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- 1) The construction of dams on large rivers has negative impacts on native species.
- Environmental flows have been proposed as a tool to mitigate these impacts, but in order for these strategies to be effective they must account for disparate temperature and flow needs of different species.
- 2) We applied a multi-objective approach to identify tradeoffs in dam release discharge and temperature for imperiled fishes with contrasting habitat requirements, while simultaneously meeting the needs of human water users.
- 3) Using the Sacramento River (California, USA) as a case study, our model suggests that current management aimed at providing high discharge for downstream water users and cold water for endangered winter-run Chinook salmon (*Oncorhynchus tshawytscha*) has detrimental impacts on threatened green sturgeon (*Acipenser medirostris*), which require warm water for juvenile growth.
- 4) We developed an optimal dam release scenario that can be used to meet the needs of salmon, sturgeon, and human water users. Our results show that dam releases can be managed to successfully achieve these multiple objectives in all but the most severe drought years.
- *5) Synthesis and applications.* This study shows that managing dam releases to meet the needs of a single species can have detrimental effects on other native species with different flow and temperature requirements. We applied a multi-objective approach to balance environmental requirements of multiple species with the needs of human water users. Our findings can be used to guide management of Shasta Dam and our approach can be applied to achieve multi-object management goals in other impounded rivers. We applied a
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 Keywords: Endangered Species Act, designer flows, green sturgeon, multi-species management, multi-object optimization, winter-run Chinook, Paris Agreement, hydropower proliferation

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INTRODUCTION

 In the last decade, there has been a massive increase in the number of proposed hydropower projects around the world (Zarfl et al. 2015). This proliferation has gained momentum in response to the 2015 Paris Agreement, which identified hydropower as the renewable energy replacement for fossil fuels (UNFCCC 2015, Hermoso 2017). It has been well documented that dams alter downstream conditions such as flow timing, flow amplitude, and river temperature (Richter & Thomas 2007, Olden & Naiman 2010). The disturbance of the river environment downstream from dams reduces biodiversity and changes community structure (Wootton et al. 1996, Stanford & Ward 2001, Poff et al. 2007). However, dams are also used to deliver water, prevent floods, and generate electricity at peak times. Dam releases must therefore be managed to sustain aquatic habitat while delivering human services. The United States Endangered Species Act (ESA) mandates flow targets for individual species, which are met using dam releases to modify discharge and/or temperature (Poff et al. 1997, Olden & Naiman 2010). Specific flow designs may provide opportunities to simultaneously meet downstream human and wildlife needs (Chen & Olden 2017). Dams prevent cold-water reliant fish species from reaching lower order streams while 199

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 must instead carry out their life history in the warmer mainstem. Targeted flows can release cold water (Olden & Naiman 2010), but the release of cold water can negatively impact warm-water species. This alters mainstem habitat, pushing warm-water organisms further down in the river system where temperatures warm to acceptable levels**.** Natural flow regimes can be restored for communities of native fishes using targeted releases (Kiernan et al. 2012, ESSA 2017), and many studies focus primarily on identifying and mimicking ecologically relevant components of the natural hydrograph (Poff et al. 2010, Yarnell et al. 2015). However, flows have not yet been designed for co-occurring species with conflicting temperature tolerances. Here, we use a case study of a warm- and cold-water Endangered Species Act (ESA) listed species in California's Sacramento River to ask whether flows can be designed to simultaneously meet the needs of cold- and warm-water fish species and downstream human use.

 The Sacramento River provides 35% of California's water supply but also contains unique genetic and life history diversity for several anadromous fish species listed under the US Endangered Species Act (ESA) (Grantham et al. 2017). The spawning grounds of two ESA- listed species, endangered Sacramento River winter-run Chinook salmon (hereafter referred to as winter-run; *Oncorhynchus tshawytscha*) and threatened green sturgeon (*Acipenser medirostris*), did not overlap in the Sacramento River. Winter-run spawned in high-elevation cold habitat while green sturgeon spawned in the warm mainstem (Figure S1; Fisher 1994, Mora et al. 2009). 134 The optimal rearing temperature for larval green sturgeon is 19° C while survival of incubating winter-run eggs begins to decrease above 12° C (Martin et al. 2017, Poletto et al. 2018). These differences in temperature tolerance between the two species lead us to classify green sturgeon as a "warm-water species" and winter-run as a "cold-water species" for the purposes of this manuscript, although these are relative classifications that are specific to this system. After the construction of Shasta Dam in 1945 blocked access to historical spawning habitat, both species began spawning in the mainstem below the dam (Figure 1). Winter-run chinook dig gravel redds in the cold outflow from the dam, while green sturgeon broadcast spawn further downstream in strong eddies with varying benthic habitat (Wyman et al. 2017). These habitat displacements are a conservation concern because both distinct population segments are endemic to Central Valley watersheds, and these compounding factors have led to the ESA-listing of both species. Current management provides cold water for winter-run egg survival using a temperature control device 22 communities of native fishes using targeted releases (Kiernan et al. 2012, ESSA 2017), and

232 communities of native fishes using targeted releases (Kiernan et al. 2012, ESSA 2017), and

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 from Shasta Reservoir. Selective withdrawal is the most effective method of control release temperature, although there are several other techniques (Olden & Naiman 2010). The river below Shasta Dam is now much colder than it was historically, and this cold water extends into current green sturgeon spawning grounds (Figure S1). Cold water pollution below dams dramatically impacts mainstem ecosystems that are adapted for warmer temperatures (Astles et al 2003). Larval green sturgeon growth, food consumption, food conversion efficiency, and diet indices are positively influenced by warmer temperatures (Mayfield & Cech 2004, Poletto et al. 2018, Zarri & Palkovacs 2018), suggesting that cold releases for winter-run may negatively impact green sturgeon.

 During the temperature management season for winter-run (May–November), Shasta Dam releases maintain cold temperatures for incubating eggs and deliver adequate discharge for downstream water users. The current management strategy aims to maintain river temperature at or below the experimentally derived threshold of 13.3° C for winter-run egg survival (USFWS 1999). Recent work suggests that dam releases should be even colder to reduce winter-run egg mortality (Martin et al. 2017). Green sturgeon spawning temporally overlaps with the temperature management season and winter-run spawning, and previous models suggest that there may be a temperature management tradeoff between the two species (Hamda et al. 2019). Downstream water users and winter-run require certain minimum discharge levels but the impact of discharge on wild larval green sturgeon remain unknown. We examined the water management options for the Sacramento River to determine if there is an optimal balance for winter-run, green sturgeon, and downstream water users. 1713 drammeters ministran cocoysterns that are adopted for warmer temperatures (Astles et al. 2003). Laveal green sturgeon growth, food consumption, food conversion efficiency. And diet
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 We used five years of green sturgeon and winter-run data from 2012 and 2016 to ask three questions: (1) Do the water temperature targets for winter-run egg development create suboptimal conditions for larval green sturgeon? (2) Do dam release strategies exist that optimize management of winter-run, green sturgeon, and downstream water users, and (3) how often are optimal release strategies feasible given inter-annual variability in hydrology and meteorology? We adapted models of winter-run egg survival (Martin et al. 2017) and developed a statistical predictive model for green sturgeon body condition to understand their responses to dam release temperature and discharge. There are other ESA-listed species in this system such as California Steelhead (*Oncorhynchus mykiss*) which are likely impacted by altered flow regimes, but there is

 tradeoffs in dam release scenarios for both species and water users, we combined the two species models in a multi-object optimization model (Polasky et al. 2005, Horne et al. 2017). We optimized dam releases for winter-run and green sturgeon during the months they are both present (Figure 2b) after constraining management scenarios to those which meet the discharge requirements of water users, based on the past 20 years of dam discharge release (Figure 2a). Finally, we used a mechanistic water temperature model of Shasta Reservoir to estimate the proportion of years the scenario was feasible.

MATERIALS AND METHODS

 We first compared health metrics for both species across 2012-2016. Winter-run egg-to- fry survival was calculated as the estimated number of surviving fry in Red Bluff Diversion Dam (RBDD) screw traps divided by estimated egg production (National Marine Fisheries Service, 190 2013-2017; Figure 1). We limited our analysis to exogenously feeding larval green sturgeon at approximately two weeks post hatch (*Supporting Information*). Samples were collected via rotary screw traps which we assumed to sample fish randomly and not select for specimens of particular body condition. The green sturgeon health metric was body condition, because there no data are available on green sturgeon egg production. Larval body condition is a commonly used indicator of fat reserves and health, and has been associated with health in sturgeon (Froese 2006, Kappenman et al. 2009). To estimate the temperature and discharge dam releases across the season, we modeled average temperature and discharge for each month of the year that early life stages of either species were present in the study area using data from the River Assessment for Forecasting Temperature model (RAFT; Pike et al. 2013, Daniels et al. 2018). 218 Experiments of weater and the state of the state of the state of larval green states of the state of

 Next, we developed statistical submodels elucidating the impact of river temperature and discharge on winter-run and green sturgeon. To place both submodels in the context of dam release scenarios, we estimated differences in discharge and temperature between Keswick Dam (the afterbay to Shasta Dam) and each species' environment. During the summer and fall, the 204 river warms as it moves downstream from Keswick Dam, increasing $0.46^{\circ}C$ (σ = $0.06^{\circ}C$) to the 205 downstream boundary of winter-run redd locations and 2.20° C (σ =0.52°C) to the green sturgeon spawning locations. We assumed constant temperature and discharge throughout winter-run embryonic development as data on individual redds was not available. Standard deviation in

209 not a significant predictor in our model and therefore we included only mean development

210 temperature and discharge. The winter-run model identified the probability of egg temperature-

211 based mortality (Martin et al. 2017). This is an additive model across the egg incubation period,

212 given by:

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$$
M_T = 1 - \prod_{i=1}^{n} \exp(-(b_T \max(T_i - T_{crit}, 0)))
$$

214 where M_T is predicted temperature dependent mortality between egg fertilization and completion 215 of the alevin stage T_{crit} is the temperature threshold above which mortality begins to increase and 216 *Tⁱ* T_i is the daily temperature for day *i* until alevins emerge at day *d*. b_T is the slope of mortality rate 217 above T_{crit} and these parameters are estimated in Martin et al. (2017) as 0.024 and 12^oC, 218 respectively. *n* is number of days to maturation, modeled using relative developmental state 219 which is 0 at fertilization and increases at rate 0.001044 ($^{\circ}$ C⁻¹d⁻¹) *T_i +0.00056(d⁻¹) until 220 completion of the alevin stage at 1 (Zeug et al. 2012). Due to lack of supporting data, we 221 assumed no impact of discharge on egg survival. Low discharge can cause redd desiccation, but 222 this is rare with high summertime water demands downstream. We developed the green sturgeon 223 submodel (See *Supporting Information*) to predict body condition over the ~14 days until they 224 pass RBDD: 238

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K = b_T \cdot T_i + b_D \cdot D_i + x
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226 where *K* is predicted body condition, b_T is the coefficient for the effect of mean temperature T_i 227 until individuals pass RBDD, b_D is the coefficient for the effect of discharge D_i until individuals 228 pass RBDD, and *x* is the intercept (estimated in *Supporting Information*).

 We combined both statistical submodels in a multi-object optimization model to calculate optimal dam release temperature and discharge when early life stages of both species are present. No weighting was applied to either objective, and data came from 2012-2016. Each management strategy was plotted with *x* as the response of objective 1 and *y* as the response of objective 2. A Pareto frontier indicated optimal solutions (Deb 2014). A Pareto frontier containing a corner on a high value for both objectives highlights the optimal strategy, while a straight or curved line indicates tradeoffs. The optimal dam release scenario was calculated by scaling each response from zero to one, then multiplying the scaled response for each species against one another for each scenario. The highest score indicated the optimal scenario. Dam release discharge is limited

 of cold water in the reservoir hypolimnion and warm water in the epilimnion. Therefore, we 240 constrained monthly discharge to the $25th$ -75th percentile and temperature to the $10th$ -90th percentile of 1996-2016 (Figure 2a).

 To evaluate the probability of achieving the optimal dam release scenario through the season, we used a mechanistic reservoir water temperature model of Shasta Reservoir that has been calibrated to the system (Daniels et. al. 2018). We ran each year independently with inputs 245 of observed hydrological and meteorological conditions from 2000-2015. Rather than using actual dam release discharge and temperature, discharge was set to the optimized monthly value and a selective withdrawal algorithm was used to select the TCD gate to open on a given day such that reservoir discharge temperature not exceed the optimal temperature target (Figure S4).

RESULTS

251 Body condition of larval green sturgeon was positively correlated with temperature 252 (linear regression: $p < 0.001$, $R²=0.07$, F-statistic=19.21, 95% confidence interval of slope=0.13-253 0.24), and negatively correlated with discharge (linear regression: $p<0.001$, $R^2 = 0.13$, F- statistic=39.63, 95% confidence interval of slope=-0.002 - -0.0009) (See *Supporting Information*). The cold, high discharge years of 2012- 2013 had high winter-run egg survival and poor green sturgeon condition (Figure 3). The warm, low flow drought years of 2014- 2015 had low winter-run egg survival and higher green sturgeon condition. In 2016 both winter-run and green sturgeon biological metrics were higher than average.

 Combining the two statistical submodels in a multi-object optimization model indicated that there is an optimal management strategy. The submodels predict how a range of dam releases observed through the season (10°C-13°C, 150cms–450cms) alter green sturgeon body condition and winter-run egg-to-fry survival (Figure 4a). The multi-object optimization model combined submodels for each species across their development periods (x-axis and y-axis, respectively, Figure 4b). The Pareto frontier identified an optimal release corner for both species that was also constrained by thresholds of water user discharge, located at the dam release of 150cms discharge with 11.5°C Keswick temperature (Figure 4b). 268

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The optimal management scenarios with the reservoir temperature model indicated which

269 S4). The water user objective was minimum dam release discharge $(25th$ quartile, Figure 2a) and species objectives are listed in Table 1. The minimum discharge objective for water users was achievable in all years except for the critically dry 2014. The temperature objective of below 11.5˚C at Keswick from June-December for winter-run was achievable in 75% of years. The 273 temperature objective of warm temperatures from March-May for larval green sturgeon was achievable in 56% of years, and warm temperatures were usually only reached at the end of the larval green sturgeon season. However, the low discharge objective from March-May for larval green sturgeon was achievable in 94% of years. All three objectives are met in 69% of years if the larval green sturgeon discharge threshold is used, while the three objectives are met in only 50% of years if the larval green sturgeon temperature threshold is used. These probabilities can be projected into the future, assuming that the past 20 years are reflective of the future.

DISCUSSION

 California's Sacramento River supports the largest agricultural economy in the U.S. and is home to unique and imperiled cold- and warm-water fish species (Grantham et al. 2017). Here we show that flow regimes can be designed to balance the needs of warm- and cold-water fishes while simultaneously meeting downstream water user requirements. The current management approach for the Sacramento River uses water releases from Shasta Dam to maintain cold temperatures for developing ESA-endangered winter-run eggs while delivering adequate discharge for downstream water users. These two objectives are of primary importance for Shasta Dam releases but likely harm ESA-threatened green sturgeon, which depend on warm low flow conditions to support larval growth. High discharge has a strong impact on developing green sturgeon larvae swimming ability and is associated with decreased prey richness and diet count (Verhille et al 2014, Zarri & Palkovacs 2018). By introducing larval green sturgeon condition to a winter-run egg survival model in multi-object optimization, we identify a Pareto frontier with a corner that is optimal for both species. Our study corroborates others which found 295 that indices of health in larval green sturgeon are enhanced at higher temperatures (Mayfield $\&$ Cech 2004, Poletto et al. 2018, Zarri & Palkovacs 2018, Hamda et al. 2019) but body condition appears to be more sensitive to changes in discharge at the range of environmental variables 298 complete in our study results and the positive of warm (Figure 4a). The positive correlation of green study results and a derivative study region of green study only reached at the cord of the green study only reached

 body condition with temperature may be moderated by food availability, as fish exposed to warm temperatures with low food availability show very low body condition (Poletto et al. 2018). The optimal dam release, which is only necessary during the time that both species are present in the managed portion of the river, is 11.5°C and 150cms (Figure 4b).

 Optimal temperature management for both species is possible given the natural warming of water as it flows downstream from winter-run redd sites to green sturgeon spawning sites. The low discharge requirements of green sturgeon conflict with high discharge requirements of water users, but larval green sturgeon are mostly present in May while peak agricultural water demand is June-July. Given the temporal variation in species presence and water user requirements, we proposed environmental flows to balance winter-run egg survival and larval green sturgeon body condition while meeting requirements of downstream water users (Table 1). Releasing warm water earlier in the season for larval green sturgeon may preserve cold water for winter-run later in the season (Hanna 1999, Nickel et al. 2004). In most years this strategy would improve conditions for larval green sturgeon without harming winter-run or water users. However, conflict is unavoidable under severe drought conditions, as occurred in 2015. 339 considered in the this manuscript in the multiple in the state of the this and consideration of the state in the state of the s

 The reservoir water temperature model indicated that discharge and temperature optimums were achievable in 69% of years from 2000-2015. Winter-run temperatures were possible to release in 75% of years, water user discharge was possible in 94% of years, and larval green sturgeon releases were possible in 94% of years if discharge is the only criteria used. Cool water for winter-run was the most challenging objective because drought conditions resulted in low reservoir storage and high air temperatures. Global warming will continue to alter air temperature and precipitation patterns (Alexander et al. 2006), which may decrease the probability that the cold-water winter-run objective is met. While difficult to manage, these factors help set reasonable targets for water users, cold-water, and warm-water species in this temperate river.

 Our results show that changes in management could benefit green sturgeon while maintaining conditions for winter-run and water users, yet there are several challenges that remain. Green sturgeon display "sweepstakes" reproduction (Hedgecock & Pudovkin 2011) and experience massive early life-stage mortality, which is likely impacted by more environmental factors than the temperature and discharge parameters we analyzed. Other important factors not

 personal communication), which could be indirectly impacted by other environmental variables such as water quality and substrate type. The optimal solution is to manage water temperatures up to the threshold for winter-run, so errors in the threshold model could lead to errors in this optimization. The reservoir model algorithm assumed that TCD gates could be adjusted daily, which rarely occurs. The reservoir simulations were also run independently from year to year and did not account for the propagating effects associated with the proposed discharge and temperature management scenarios across years. Nonetheless, our results show that it is possible to design dam releases to simultaneously support warm- and cold-water species and water users in all but the most extreme drought years.

 Our approach to developing an optimal dam release scenario can be extended to other ecosystems where the environment can be manipulated to provide anthropogenic resources while making habitat for multiple species. Potential applications beyond environmental flows include the management of ESA-listed species in timber harvest regions (Nalle et al. 2004), and seagrass ecosystem restoration amidst oyster bed aquaculture (Dumbauld et al. 2009). However, few systems exist where the environment can be engineered as completely as a dam controls river temperature and discharge. There are many methods for controlling dam release temperature (Sherman 2000), and the challenge for managers thus becomes identifying species-specific (or even population-specific) thermal and discharge requirements (Poff et al. 1997, Olden & Naiman 2010). By analyzing three objectives, our model suggests that the main water management conflict in this system is between low discharge, required by larval green sturgeon, and high discharge, demanded by downstream water users. The dilemma of managing for multiple imperiled species is likely to become more common in the future, as the number of species at risk of extinction continues to increase (Chapin et al. 2000). In these circumstances, optimization models are an effective tool to evaluate tradeoffs in management (Polasky et al. 2005, Horne et al. 2017). Our results show that balancing the needs of multiple species and water users in this highly altered ecosystem can be achieved in most years. which randy occurs. The reservoir simulations were also run independently from year and did not account for the propagating effects associated with the proposed discharge compending the membersion sections years. Noncthele

AUTHORS' CONTRIBUTIONS

L.J.Z. contributed ideas, data generation, data analysis, and manuscript preparation. E.M.D

 generation, data analysis, and manuscript preparation. E.P.P. contributed ideas, manuscript preparation, and funding.

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DATA Availability Statement

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- Data available via the Dryad Digital Repository. DOI: 10.5061/dryad.898ks73 (Zarri et al. 2019)
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- Figure 1. Map of the Sacramento River below Keswick Dam (the afterbay to Shasta Dam) to Red
- Bluff, with river regions of Sacramento River winter-run Chinook redds, green sturgeon
- spawning, and temperature management

562 Figure 2. (A) Historic temperature (10th and 90th quartiles) and discharge (25th and 75th quartiles) releases from Keswick Dam by month from 1990-2016, and (B) temporal distribution of

 Figure 3. Average environment and biological response across the 5 years of this study. (A) The mean temperature (solid line) and discharge (dashed line) at Keswick Dam from April to November across the 5 years of this study. (B) Green sturgeon body condition (dotted and dashed line) and Sacramento River winter-run Chinook egg-to-fry survival (dotted line).

Figure 4. (A) Impact of Keswick Dam temperature and discharge on relative body condition of

 Multi-object optimization model generated by modeled response of Sacramento River winter-run Chinook and green sturgeon to Keswick dam release temperature and discharge. The optimal solution can be visually identified as there are just two objectives. The colored lines indicate the minimum discharge Pareto frontiers. For example, "150 cms" is the Pareto frontier for discharge of 450-150cms and "250 cms" is the Pareto frontier for discharge of 250-250 cms. Each line is colored by temperature. The black box represents the optimal strategy.

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 Table 1. Management recommendations to balance Sacramento River winter-run Chinook and green sturgeon. Management recommendation temperature and discharge is based on release from Keswick Dam. $\sum_{i=1}^n$

Winter-run chinook redd locations

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Red Bluff

