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Water storage decisions will determine the distribution and persistence of imperiled river fishes

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Abstract. Managing the world's freshwater supply to meet societal and environmental needs in a changing climate is one of the biggest challenges for the 21st century. Dams provide water security; however, the allocation of dwindling water supply among reservoirs could exacerbate or ameliorate the effects of climate change on aquatic communities. Here, we show that the relative sensitivity of river thermal regimes to direct impacts of climate change and societal decisions concerning water storage vary substantially throughout a river basin. In the absence of interspecific interactions, future Colorado River temperatures would appear to benefit both endemic and nonnative fish species. However, endemic species are already declining or extirpated in locations where their ranges overlap with warmwater nonnatives and changes in water storage may lead to warming in some of the coolest portions of the river basin, facilitating further nonnative expansion. Integrating environmental considerations into ongoing water storage negotiations may lead to better resource outcomes than mitigating nonnative species impacts after the fact.

Key words: climate change; Colorado River; dam operations; drought; endangered species; endemic fishes; nonnative species; reservoir storage; water policy; water temperature.

Introduction

Reservoir operations that govern water storage and its release downstream are typically determined by large-scale water-supply policy that rarely considers ecological impacts to the river segments between reservoirs (Bair et al. 2019). River regulation has fragmented rivers on a global scale, altered natural flow regimes, disrupted sediment and organic material flux, severed long-distance fish migrations, and created thermal discontinuities that profoundly influence aquatic communities (Ward and Stanford 1983, Schmidt and Wilcock 2008, Poff and Zimmerman 2010). Below large reservoirs, changes in storage affect river temperature and by extension aquatic communities. When full, most large reservoirs stratify and release cold water from the hypolimnion, and there is little seasonal variation. When relatively empty, water released from these same reservoirs is warmer, because withdrawals occur from the epilimnion (Caissie 2006, Olden and Naiman 2010). As such, the extent of thermal modification can be strongly correlated with the depth of reservoir withdrawals (Appendix S1: Fig. S1).

Human consumption of water supply is expected to exacerbate climate-driven reductions in water availability in many areas (Haddeland et al. 2014), especially in arid regions already experiencing intensified drought and warming air temperatures (Udall and Overpeck 2017, Xiao et al. 2018). In some arid regions where water supply is already fully appropriated for human consumption, any additional decrease in water availability due to climate change will force reconsideration of longstanding water-supply allocation agreements, with inevitable changes in the rules governing reservoir storage and

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operation. We hypothesize that decisions arising from the renegotiation of water supply agreements have the potential to exacerbate or ameliorate the direct thermal effects caused by a warming climate on river segments below large reservoirs because the depth of water withdrawals can have a profound effect on riverine thermal regimes.

The Colorado River basin (hereafter, "basin") is among the most highly regulated and overallocated river networks in the world, having the largest ratio of reservoir storage to mean annual flow in North America (Hirsch et al. 1990). The basin is also experiencing increasing air temperatures and declining watershed runoff, with subsequent reductions in water available for human consumption (Brekke et al. 2013, Udall and Overpeck 2017). Basin reservoirs, including the two largest in the United States, Lakes Mead and Powell, store water to support agriculture, large human populations, and regional economies of the United States and Mexico. The administrative framework that governs management of the river is known as *The Law of the River* and includes a bi-national treaty and its amendments, federal and state laws, a Supreme Court ruling, records of decisions arising from environmental impact statements, and other agreements. Starting in 2020, stakeholders will begin renegotiations concerning water supply allocation and reservoir operations that will shape releases and storage volumes in response to future drought and water shortages. These negotiations have the potential to further alter thermal regimes through reservoir releases, and as such, native and nonnative fish assemblages across the basin.

The Colorado River basin was historically home to more than thirty mostly endemic native fish species, including the four "big river" fishes that are federally endangered: Colorado pikeminnow (*Ptychocheilus lucius*), razorback sucker (*Xyrauchen texanus*), humpback chub (*Gila cypha*), and bonytail (*Gila elegans*) (Minckley and Deacon 1991, Mueller and Marsh 2002). Dams, diversions, and reservoirs have fundamentally changed the physical and biological template of the river and opened niche space for nonnative species through stabilization of flow regimes and thermal regime impairment (Olden et al. 2006, Bestgen and Hill 2016). In recent decades, rapidly spreading opportunistic nonnative fish have contributed to observed declines in native species (Martinez et al. 2014, Bestgen et al. 2018).

Here, we focus on the nexus among water-supply allocation policy, riverine thermal regimes controlled by reservoir releases, and fish community dynamics, and we examine how these relations might change in a warming climate where Colorado River watershed runoff declines. We describe the current thermal regime and its suitability for fish communities, predict water temperatures under climate change scenarios and water allocation strategies, and consider potential responses of native and nonnative fish populations to anticipated changes in water temperature. Further, we illustrate how societal decisions concerning water supply have the potential to trigger changes in fish communities across this highly engineered riverscape.

Methods

Water temperature model

We modified a heat-exchange model previously described by Wright et al. (2009) and empirically estimated parameters by fitting relationships to monthly average water temperature data collected from 1985 to 2015 at 44 gages along the Colorado, Gunnison, Green, Yampa, Duchesne, White, San Juan, and Animas rivers (Appendix S2). Solar radiation and air temperature represent the primary components in the simplified heat budget that determines river temperature. Our model also accounted for major tributaries (i.e., mean annual flow ≥10% of the mainstem river). To estimate model suitability, we first fit the model to data from odd years and used data from even years to calculate the root mean square error (RMSE) and overall bias of out-of-sample prediction aggregated by river segment and month of year (Appendix S2: Table S5). We then fit the model using all data, producing estimates with similar means, but higher precision, and used these estimates to predict water temperatures for the current period (1985–2015) at a 1-river-kilometer (rkm) resolution along 2,560 rkm of river.

Linking fish to temperature

We linked the distribution of native and nonnative species to river temperatures by first developing a thermal suitability metric for each of six important fish species based on literature review (Appendix S3), and then fitting a generalized linear mixed model using this thermal suitability metric to predict the current status of each species in 16 river segments in the basin. The six species we modeled include three of the four endangered big-river fishes: Colorado pikeminnow, razorback sucker, and humpback chub. The fourth, bonytail, is extremely rare (Minckley and Deacon 1991). We also included three warmwater nonnative species in our analysis, smallmouth bass (*Micropterus dolomieu*), red shiner (*Cyprinella lutrensis*), and channel catfish (*Ictalurus punctatus*); these species have likely contributed to the decline of endangered big-river fishes via competition and predation (Johnson et al. 2008, Bestgen et al. 2018). We calculated the thermal suitability metric for each species in each segment by comparing monthly average water temperatures to the minimum, maximum, and optimal range of temperatures for growth of that species (Appendix S3: Table S1), and assigned a score from 0 (temperature too high or too low) to 1 (optimal temperature), with fractions when temperatures were within minimum and maximum but not within the optimal range. These proportions were multiplied by the number of days in a month and summed across months. We categorized the status of each species as “never present,” “extirpated,” “rare,” or “common/abundant” following Holden and Stalnaker (1975) using recent data from fish sampling efforts, government reports, and journal articles (Appendix S3: Table S2). For our analysis, we excluded river segments with a “never present” status for a given species and classified extirpated/rare as 0 and common/abundant as 1. One exception was Colorado pikeminnow, which have not been common anywhere since the early 1900s when Laguna Dam was constructed (Mueller and Marsh 2002), so we classified extirpated as a 0 and rare a 1 (Appendix S3: Table S2). The generalized linear mixed model included random intercepts and slopes for species, a logit link, and a binomial error structure.

Case studies

While we hypothesized that thermal suitability would correlate with the current status of both native and nonnative fish species (see *Linking fish to temperature*), we were also aware the long-term trend of the three native species was declining in segments that also support large populations of warmwater nonnatives. To highlight this important nuance, we summarized population-level data for humpback chub and Colorado pikeminnow as case studies relative to data on warmwater nonnatives. We compare Colorado pikeminnow abundance estimates to smallmouth bass removal efforts, which were modest prior to 2003 because the species had just invaded. Large smallmouth bass numbers in 2007 and 2012–2014 portray possible future responses where warm low flows may prevail.

Future water temperature scenarios

We used air temperature predictions from CMIP3 (SRES A.1B) and CMIP5 (RCP 4.5) models (n = 109) to understand how climate change under moderate (somewhat reduced by mitigation) greenhouse gas emissions may change air temperatures by mid-century (2040–2059) relative to 1950–1999. On average, air temperatures in the basin are predicted to increase by 1.85°–3.01°C per month by mid-century, averaging ~2.6°C on an annual basis (Brekke et al. 2013). An annual air temperature increase of ~2.6°C would reduce mean annual flow in the basin by ~17% through greater evaporation, evapotranspiration, and sublimation, among others (Udall and Overpeck 2017). We used predicted increases in monthly air temperature per Brekke et al. (2013), combined with predicted declines in Colorado River flow from Udall and Overpeck (2017), as inputs into our “climate change only” model (Appendix S2: Table S6).

For our “storage + climate change” scenario, we used nonlinear regression (least squares) to predict reservoir release temperatures as a function of storage elevation by month, which permitted an assessment of the degree to which changes in reservoir storage affect riverine thermal regimes relative to climate warming alone. This analysis included data spanning 1965–2015 from five large storage reservoirs in the basin (Fontenelle, Flaming Gorge, Navajo, Glen Canyon, Hoover; Appendix S2: Table S6). The predicted water temperature associated with the lowest recorded storage elevation for each reservoir was used to predict potential warming of releases if storage was deemphasized. As such, the low storage adjustment (Δ°C) represents predicted river temperature at the lowest storage after reservoirs initially filled relative to the base model (Appendix S2: Table S6). We calculated future thermal suitability and predicted status by fish species, in the absence of species interactions, using outputs from the climate change only and storage + climate change scenarios and compared outputs to current conditions.

Uncertainty

While our approach does not consider the full uncertainty in climate change forecasts, there is equal or greater uncertainty in how monthly flows out of or storage in reservoirs in the basin will be managed, because the rules for these decisions are currently being negotiated. There is also considerable uncertainty in nonflow management alternatives that may be developed to mitigate threats posed by warmwater nonnatives. Our intent in comparing scenarios is to highlight the potential importance of reservoir storage decisions for water temperature and fish communities, acknowledging that more detailed modeling that fully incorporates uncertainties is an important next step. Data, models, and code generated during this study are available from the USGS ScienceBase-Catalog (Dibble et al. 2020).

Results

Water temperature model

The mean signed error (bias) of our water temperature model was −0.003°C and absolute error (RMSE) averaged 0.5°C. By month, RMSE ranged from 0.4°C to 0.6°C. For individual river segments, signed error ranged from −0.2°C to + 0.1°C and RMSE ranged from 0.3°C to 1.2°C, with most segments <0.7°C (Appendix S2: Table S5). We used parameters from the model that incorporated all data from 1985 to 2015 to generate temperature predictions throughout the basin at a 1-rkm resolution (Fig. 1). Different segments differ in the timing of their warmest six-month period (Appendix S2), the degree of discontinuity created by reservoirs (also see Appendix S1: Fig. S1), and the downstream rate of temperature recovery (Fig. 1). Artificially cold release temperatures persist over the entire length of some river segments, such as the Colorado River downstream from Lake Powell (476 rkm), never approximating ambient temperatures. In contrast, cool release temperatures in

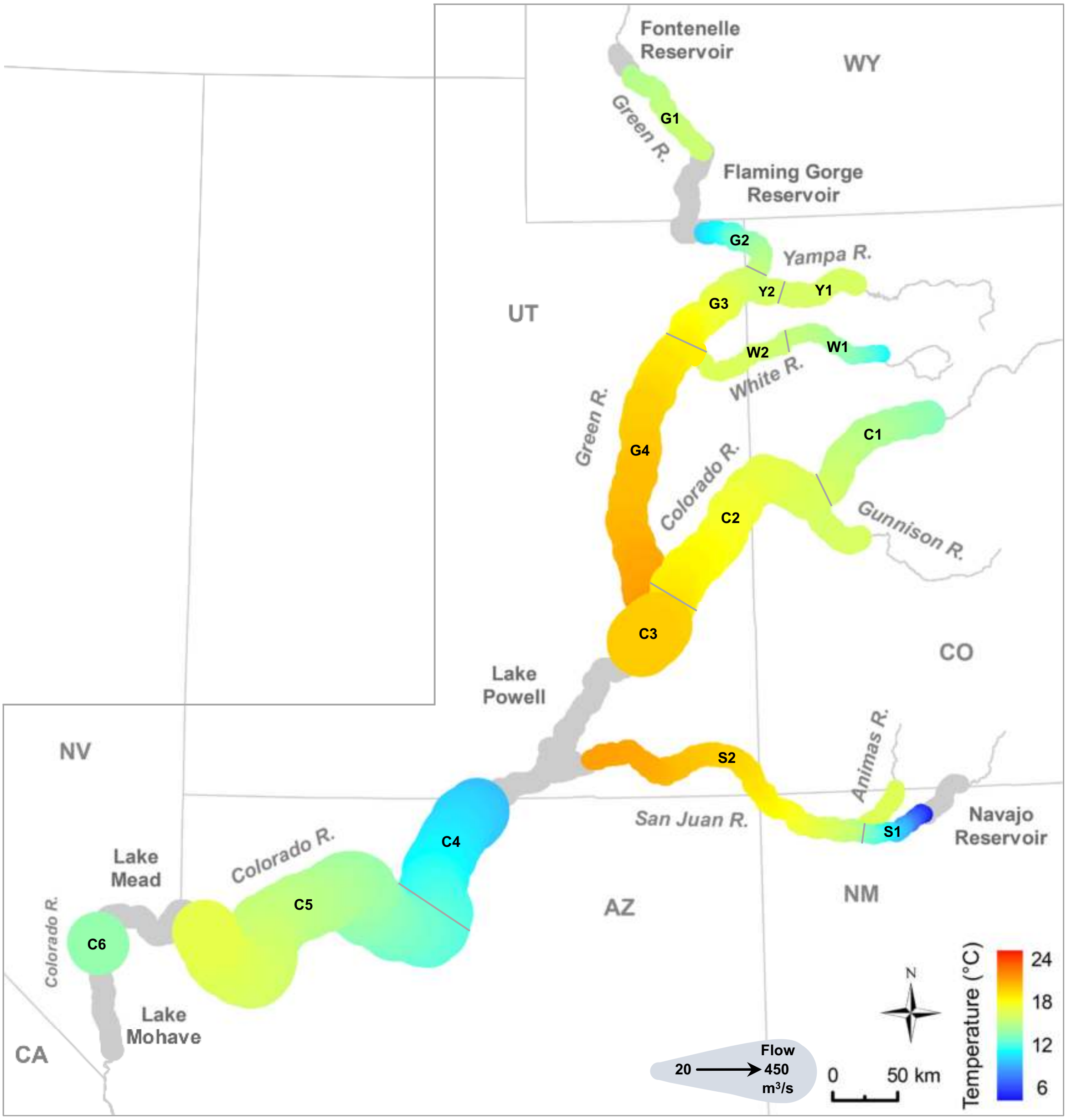

Fig. 1. Predicted river temperatures from the base model for the warmest growing season months by river segment (see Appendix S2). Segment width is proportional to mean monthly flow. States are WY, Wyoming; UT, Utah; CO, Colorado; NV, Nevada; AZ, Arizona; NM, New Mexico; CA, California.

the Green River downstream from Flaming Gorge Reservoir persist for ~90 rkm but then nearly equilibrate to unregulated tributary temperatures at the Yampa River confluence, 105 km downstream (Fig. 1).

Fish status and trends

There was a positive relationship between thermal suitability and current status for all six fish species (Appendix S3: Tables S3, S4); however, closer examination of trends in humpback chub and Colorado pikeminnow illustrate the importance of interspecific interactions. In our statistical model describing current status, nonnative species all had higher slopes (and intercepts) than endangered species, indicating greater nonnative species response to increasing thermal suitability (Fig. 2; Appendix S3: Table S4). Throughout the basin, humpback chub populations have declined where warmwater nonnative species are common (red arrows) and are increasing where these species are rare (blue arrows, Fig. 3a). The greatest increases in humpback chub populations have occurred in segments where thermal

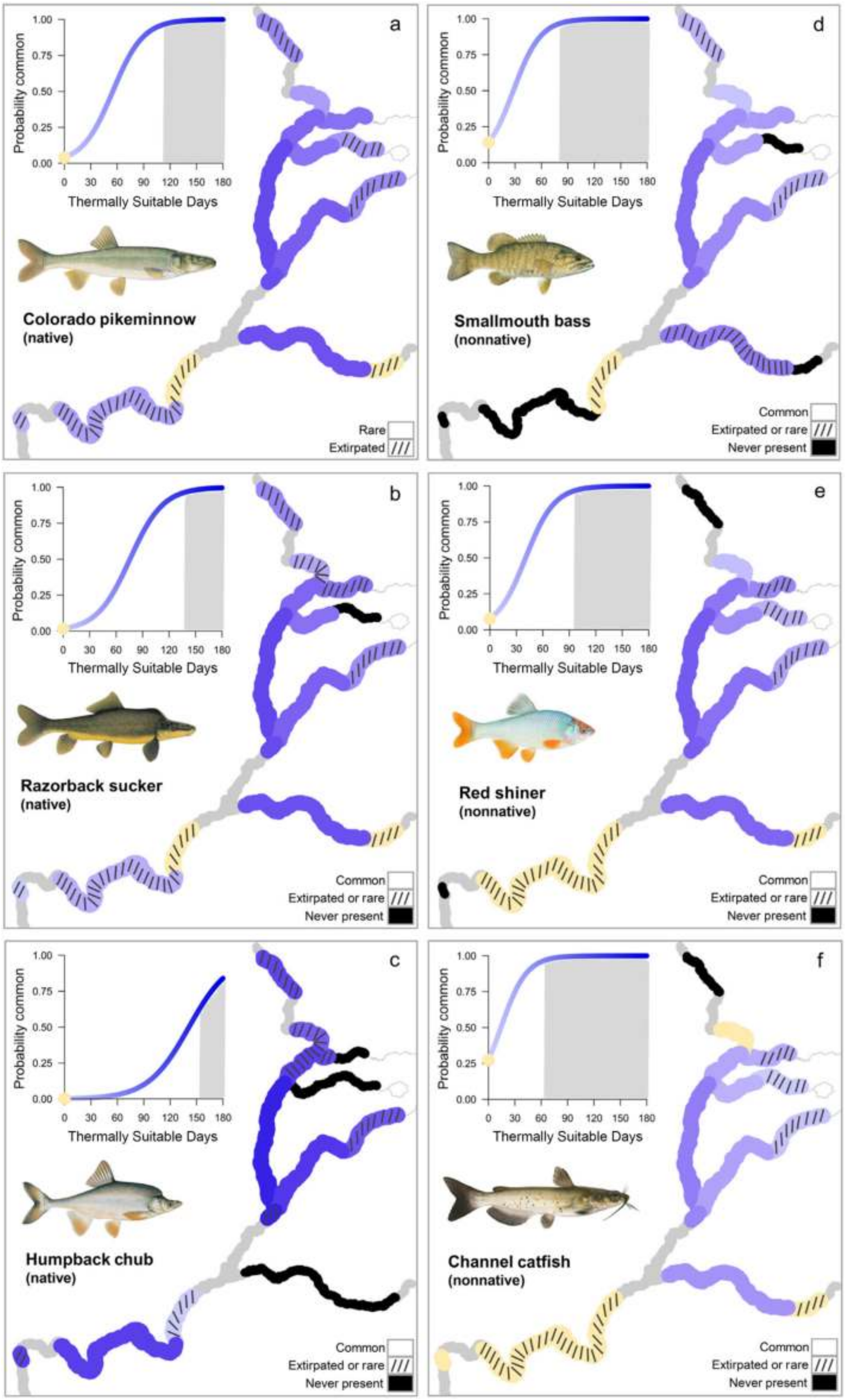

Fig. 2. Thermal suitability for (a) Colorado pikeminnow, (b) razorback sucker, (c) humpback chub, (d) smallmouth bass, (e) red shiner, and (f) channel catfish. Maps include a logistic regression of the probability a species is common relative to the number of thermally suitable days (TSDs) from the base model. Gray on LR plots shows predictions beyond the data range; orange, zero TSDs; purple, increasing thermal suitability; black, species never present; hash marks, current species status. Illustrations: Joseph R. Tomelleri.

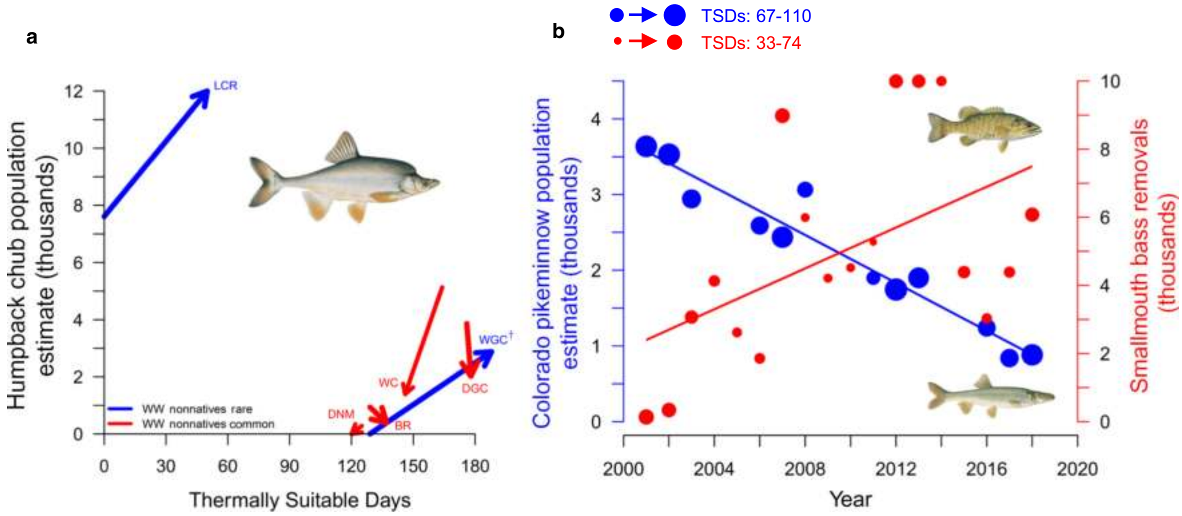

Fig. 3. (a) Mean humpback chub population estimates for Dinosaur National Monument (DNM), Desolation/Gray Canyons (DGC), Black Rocks (BR), Westwater Canyon (WC), Little Colorado River (LCR), and western Grand Canyon (WGC) relative to TSDs. A dagger † indicates estimate based on a portion of the population. Arrow bases represent 1990–1999 or 2000–2009, arrow tips represent 2010–2018. Red arrows represent overlap with warmwater (WW) nonnatives, blue lack overlap. (b) Adult Colorado pikeminnow estimates in the Green, Yampa, and White rivers (819 rkm; G3, G4, Y1, Y2, W2 in Fig. 1; blue), compared to smallmouth bass removed from a subset of that reach (247 rkm; G3, Y2 in Fig. 1; red). Smallmouth bass removals from 2012 to 2014 (15,750, 21,869, and 10,187, respectively) capped at 10,000 to better show patterns. Point size proportional to TSDs. Illustrations: Joseph R. Tomelleri.

suitability has increased *and* nonnatives are rare, illustrating the interactive effects of water temperature and nonnative abundance (Fig. 3a). Similarly, Colorado pikeminnow are not currently found anywhere in the absence of nonnatives, and their rate of decline has increased concomitant with increases in warmwater nonnative fish, likely due to reduced juvenile survival leading to low recruitment and a smaller adult population (Fig. 3b). Notably, smallmouth bass populations have increased, requiring intensive removal efforts, even though the habitat is currently less thermally suitable for this species than Colorado pikeminnow (Fig. 3b). This is likely because nonnative fish have a higher probability of being common in habitats with fewer thermally suitable days (Fig. 2).

Future scenarios

Climate change will increase water temperatures throughout the basin; however, water storage decisions have greater potential to impact water temperature in some river segments. Upstream from Lake Powell, release temperatures are less dependent on storage levels, and warming occurs quickly downstream from reservoirs, so storage decisions are not as significant for thermal regimes as the direct impacts of climate change on air temperature and river flows. For example, the biggest change in thermal regime for the Green and San Juan rivers occurs from the base model (interior color, Fig. 4a) to the climate model (middle color), whereas additional heating from the storage model (exterior color) is minimal. In contrast, release temperatures from Lakes Powell and Mead are very sensitive to reservoir elevation and warming is relatively slow. Warming temperatures increased thermal suitability for most species in most river segments (Figs 4b–g; Appendix S3: Table S3). Consequently, models that ignore species interactions suggest increasing probabilities that both native and nonnative species will become common in areas where they are not already common. Similar to raw temperature predictions, thermal suitability predictions are more sensitive to climate change in the upper portions of the basin, and more sensitive to water storage decisions below the large dams lower in the basin.

Discussion

Fish are ectotherms, and as such, the thermal regime of their environment is critically important in determining species distribution, abundance, and growth (Neuheimer and Taggart 2007, Isaak et al. 2017, Yackulic et al. 2018). There is substantial overlap in the thermal suitability of river segments for growth of warmwater native and nonnative fishes across the basin, and current evidence suggests nonnative species have a competitive or predatory advantage over native species in places where their ranges overlap (Olden et al. 2006, Johnson et al. 2008). Our analysis demonstrates that nonnative species in the basin have responded more strongly to recent river warming than native species. Thus, in the absence of effective management interventions, future warming is likely to disproportionately benefit nonnative species to the detriment of native species.

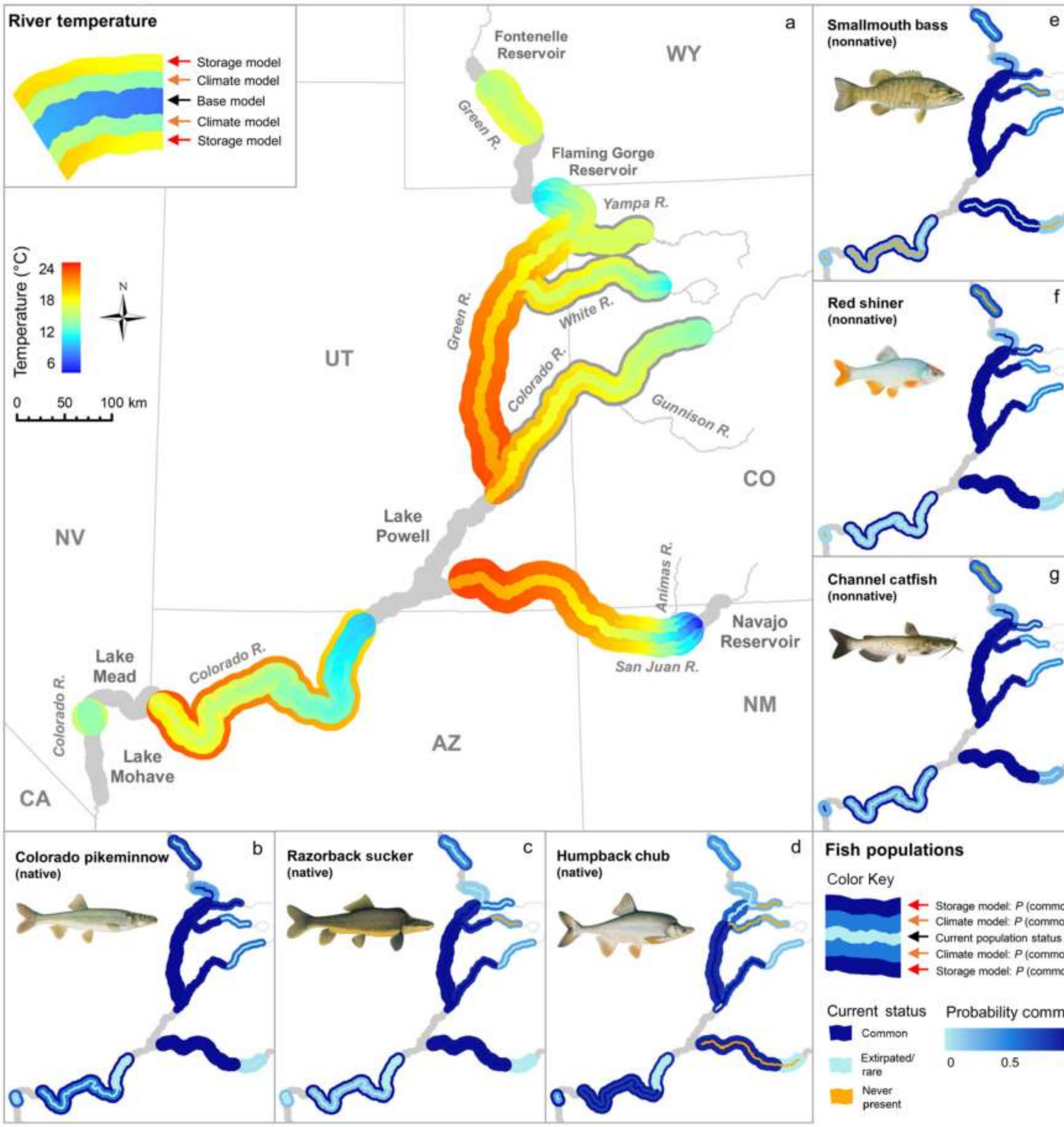

FIG. 4. (a) Predicted river temperatures in the warmest months for the base (interior), climate (middle), and storage models (exterior). Water temperatures not substantially influenced by reservoir storage decisions shaded in gray (exterior). Probability (b) Colorado pikeminnow, (c) razorback sucker, (d) humpback chub, (e) smallmouth bass, (f) red shiner, and (g) channel catfish will become common based on predicted TSDs. Interior color represents current species status, middle and exterior colors indicate probability the species will become common based on predicted temperatures from the climate and storage models, respectively. Projections in reaches where fish species were historically absent can be interpreted as future thermal suitability. Illustrations: Joseph R. Tomelleri.

Resource managers are currently exploring flow management strategies to suppress smallmouth bass reproduction while also benefitting native endemic species through the timing of flood disturbance events (Bestgen and Hill 2016). These types of designer flood-flow regimes have been evaluated in other southwestern U.S. rivers to maximize spawning and recruitment benefits to native fishes while disadvantaging nonnative predators (Tonkin et al. 2020). If flow management strategies are successful, then prioritizing storage rules that provide water for these flows will be important for the recovery of listed species. Upcoming renegotiations of storage rules are likely to consider how much water is consumptively used and where reservoir water is stored during periods of extended drought, thereby determining the proportional changes in mean annual streamflow in different parts of the river network. Since less than 10% of the total reservoir storage capacity of the entire watershed occurs in reservoirs upstream from Lake Powell, modifying water storage rules to provide maximum flexibility in implementing designer flows will have a minimal impact on overall storage compared to the debate over the allocation of storage between the two largest reservoirs in the United States: Lakes Powell and Mead.

Recent declines in Lake Mead elevation have increased the extent of the Colorado River in western Grand Canyon by more than 100 rkm, and this warming river segment is now dominated by native fish species (Van Haverbeke et al. 2017, Rogowski et al. 2018, Kegerries et al. 2020). Lake Mead reduction below 346 m above sea level (masl) has also led to the development of Pearce Ferry Rapid, where the river has cut through the reservoir delta outside the original channel, such that water now flows over a bedrock ledge. Fish biologists hypothesize this rapid is a barrier to movement of warmwater nonnative fishes from Lake Mead into upstream habitats that are currently suitable for nonnatives. Thus, if storage in Lake Powell were prioritized over Lake Mead in the future, Pearce Ferry Rapid would likely be maintained, but water temperatures in eastern Grand Canyon may return to unsuitably cold conditions for native fish species, similar to the 1980s and 1990s. Alternatively, prioritizing storage in Lake Mead over Lake Powell could lead to warmer water temperatures throughout Grand Canyon improving its thermal suitability for native and nonnative species alike. Two of the three native species we modeled (humpback chub, razorback sucker) are already present in this river segment and could benefit from improved thermal conditions, assuming of course that warmwater nonnatives can be effectively managed. Colorado pikeminnow, the third species we modeled, was last recorded in Grand Canyon in 1972 and it is thought that unfavorable thermal conditions played a major role in their extirpation; more favorable thermal conditions in Grand Canyon might aid potential reintroduction and recovery efforts for this species. The strategy of prioritizing storage in Lake Mead over Powell would also open more than 100 rkm of riverine habitat upstream from Lake Powell in the lower San Juan and upper Colorado rivers. However, management of nonnatives in Grand Canyon under this scenario would be especially problematic because it could remove barriers to invasions by warmwater nonnatives from both Lake Mead via elimination of Pearce Ferry Rapid, and Lake Powell via elimination of the cold to cool-water barrier. An intermediate strategy would be to maintain the current, modified thermal regimes and physical barriers to invasion that exist in Grand Canyon by installation of selective water withdrawal on upstream Glen Canyon Dam or by maintaining intermediate storage levels in Lake Powell. This strategy would prevent water temperatures in Grand Canyon from recovering to natural patterns but may support persistence of the native-dominated fish community and aid continued growth and recovery for endangered humpback chub and razorback sucker by suppressing nonnative species.

Policy makers will soon commence a formal renegotiation process of the 2007 Interim Shortage Guidelines that are part of the *Law of the River*. This renegotiation has the potential to shape water policy across the basin for the next few decades. Central to this discussion will be allocation of the basin's dwindling water supply and changing the rules of reservoir storage and operation. During past negotiations, the consideration of impacts of storage decisions on resources in the intervening river segments between dams have not been a priority. However, as our analysis demonstrates, these future negotiations will have important implications for the recovery of endemic fishes basin-wide. While we have focused on evaluating conditions in the Colorado River basin, global climate change is likely to present similar challenges in other large river networks, particularly those in arid regions associated with declining watershed runoff. We suggest that our approach to modeling water temperatures, which explicitly considers the twin levers of climate change and storage decisions in driving river temperatures, could inform management of native and nonnative fish populations globally.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2279/full

Data Availability

Data are available via a USGS ScienceBase release (Dibble et al. 2020): https://doi.org/10.5066/P9HFKV7Q.