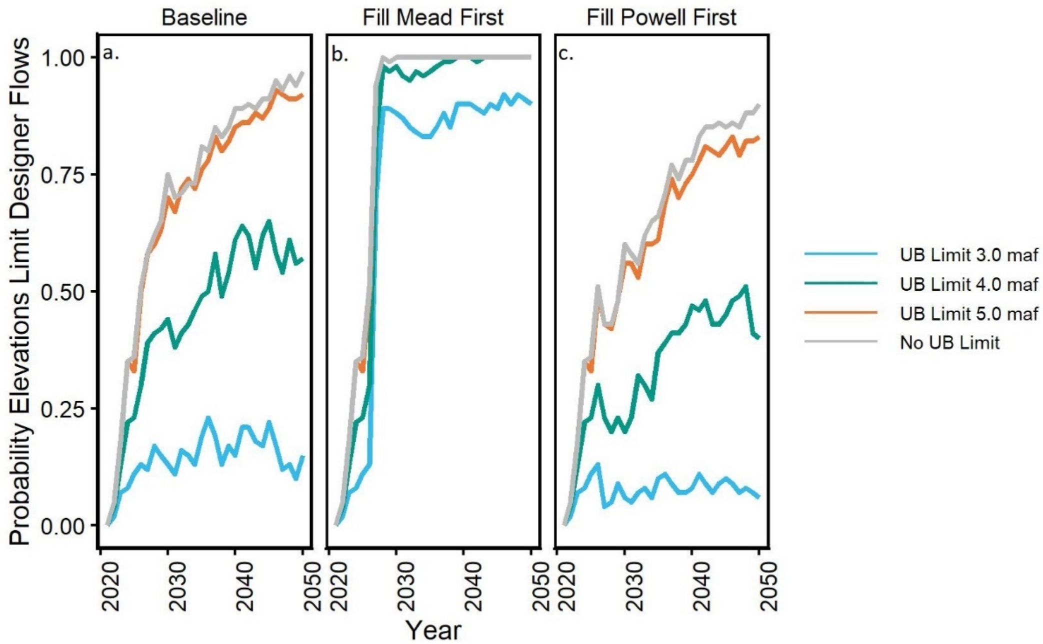

Figure 4. The probability that Lake Powell reservoir elevations will fall below 1082m, a threshold in which designer flows would likely cease to be implemented varied across storage and use alternatives. Probabilities were calculated as the number of hydrologic traces in which reservoir elevations fell below the threshold out of all 50 traces and were calculated across combinations of baseline conditions (a), the Fill Mead First (b), and the Fill Powell First (c) alternatives crossed with different Upper Basin (UB) limit scenarios.

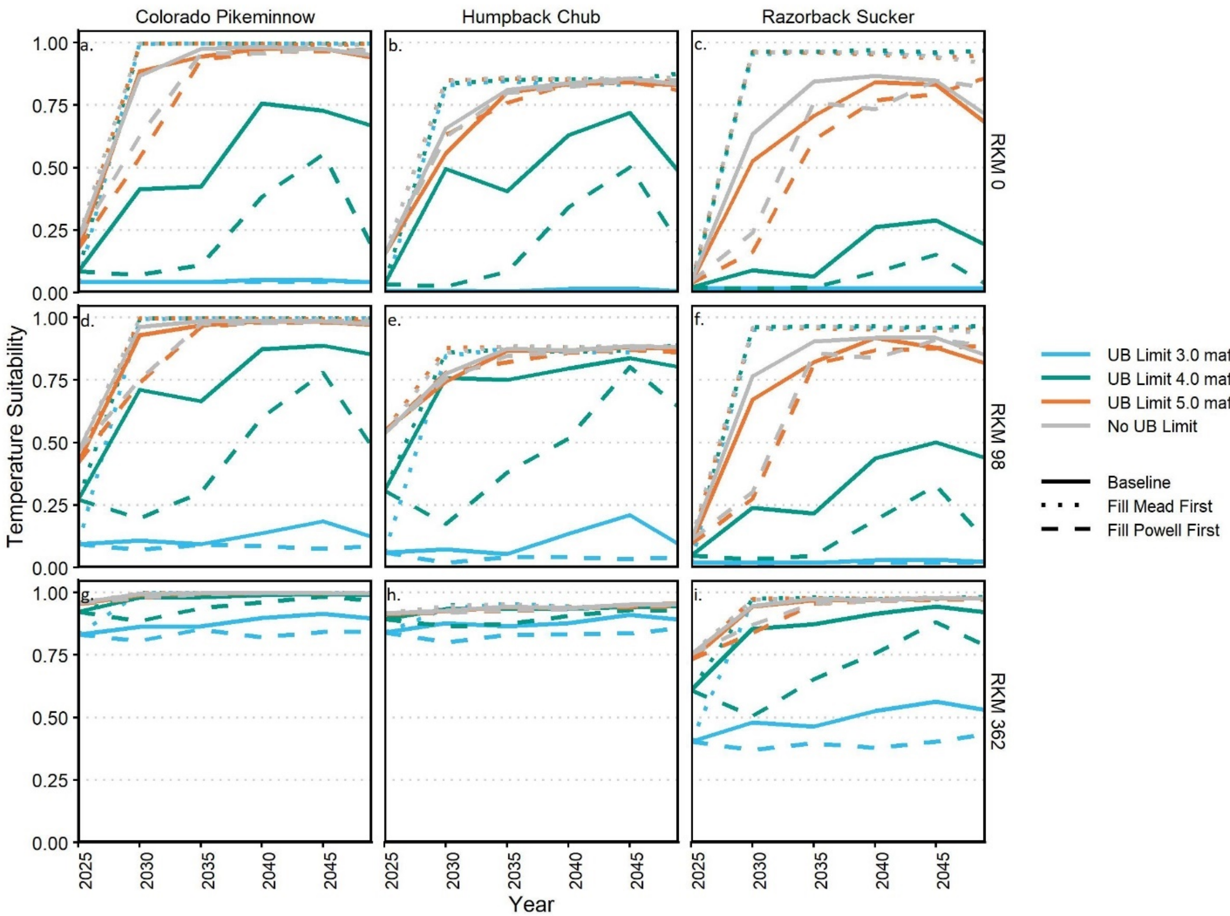

Figure 5. Temperature suitability for several native (Colorado pikeminnow, humpback chub, and razorback sucker) fish was measured using the model developed by Dibble *et al.* 2021 predicting the probability these species would be common or rare as a function of river temperature. Probabilities were calculated using predicted river temperatures at three locations along the Colorado River, including Lees Ferry (RKM0), 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, Fill Mead First, and Fill Powell First crossed with different Upper Basin (UB) limit scenarios. Lines represent medians of predicted probabilities of each species being common across hydrologic traces.

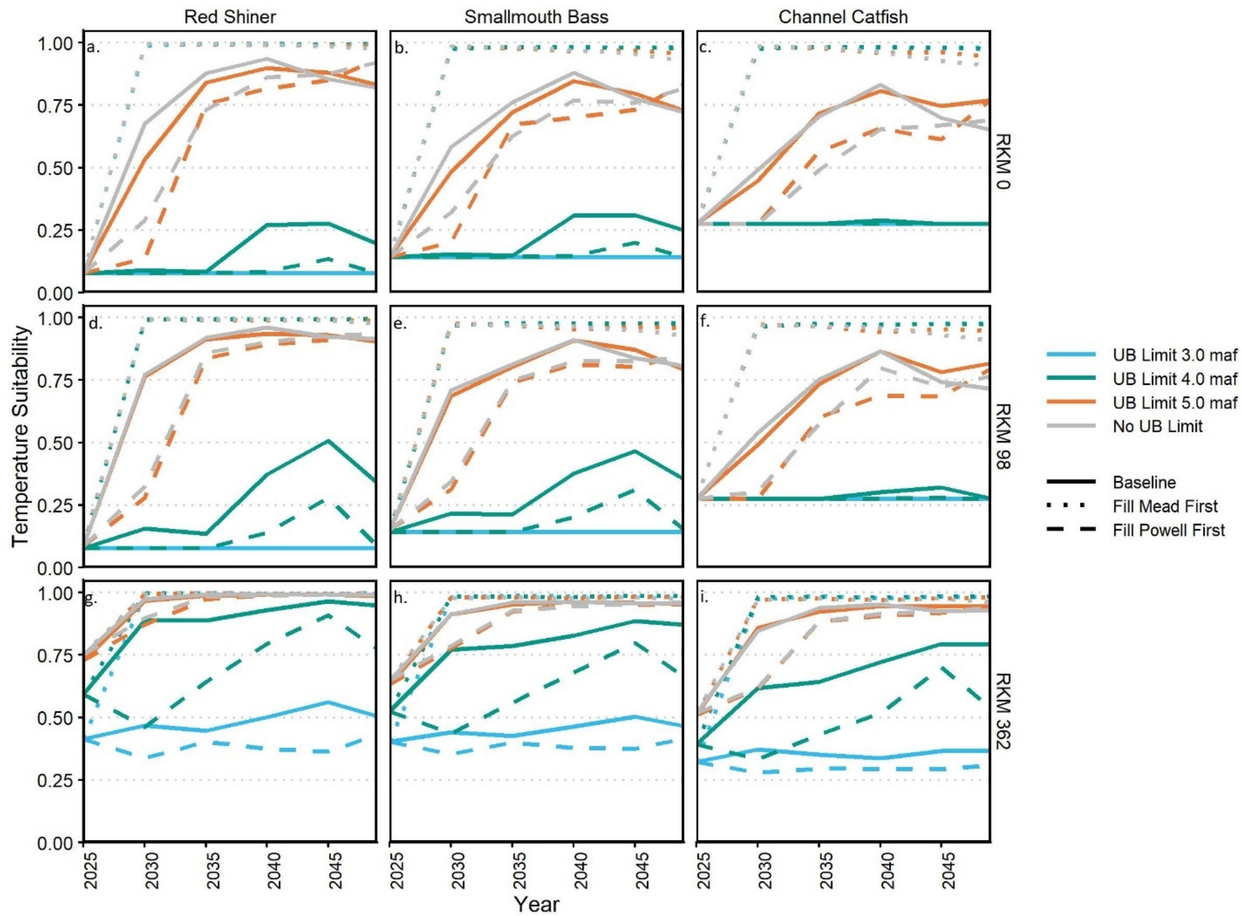

Figure 6. Temperature suitability for several non-native (red shiner, smallmouth bass, and channel catfish) fish was measured using the model developed by Dibble *et al.* 2021 predicting the probability these species would be common or rare as a function of river temperature. Probabilities were calculated using predicted river temperatures at three locations along the Colorado River, including Lees Ferry (RKM0), 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, Fill Mead First, and Fill Powell First crossed with different Upper Basin (UB) limit scenarios. Lines represent medians of predicted probabilities of each species being common across hydrologic traces.

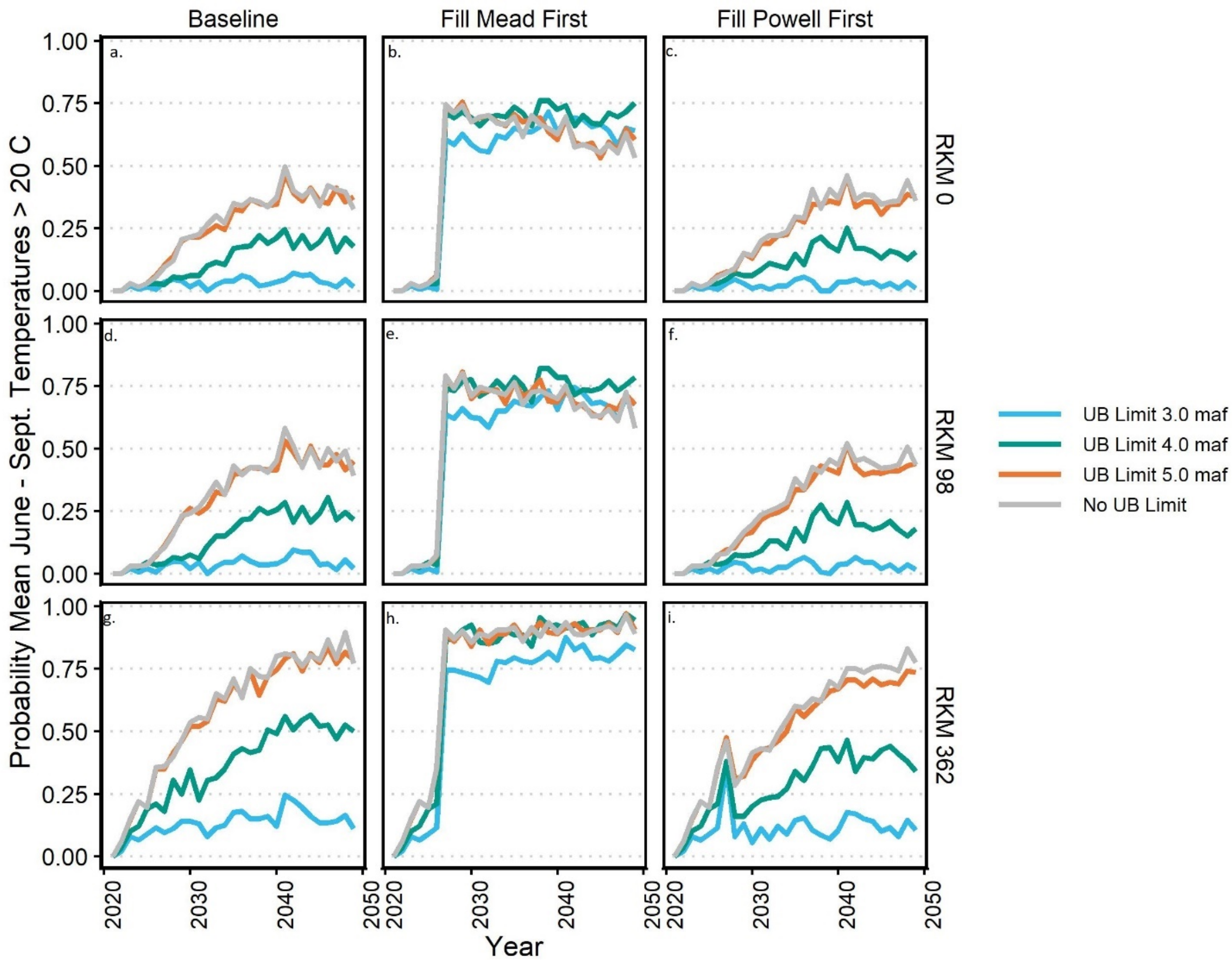

Figure 7. The probability mean summer (June through September) temperatures would exceed 20 °C, the predicted sustained upper tolerance for brown and rainbow trout, increased over time at three locations along the Colorado River downstream from Glen Canyon Dam. Probabilities were calculated as the number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

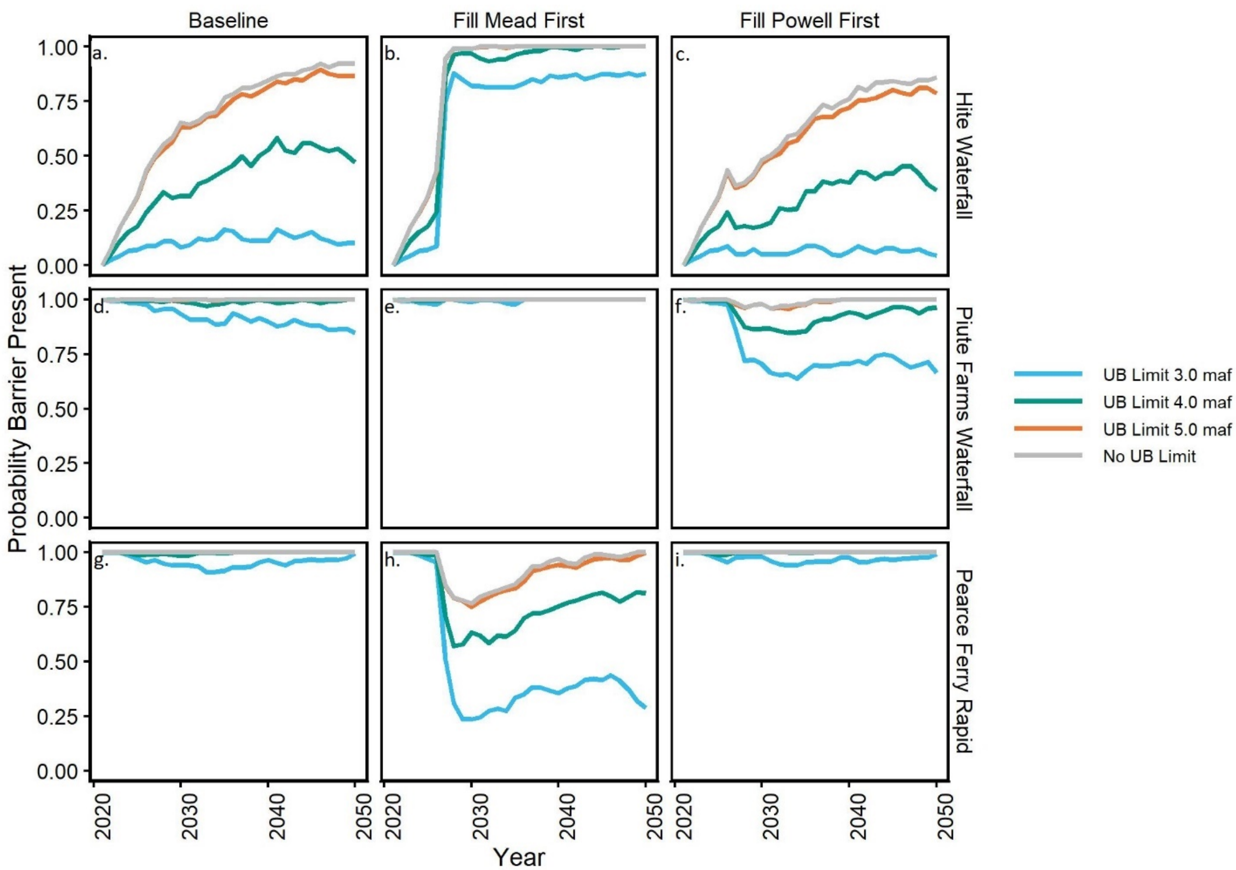

Figure 8. The probability three barriers, including the Hite Waterfall on the Colorado River arm of Lake Powell, Piute Farms Waterfall on the San Juan River arm of Lake Powell, and Pearce Ferry Rapid on the Colorado River upstream from Lake Mead will be present under future management alternatives. Probabilities 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, Fill Mead First, and Fill Powell First alternatives crossed with different Upper Basin (UB) limit scenarios.