

UC Davis

UC Davis Previously Published Works

Title

Identifying cost-effective invasive species control to enhance endangered species populations in the Grand Canyon, USA

Permalink

<https://escholarship.org/uc/item/7tj1h1f8>

Authors

Bair, Lucas S
Yackulic, Charles B
Springborn, Michael R
et al.

Publication Date

2018-04-01

DOI

10.1016/j.biocon.2018.01.032

Peer reviewed

1 **Title**

2 Identifying cost-effective invasive species control to enhance endangered species populations in
3 the Grand Canyon, USA

4 **Running Head**

5 Cost-effective invasive species control

6 **Authors**

7 **Lucas S. Bair***, U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon
8 Monitoring and Research Center, 2255 N. Gemini Dr. Flagstaff, Arizona 86001, USA

9 **Charles B. Yackulic**, U.S. Geological Survey, Southwest Biological Science Center, Grand
10 Canyon Monitoring and Research Center, 2255 N. Gemini Dr. Flagstaff, Arizona 86001, USA

11 **Michael R. Springborn**, University of California, 1 Shields Avenue Davis, CA 95616, USA

12 **Matthew N. Reimer**, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, AK,
13 99508, USA

14 **Craig A. Bond**, RAND Corporation, 1200 S. Hayes St. Arlington, VA, 22202, USA

15 **Lewis G. Coggins**, U.S. Fish and Wildlife Service, PO Box 346, Bethel, AK, 99559, USA

16

17

18

19

20

21

* Corresponding author: lbair@usgs.gov

22 **Abstract**

23 Recovering endangered species populations when confronted with the threat of invasive species
24 is an ongoing natural resource management challenge. While eradication of the invasive species
25 is often the optimal economic solution, it may not be a feasible nor desirable management action
26 in other cases. For example, when invasive species are desired in one area, but disperse into
27 areas managed for endangered species, managers may be interested in persistent, but cost-
28 effective means of managing dispersers rather than eradicating the source. In the Colorado River,
29 a nonnative rainbow trout (*Oncorhynchus mykiss*) sport fishery is desired within Glen Canyon
30 National Recreation Area, however, dispersal downriver into the Grand Canyon National Park is
31 not desired as rainbow trout negatively affect endangered humpback chub (*Gila cypha*). Here,
32 we developed a bioeconomic model incorporating population abundance goals and cost-
33 effectiveness analyses to approximate the optimal control strategies for invasive rainbow trout
34 conditional on achieving endangered humpback chub adult population abundance goals. Model
35 results indicated that the most cost-effective approach to achieve target adult humpback chub
36 abundance was a high level of rainbow trout control over moderately high rainbow trout
37 population abundance. Adult humpback chub abundance goals were achieved at relatively low
38 rainbow trout abundance and control measures were not cost-effective at relatively high rainbow
39 trout abundance. Our model considered population level dynamics, species interaction and
40 economic costs in a multi-objective decision framework to provide a preferred solution to long-
41 run management of invasive and native species.

42 **Key Words**

43 Bioeconomic model, conservation, Monte Carlo simulation, social-ecological system, population
44 modeling, fisheries management, humpback chub, rainbow trout

45 **Introduction**

46 Endangered species recovery efforts sometimes focus on the reduction or eradication of invasive
47 species that negatively impact recovery (Wilcove et al. 1998). While eradication has been
48 possible in some situations (e.g., in isolated areas like islands, Ebbert and Byrd 2002), it may not
49 be a feasible nor desirable management action in other cases. In particular, limited budgets
50 and/or beneficial economic, social, and biological effects stemming from the invasive species
51 may preclude eradication as an optimal management action (Schlaepfer et al. 2011, Lampert et
52 al. 2014). For example, resource users may favor maintaining an invasive species in areas
53 adjacent to an area intended for endangered species conservation, and resource managers may
54 focus on limiting the number of dispersing individuals. In these cases, the endangered species
55 may require ongoing threat reduction to sustain viable populations in the wild.

56 An important consideration in ongoing endangered species management is the allocation of
57 resources over time to meet species recovery goals. Species conservation strategies involves
58 trade-offs between short- and long-run management actions, along with the potential for the
59 reallocation of resources to alternative conservation objectives with higher return on investment
60 (Polasky 2008). An effective way to explicitly incorporate trade-offs in conservation planning is
61 through the inclusion of economic costs (Naidoo et al. 2006, Polasky 2008). Economic
62 information can convey the opportunity cost of conservation, or the foregone benefit of
63 undertaking an alternative conservation action, allowing comparison among competing
64 conservation priorities over the period of analysis. This is particularly important when the
65 dynamics of invasive species management for endangered species recovery may include a series
66 of competing or complementary management actions over time.

67 Cost-effectiveness analysis—i.e., assessing how a given objective can be achieved at the least
68 possible cost—is a useful tool for allocating resources for meeting endangered species recovery
69 goals (Moran et al. 2010, Rose et al. 2016). Conservation objectives are typically set in
70 accordance with societal goals, often embodied in legal directives governing actions of resource
71 management organizations (Murdoch et al. 2007). In this context, when implicit social or
72 economic valuation occurs as legislative bodies or other governing organizations establish
73 endangered species protection goals, the act of minimizing costs maximizes the return on
74 investment. Further, in the context of population abundance goals, cost-effectiveness analysis
75 must be inherently dynamic, i.e. focused on the optimal allocation of management resources over
76 time.

77 Cost-effectiveness analysis also has the characteristic of shifting the focus in the decision
78 framework from justifying conservation ends (e.g., economic value of a species) to the various
79 management actions available to best achieve conservation goals (Sagoff 2009). This is an
80 important distinction when stakeholders have different objectives or may fundamentally reject
81 attempts to economically value aspects of ecosystem resources. In addition, cost estimates in
82 conservation may be easier to generate than estimates of benefits (Naidoo et al. 2006). Therefore,
83 cost-effectiveness analysis can provide a more suitable approach to endangered species
84 conservation planning than benefit-cost analysis (which requires a much more comprehensive
85 assessment of the benefits generated by species).

86 In this paper we developed a bioeconomic model to identify the least-cost management strategy
87 to control invasive rainbow trout (*Oncorhynchus mykiss*; hereafter, RBT) subject to achieving
88 juvenile humpback chub (*Gila cypha*; hereafter, HBC) survival targets. We modified established
89 population models for RBT and HBC and utilized management cost information generated from

90 long-term monitoring and research at the Grand Canyon Monitoring and Research Center
91 (GCMRC) (Korman et al. 2012, Yackulic et al. 2014, Yackulic, *In Press*). We identify the least-
92 cost management action given juvenile HBC survival targets, which supports long-run viability
93 of the adult population over time. Further, we explore the sensitivity of the model across
94 assumptions regarding RBT population parameters and risk preferences, and discuss the potential
95 environmental conditions that would affect fundamental model assumptions and results.

96 **Methods**

97 *Study Area*

98 This study is focused on the HBC habitat in the lower Little Colorado River (LCR) and its
99 confluence with the mainstem of the Colorado River (mainstem) in Grand Canyon National Park
100 (GCNP) (Figure 1). HBC were widely dispersed in the mainstem prior to construction of dams
101 and the introduction of invasive species (USFWS 1994). Most HBC in LCR aggregation spawn
102 in the lower 13.6 km of the LCR and a large portion of juvenile HBC disperse into and rear in
103 the mainstem, with the majority of dispersal occurring between July and October (Yackulic et al.
104 2014). A variety of factors, including both biotic (i.e., interspecific and intraspecific interactions,
105 food availability, etc.) and physical factors (temperature, turbidity, etc.) determine how many
106 juvenile HBC survive into larger size classes (Yackulic, *In Press*); however, the roles of
107 temperature (positive) and RBT (negative) have typically been the focus of management debate.
108 Glen Canyon Dam (GCD) impounded the Colorado River in 1963 for the primary purposes of
109 water storage, flood control, and hydroelectric power generation (Bureau of Reclamation 1995).
110 Construction of GCD substantially altered the temperature, turbidity and flow regime of the
111 mainstem (Schmidt et al. 1989). Following dam construction, RBT were introduced immediately
112 downstream, creating a clear, cold-water sport fishery in an approximately 26 kilometer reach of

113 Glen Canyon, often referred to as Lees Ferry. Rainbow trout recruitment in the tailwater of the
114 GCD (i.e., Glen Canyon reach) is driven by many factors, including within-day, seasonal and
115 annual variation in flows from the GCD, and a proportion of RBT move downstream (Korman et
116 al. 2012, Korman et al. 2015). Rainbow trout that move downstream along the mainstem to the
117 LCR confluence prey on, and compete with, HBC (Yard et al. 2011) and increased RBT
118 abundances are associated with lower survival of juvenile HBC (Yackulic, *In Press*).
119 In an effort to reverse declining HBC abundance, mechanical removal of RBT was performed
120 from 2003 to 2006 and in 2009 (Interior 2016). Mechanical removal involves boat electrofishing
121 for RBT, which are subsequently processed (e.g., cleaned, frozen) for beneficial use outside of
122 GCNP¹. Humpback chub abundance appeared to increase following RBT removals; however,
123 these increases coincided with two favorable changes in the environment from the perspective of
124 HBC: warming mainstem temperatures and declining RBT numbers system-wide (Coggins et al.
125 2011). The GCMRC has continued to monitor and collect data on RBT and HBC, along with
126 environmental conditions, since RBT removals began in the 2000s. Concerted juvenile HBC
127 research beginning in 2009 allowed us to develop an empirically-grounded model to explore the
128 ability of RBT removals to meet HBC long-run population recovery goals under historically
129 demarcated periods of cold and warm mainstem temperatures. The bioeconomic model modified
130 recent approaches to modeling HBC and RBT demographics and utilized existing empirical data
131 to inform parameter estimates, as summarized in the Long-Term Experimental and Management
132 Plan Final Environmental Impact Statement (LTEMP FEIS) (Interior 2016).

133 ***Model Framework***

¹Beneficial use is a mitigation action established during federal consultation with Native American tribes to address the live removal of fish during management actions in the Grand Canyon (Reclamation 2011). An example is the use of removed rainbow trout in the Pueblo of Zuni aviary.

134 In our model, the manager’s hypothetical objective is to identify the least-cost management
135 strategy that reduces downstream RBT abundance to maintain long-term adult HBC (200 mm+)
136 abundance. Since HBC have complex population dynamics and relatively slow growth in the
137 colder mainstem, we used our understanding of HBC life history to translate this adult HBC
138 abundance goal into a shorter-term annual juvenile HBC survival target. Specifically, we
139 determined the annual juvenile HBC (40 – 100 mm total length) survival target required to
140 maintain a long-term adult abundance of 7000 or greater (see below for specifics). Estimated
141 abundance of adult HBC in the LCR aggregation has ranged from 5 – 11 thousand in the last
142 several decades (Interior 2016). We developed the bioeconomic framework by integrating HBC
143 and RBT population dynamics with RBT control actions, where RBT populations are determined
144 by stochastic recruitment in the tailwater of GCD and the manager’s choice of up to 6 control
145 actions in a year is a function of RBT abundance in the Juvenile Chub Monitoring (JCM) reach.
146 The control action is comprised of mechanical removal to reduce RBT abundance from river
147 kilometer 116.5 to 147.1 of the mainstem, near the JCM reach. Complete eradication of RBT in
148 Lees Ferry is not considered given the undesirable loss of upstream recreational fishing. The
149 RBT fishery has an estimated \$2.6 million annual economic value (Bair et al. 2016),
150 considerably greater than the cost of proposed RBT control actions. The population model
151 schematic appears in Table 1 and population and management variable definitions and
152 parameters are specified in Table 2 (See Appendix A for bioeconomic model code (R Core
153 Team, 2016)).

154 **Population Model**

155 The population model depicts the stylized dynamics, or simplified configuration of empirical
156 findings, of RBT and HBC along a ~130-kilometer reach of the mainstem, from Glen Canyon to

157 just past the LCR confluence (see Table 1). The population model is comprised of the following
158 three components: 1) RBT recruitment in Glen Canyon; 2) outmigration of RBT and their
159 movement and survival in Marble Canyon between Glen Canyon and the JCM reach; and 3)
160 juvenile HBC survival in the JCM reach in response to RBT abundance from September through
161 August of each year.

162 *Rainbow trout recruitment*

163 Rainbow trout recruitment, which largely occurs in the Glen Canyon reach, is highly variable
164 and is determined by factors exogenous to our model. We follow Korman et al. (2012) and
165 model annual RBT recruitment r_y , where y denotes year, as density independent according to a
166 stochastic exponential function e^z , where z is a random variable that follows a uniform
167 distribution, $z \sim \text{unif}(\alpha, \beta)$. The parameters α and β are chosen such that all potential recruitment
168 events r_y lie within the range of historical estimates (Korman et al. 2012, Interior 2016).

169 Estimated abundance of RBT in Glen Canyon over the last several decades has ranged from ~0.2
170 – 1.0 million individuals (Korman and Yard 2017).

171 *Rainbow trout outmigration and movement*

172 Outmigration of age-1 RBT from Glen Canyon down the mainstem is a function of the previous
173 year's recruitment and survival of RBT (Korman et al. 2012). For simplicity, the age-size
174 structure is not modeled and the effect of RBT abundance on survival is considered constant
175 (Interior 2016). Specifically, in year y , we model the outmigration of RBT from Glen Canyon
176 into Marble Canyon as:

$$177 \rho_y = \tau\psi_1 r_{y-1}, \tag{1}$$

178 where ψ_1 is the average annual age-1 RBT survival rate and τ is the annual outmigration rate
179 from the Glen Canyon reach, both of which are assumed to be constant within and between years
180 (Interior 2016).

181 For the purposes of implementing mechanical removal, we model monthly movement and
182 dispersion of RBT between each of the J river segments (approximately 1.6 km in length) of the
183 mainstem between river-kilometer 26.4 and 267.8. We assume that movement is independent of
184 RBT density and follows a Cauchy distribution $f(x; 0, 3.38)$, a continuous distribution with a
185 lower probability than a normal distribution of RBT moving long distances (Interior 2016).

186 Letting $\mathbf{N}_{y,t}$ denote a $J \times 1$ vector containing the abundance of RBT within each river-segment
187 along the mainstem in year y and month t , the movement and survival of RBT can be
188 characterized as:

$$189 \quad \mathbf{N}_{y,t+1} = \psi_0 \mathbf{\Phi} \mathbf{N}_{y,t}, \quad (2)$$

190 where ψ_0 is the monthly survival rate of RBT in each river-segment and $\mathbf{\Phi}$ is a $J \times J$ matrix that
191 specifies how RBT movement from a particular river-segment is distributed to other segments
192 (Interior 2016). We assume that an equal proportion of annual outmigration of RBT from Glen
193 Canyon ($\rho_y/12$) is added to the first element (river-kilometer 26.4) of the RBT abundance
194 vector ($\mathbf{N}_{y,t}$) for every month. Further, we assume that both ψ_0 and $\mathbf{\Phi}$ are constant over time,
195 that the monthly survival rate of RBT is constant along the mainstem (Korman et al. 2012), and
196 that the JCM reach is a sink habitat for RBT with no local recruitment (Korman et al. 2015). The
197 annual rate of change in RBT abundance in the vicinity of the JCM reach has varied from -75 –
198 150 percent since 2012 (Korman and Yard 2017).

199 *Juvenile humpback chub survival*

200 Past modelling of HBC population dynamics has been based on a size- and location-structured
201 multistate model with 10 states (5 size groups in 2 locations representing the Colorado River and
202 its tributary the Little Colorado River; Yackulic et al. 2014). Given monthly values of
203 temperature and rainbow trout, it is possible to generate monthly transition matrices between
204 these 10 states that incorporate both survival of the 10 states, but also contributions from one
205 state in one month, t , to another state in the next month $t + 1$ as a result of movement, growth,
206 and/or fecundity (i.e., juvenile recruitment divided by the target adult population size). These
207 monthly values can in turn be used to create an annual transition matrix. The first eigenvalue of
208 this annual transition matrix is the population growth rate expected for a population with a value
209 of 1 indicating a stable population. Therefore, if juvenile survival is treated as an unknown
210 variable, but all other parameters are treated as fixed, it is possible to determine the juvenile
211 survival that would lead to a stable population of a given size (i.e., a juvenile survival target) by
212 finding the juvenile survival value that minimizes the square of the difference between its
213 eigenvalue and 1 (i.e., by identifying the juvenile survival that yields a stable population) (See
214 Appendix B for details (R Core Team, 2016)).

215 We used estimates from past work to populate monthly transition rates for the HBC states.
216 Yackulic et al. (2014) estimate constant survival and growth rates, as well as movement rates
217 that varied seasonally, but were constant across years. Yackulic (*In Press*) estimated growth and
218 survival of juvenile HBC only in the mainstem, but allowed for monthly variation in survival and
219 growth of juvenile HBC based on various covariates including RBT abundances and
220 temperature, respectively. Recruitment is the most poorly understood population process. Past
221 work has defined recruitment in terms of juvenile abundances in the LCR in the month of July
222 and has based estimates on back-calculations of juvenile HBC from the month of September

223 (Interior 2016). While ongoing field studies refine these estimates, we use back-calculations to
224 estimate 19,000 individuals as the average annual density-independent recruitment (Interior
225 2016).

226 We used the HBC recruitment estimate to calculate the annual juvenile survival under both warm
227 and cold scenarios required to maintain a population of 7000 adults, which is often used as a
228 target for this population (Interior 2016). To simplify, we focused solely on the effects of RBT
229 on survival of juvenile HBC and considered the effects of two mainstem temperature regimes on
230 growth of juveniles (warm - average monthly water temperatures from 2009-2016, cold - average
231 monthly water temperatures from 1990-1999 – all data from USGS gauge 09383100). Colder
232 temperatures decreased the growth rate of juvenile HBC leaving the vulnerable size class (40-
233 100 mm) exposed to prolonged periods of negative interactions (predation, competition) with
234 RBT. Historically low Lake Powell reservoir levels have resulted in a relatively warm mainstem
235 temperature. We include cold mainstem temperature in our analysis to consider both possible
236 futures. To account for uncertainty in survival, growth, and movement parameters, we based
237 inferences on 1000 draws from the multivariate normal distribution given by the estimated
238 means and associated variance-covariance matrix from Yackulic et al. (2014) combined with
239 1000 draws from the posterior distributions in Yackulic (*In Press*). For each set of parameters,
240 we used the approach described above and in Appendix B to calculate the associated target.

241 For each of two scenarios (hot or cold water temperatures), we calculated the median as well as
242 the 2.5% and 97.5 quantiles of the 1000 values of the target. We then compared these values of
243 the target to survival estimates based on simulated rainbow trout abundances. In particular, to
244 estimate annual juvenile HBC survival in the JCM reach, we modeled juvenile HBC survival as a
245 function of RBT abundance with the following equation based on monthly survival estimates:

246 $\varphi_y = \prod_{t=1}^T \varphi_{y,t}(N_{y,t}^{JCM}),$ (3)

247 where $\varphi_{y,t}$ is monthly juvenile HBC survival, $N_{y,t}^{JCM} = \sum_{j \in J^{JCM}} N_{y,t,j}$ is the sum of RBT
 248 abundance in the set of JCM reach river segments (J^{JCM}), i.e., river kilometers 127.8 to 130.2,
 249 and $T = 12$ months. See Table 2 for the functional form of φ_y .

250 **Management Model**

251 The objective of the management model is to identify a feedback rule, or policy function, that
 252 takes the estimated level of RBT abundance in the JCM reach and selects a level of removals that
 253 achieves the specified conservation goal (target average annual juvenile HBC survival likelihood
 254 σ over the planning horizon) at the lowest expected present value of management costs. The
 255 management action to control RBT involves selecting the annual number of mechanical removal
 256 trips in year $y, a_y \in \{0, 1, \dots, 6\}$, which occur from river kilometer 116.5 to 147.1 (hereafter, the
 257 removal reach). A mechanical removal trip consists of traveling downriver 363.7 kilometers with
 258 removal equipment and requires that all mechanically-removed RBT be processed for beneficial
 259 use. We therefore assume that no more than one removal trip occurs per month, done
 260 sequentially starting in February and ending July due to seasonal constraints (e.g., turbidity). We
 261 assume that removal trip costs are independent of RBT abundance and consist only of labor and
 262 equipment to remove and process the RBT. Trip length is fixed and variation in daily labor due
 263 to RBT abundance would not affect the fixed cost of labor, equipment and trip logistics.
 264 Personnel, equipment and logistical support are available through the Glen Canyon Dam
 265 Adaptive Management Program. Annual management costs are therefore given by:

266 $c(a_y) = c^T a_y,$ (4)

267 where $a_y \in \{0, 1, \dots, 6\}$ and c^T denotes the fixed cost per removal trip.

268 Each mechanical removal trip consists of five “passes” over the entire removal reach, with each
 269 pass removing a proportion (θ) of RBT from each river- segment, representing an average
 270 capture probability (Korman et al. 2012, Korman and Yard 2017). Each removal trip therefore
 271 removes $1 - (1 - \theta)^{5=\text{number of passes}}$ of the RBT from each river- segment along the removal
 272 reach. Let $a_{y,t}^j(a_y)$ be a binary variable equal to one for months t and river-segment j in which
 273 mechanical removals take place and zero otherwise. For example, if $a_y = 3$, then $a_{y,t}^j = 1$ for
 274 each river-segment j within the removal reach for the months $t = 2, 3$, and 4 , and $a_{y,t}^j = 0$ for all
 275 other months (12 in total) and each river segment within the removal reach. Mechanical removal
 276 of RBT along the removal reach can therefore be incorporated into the population model by
 277 replacing the RBT movement equation (2) as follows:

$$278 \quad N_{y,t+1} = \psi_0 \Phi \text{diag}[(1 - a_{y,t}^j(a_y)\theta)^5] N_{y,t}, \quad (5)$$

279 where $\text{diag}[\circ]$ denotes a diagonal matrix whose j^{th} diagonal element is $(1 - a_{y,t}^j(a_y)\theta)^5$. Note
 280 that equation (5) implicitly assumes that monthly removal occurs prior to the movement of RBT
 281 between river segments of the mainstem. This results in movement of RBT in the mainstem prior
 282 to estimating HBC survival, reducing the efficacy of removal. We would multiply equation (2)
 283 by a $J \times 1$ vector, with the removal reach river-segment elements equal to $(1 - a_{y,t}^j(a_y)\theta)^5$, to
 284 implement removal following RBT movement.

285 The management objective is to minimize the expected present value of annual management
 286 action costs over a defined time horizon, Y ,

$$287 \quad \min_{a_y} E\left(\sum_{y=1}^Y \delta^y c(a_y)\right), \quad (6)$$

288 subject to: $a_y \in \{0,1, \dots, 6\}$, the RBT movement and survival (including management action)
 289 process (equation 5), HBC survival rates in the JCM reach (equation 3), and the probability σ

290 that the average annual share of juvenile HBC that survive ($\varphi = \frac{1}{Y} \sum_y \varphi_y$) does not drop below a
291 target rate:

$$292 \Pr(\varphi > Target(\varphi^*)) > \sigma, \quad (7)$$

293 over the planning horizon.

294 The discount factor $\delta < 1$ in equation (6) reflects that costs are given less emphasis the further
295 they lie in the future. The expectation in equation (6) is taken with respect to stochastic annual
296 recruitment of RBT from Glen Canyon, and reflects uncertainty regarding how environmental
297 conditions, exogenous to our model, affect future abundance of RBT. The target survival rate in
298 equation (7) is established to achieve a minimum population abundance with a probability of σ
299 (e.g., 0.90) over a 20-year planning horizon, the same planning horizon specified in recent
300 environmental planning documents (Interior 2016). The probability of meeting a minimum HBC
301 population abundance (σ) was chosen to reflect the fact that RBT abundance in the JCM and
302 mainstem temperature only explain approximately 40 percent of the juvenile HBC survival
303 (Yackulic, *In Press*) and past planning documents have included similar probabilities of recovery
304 (Interior 2016). However, by not specifying $\sigma = 1$ we are diverging from an economically
305 efficient solution².

306 ***Model Solution Process***

307 The solution to the management model in equation (6) identifies a policy function, which is the
308 approximate optimal number of annual mechanical removals given an observed level of RBT
309 abundance in the JCM reach. Identifying the solution involves searching over an infinite set of
310 possible functions. For tractability, we limit our search to the set of policy functions that are

² A cost-effective solution is economically efficient when a good or service is not continuous (e.g., endangered species recovery) and exhibits significant economic value. Choosing a probability of achieving juvenile HBC survival of less than the highest feasible σ is an economically inefficient solution.

311 piecewise linear (straight-line segments) in RBT abundance, rounded to the nearest whole
 312 number of removals, bounded by the minimum (0) and maximum (6) number of mechanical
 313 removals allowed in a year, and limited to the range of RBT abundance in which mechanical
 314 removals are desirable:

$$315 \quad a(N^{JCM+}) = \begin{cases} \text{round}(\min\{\alpha + \beta N^{JCM+}, 6\}), & \text{if } \tau_{min} \leq N^{JCM+} \leq \tau_{max} \\ 0, & \text{otherwise} \end{cases} . \quad (8)$$

316 The state variable input to the policy function, N^{JCM+} , is the existing RBT population at the JCM
 317 reach (N^{JCM}) plus the expected number of new arrivals given stochastic recruitment that would
 318 arrive if no subsequent removals were implemented. The parameters τ_{min} and τ_{max} represent the
 319 lower and upper level, respectively, of RBT abundances at which removals are not cost-effective
 320 at meeting the HBC juvenile survival target rate over the planning period.

321 The process for finding the preferred policy function $a^*(N^{JCM+})$ requires finding the parameters
 322 $[\alpha^*, \beta^*, \tau_{min}^*, \tau_{max}^*]$ that minimize the objective function in equation (6) while satisfying the
 323 probabilistic HBC survival constraint σ in equation (7). We discretize α and β and then examine
 324 each feasible pair to identify the preferred policy from the set, over all parameter combinations
 325 of a partitioned set of $\tau_{min} \in \{300, 450, \dots, 950\}$ and $\tau_{max} \in \{2000, 2150, \dots, 3200\}$, the set over
 326 which mechanical removals are impactful. Specifically, we consider $\alpha \in \{0, 1, \dots, 6\}$ —this
 327 intercept parameter determines removals at the lowest RBT abundance, motivating the use of
 328 integers. The second parameter determines the rate over RBT abundance at which removals
 329 increase ($\beta > 0$) or decrease ($\beta < 0$) as the expected RBT population increase. We consider
 330 $\beta \in \{-10, -9, \dots, 0, \dots, 9, 10\}$. For each unique pair of these two parameters—i.e. for each
 331 candidate policy function—we evaluate costs and population outcomes using 1000 Monte Carlo
 332 simulations. From the set of candidate policy functions, we first exclude those that do not meet

333 the population abundance constraint. Then from the set remaining, we identify the preferred
334 policy function as the one with the lowest expected present value of management costs.
335 The preferred policy is described in the results as annual removal effort over a defined range of
336 RBT abundance in the JCM reach. The sensitivity of the preferred policy to risk preferences or
337 management strategies was tested along with RBT population parameters. This included
338 variation in the length of the simulation period, probability of successfully meeting juvenile HBC
339 survival targets, and the location of RBT removal actions. We also investigated the influence of
340 RBT abundance over the simulation period.

341 **Results**

342 Model results indicated that the most cost-effective strategy to achieve an average annual
343 juvenile HBC survival target of 81% (median estimated target) under warm mainstem
344 temperature conditions, with a likelihood of 90%, required considerable levels of RBT removal
345 at moderate RBT abundances. Under cold mainstem temperature conditions, the average annual
346 survival target of juvenile HBC required to achieve long-run population goals increased to 89%
347 (median estimated target). An average 89% juvenile HBC survival over a 20-year period was not
348 achieved in any base model simulation, under any set of parameter assumptions, even with the
349 most intensive removal strategy (6 annual removals regardless of RBT abundance). This is a
350 result of a change in the annual probability of transition of juvenile HBC out of size class (40 –
351 100 mm) from 30 to 22 percent in warm and cold mainstem temperatures, respectively
352 The expected present value of management costs that met the average annual juvenile HBC
353 survival target under warm mainstem temperatures were lowest with a policy function where
354 removals started moderately high (5), then increased to 6 with increasing RBT abundance (Fig.
355 2). Additionally, the preferred policy function was constrained by lower and upper RBT

356 abundance bounds. Specifically, delaying removal until RBT abundance exceeded ~600
357 individuals and then implementing five annual removals, followed by increasing annual
358 removals with increasing RBT abundance, until RBT abundance exceeded ~2600 individuals, at
359 which point removals ceased, led to the lowest expected present value of management costs over
360 the 20-year planning horizon (\$4.6 million). Given the expected recruitment of RBT and the
361 relatively prompt response of RBT abundance to it, removals did not occur at low RBT
362 abundances, when the juvenile HBC survival target was met. Similarly, these population
363 characteristics led to removals over the upper RBT abundance trigger being ineffective.
364 Conditional on initial parameter values, the expected number of annual removals with this
365 preferred policy function was 4.2. However, removals were typically zero and then jumped to
366 between four and six removals following larger RBT recruitment events. Absent RBT removal,
367 achieving an average annual juvenile HBC survival target of 81% over a 20-year simulation only
368 occurred 6% of the time.

369 *Model Sensitivity*

370 We assessed the sensitivity of model results under different parameter assumptions. Parameters
371 were organized into three categories (discussed further below) including policy criteria, juvenile
372 HBC survival targets, and RBT abundance. In general, variation of these parameters lead to a
373 similar removal strategy (e.g., four or five initial removals, increasing with increasing RBT
374 abundance) but with variation in the starting and ending RBT abundances over which this
375 removal strategy was applied. This variation in preferred policy functions under different
376 parameter assumptions led to differences in the average annual expected removals that occurred
377 when varying model parameters (Fig. 2). For example, we made several policy criteria
378 assumptions when specifying parameters in the base model: we set the simulation period to 20

379 years (Interior 2016), specified the risk tolerance (the required probability of staying above the
380 average juvenile HBC survival target) at 90%, and located the RBT removal reach at the
381 confluence of the LCR and mainstem (river kilometers 116.5 – 147.1). When decreasing or
382 increasing the planning horizon from 20 years, we found that average annual expected removals
383 either increased or decreased with shorter or longer planning horizons, respectively, and that the
384 preferred removal strategies became more or less intensive to meet these requirements (Fig. 2A-
385 B). The solution was sensitive to starting RBT abundance in the mainstem when reducing the
386 planning horizon. Using recent average RBT abundance in the mainstem (Interior 2016),
387 reducing the planning horizon to 10-years made meeting average annual juvenile HBC survival
388 target 90% of the time unattainable even with the most intensive removal strategy.

389 Resource managers may alter their level of risk tolerance over time. We increased (lowered the
390 probability of meeting juvenile chub survival targets) or decreased the risk tolerance parameter
391 from the base model. Increasing the risk tolerance decreased the average annual expected
392 removals required to meet juvenile chub survival target while decreasing the risk tolerance in the
393 model increased average annual expected removals (Fig. 2C-D). Specifying $\sigma=0.975$ made
394 meeting juvenile HBC survival goals infeasible.

395 The policy assumption with the largest impact on the effectiveness of RBT removal required to
396 achieve the average juvenile HBC survival target was the location of RBT removal. Relocating
397 the removal reach upriver from river kilometers 113.5 – 147.1 made meeting average annual
398 juvenile HBC survival target 90% of the time unattainable (Fig. 2E-F). Relocating removals
399 upstream from the LCR confluence takes less advantage of the slow dispersion of RBT from
400 Glen Canyon and the natural rainbow trout mortality during the interval it takes for the trout to

401 move downstream. Relocating the removal reach downstream approximately 8 kilometers,
402 increased the average annual expected removals significantly (Fig. 2E-F).

403 Expected RBT abundance in the JCM reach was dependent on recruitment in Glen Canyon,
404 outmigration into Marble Canyon and survival of those outmigrants and resident RBT in Marble
405 Canyon. To assess sensitivity of the preferred policy to RBT population dynamics, we increased
406 RBT recruitment over the planning horizon. Increasing the RBT abundance over the simulation
407 period by 10% made meeting average annual juvenile HBC survival target 90% of the time
408 infeasible, indicating a threshold in RBT abundance and a feasible model solution given the
409 annual removal constraint. Decreasing RBT recruitment by 10 or 20% resulted in fewer average
410 annual expected removals and less intensive removal policies (Fig. 2G-H).

411 In our base model, we used the median estimated target for juvenile HBC survival of 81%, the
412 juvenile HBC survival needed to maintain an adult HBC population of 7000. We also used the
413 median values for the juvenile HBC survival function (i.e., relationship between RBT abundance
414 in the JCM reach and juvenile HBC survival) (Yackulic, *In Press*). We explored sensitivity of
415 the preferred policy function using either the 2.5 or 97.5 percentile juvenile HBC survival targets
416 and parameters in the survival function (Yackulic, *In Press*). No removals are required to meet
417 the annual juvenile HBC survival target on average when using parameter estimates at the 2.5
418 percentile. When simulating the model with survival parameter estimates at the 97.5 percentile, it
419 is infeasible to meet the annual juvenile HBC survival target on average. These results indicate
420 that if actual juvenile HBC survival is far from central estimates, the preferred policy will differ
421 considerably.

422 **Discussion**

423 Efficient dynamic management of interacting invasive and endangered species populations is a
424 pressing conservation issue (Lampert et al. 2014). This challenge is compounded when invasive
425 species eradication is not a feasible or desirable option. Our model integrated a location-structured
426 RBT population model with juvenile HBC survival targets and control costs to identify the least
427 cost RBT removal strategy to meet HBC population goals over time. Our study identified an
428 efficient RBT control strategy to effectively manage the HBC population, while retaining the
429 RBT population in Glen Canyon, and identified exogenous environmental conditions that limit
430 success of applied management strategies.

431 The model demonstrated that considerable levels of RBT removal would be needed to cost-
432 effectively achieve annual juvenile HBC survival targets under the present condition of warm
433 mainstem temperatures. A considerable level of removals is required due to monthly RBT
434 movement following a removal trip, reducing the efficacy of removals. Under cold mainstem
435 temperature removals were unable to achieve annual juvenile HBC survival targets. The
436 preferred RBT removal policy was dependent on model parameter specification but was
437 insensitive to higher-order approximation of the policy function. We evaluated model sensitivity
438 by varying parameters associated with policy criteria, RBT abundance and juvenile HBC
439 survival targets. In general, variation in parameter estimates led to similar preferred policy
440 functions with variation in RBT “trigger” bounds. These ‘trigger’ bounds are defined by RBT
441 recruitment and movement parameters and the juvenile HBC survival function. Over the
442 simulation period, the frequency of large RBT recruitment events and the time it takes RBT to
443 populate the JCM govern the bioeconomic model solution. For example, implementing removals
444 following RBT movement, increasing the efficacy of removals, narrows the ‘trigger’ bounds of
445 the preferred removal strategy. ‘Trigger’ bounds are further defined by the reverse ‘S-curve’

446 shape of the juvenile HBC survival function, resulting in limited marginal benefit of removal at
447 low and high RBT abundance.

448 Increasing the probability of meeting a juvenile HBC survival target or decreasing the simulated
449 planning horizon required a higher expected number of removals. In addition, higher abundance
450 of RBT from upstream sources made the likelihood of achieving a juvenile HBC survival target
451 infeasible. For context, the largest recruitment event (2011) in the last 15 years led to RBT
452 abundance in the vicinity of the JCM reach of ~400 RBT per 1.5 km (Korman and Yard 2017).
453 Relocating removal upriver of the removal reach also resulted in infeasible model solution.

454 Given a constant proportion of RBT removed in any removal reach and the Cauchy-distributed
455 movement of RBT, removals that occurred upriver from the LCR (greater RBT abundance) were
456 less useful at reducing long-run abundance in the JCM reach. Removal of RBT at locations
457 distant to the JCM reach is further complicated by the location of RBT abundance that triggers
458 removal. Bifurcating removal and the location of the RBT abundance trigger results in less
459 effective removals. These model characteristics highlighting the tradeoffs between variation in
460 removal location and the difference in removal effort required to achieve long-run HBC
461 population goals. The confluence has cultural significance to Native American tribes tied to Glen
462 and Grand Canyons, therefore the location of the removal reach is an important aspect of the
463 model structure and consideration in exploring the preferred management strategy.

464 Because several assumptions were made in development of this model, an important
465 consideration in model implementation is the ability to accurately predict changes in estimated
466 parameters (Coulson et al. 2001). Several of the parameters used in this study could be
467 influenced by environmental conditions that were exogenous to our model, including turbidity
468 and food base conditions in the tailwater and mainstem. As Lake Powell changes and climate

469 influences the Colorado River Basin hydrology, characteristics of the tailwater are likely to
470 change, affecting RBT recruitment. Increasing mainstem temperature as a result of decreasing
471 reservoir levels has been identified as an environmental condition that may increase RBT
472 recruitment (Dibble, 2017, written comm.). In addition, long-term changes in mainstem turbidity
473 or the food base due to environmental or management perturbations are factors that would affect
474 RBT and HBC populations or further constrain the number of annual removals (Cross et al.
475 2013, Dodrill et al. 2016; Dzul et al., 2016; Yackulic, *In Press*). Another significant model
476 assumption concerning RBT population dynamics is that no local recruitment occurred in Marble
477 Canyon (Korman et al. 2015). The dynamic between RBT abundance and characteristics of
478 removal (timing, intensity and location) could be increased if this condition changed. It is also
479 important to recognize that HBC recruitment and movement is predicated on historical
480 hydrologic conditions in the LCR (Interior 2016). If historical flooding patterns change, in the
481 winter or during monsoon season, HBC recruitment and movement (i.e., dispersal into the
482 mainstem) parameters could be altered significantly.³ This in turn would affect target rates of
483 survival, influencing the preferred RBT removal strategy. Continued monitoring and research of
484 RBT and HBC populations would allow for the identification of any departure from the
485 estimated population parameters as a result of changing environmental conditions.
486 Future development of this bioeconomic model could include alternative RBT control options
487 and/or RBT and HBC population triggers that prompt management actions. An example is the
488 tradeoff between managing RBT recruitment in Glen Canyon, immediately below Glen Canyon
489 Dam, and RBT removals at the confluence of the LCR. The LTEMP FEIS (Interior 2016) has
490 proposed RBT management flows at Glen Canyon Dam to reduce high RBT recruitment events.

³ The monsoon is a pattern of increased rainfall in the southwestern United States and northwestern Mexico, typically occurring between July and September (Adams and Comrie 1997).

491 The proposed RBT management flows maintain high steady flows for a period of time and then
492 reduce flows dramatically to strand young-of-year RBT. Our model could be refined to inform
493 on the effectiveness and overall economic costs (e.g., foregone hydropower) of RBT
494 management flows for achieving juvenile HBC survival targets. Model results indicated that
495 reduced RBT recruitment in Glen Canyon would reduce removal efforts needed to maintain the
496 target juvenile HBC survival target. This is based on the assumption that population parameters
497 in the HBC population remain constant and that focusing on the invasive species trigger is most
498 effective (Baxter et al. 2008). Furthermore, we assumed that variation in the need for control was
499 best captured by the abundance of RBT (given the impact on juvenile HBC survivorship).
500 However, it may be the case that optimal control should also vary depending on the level of adult
501 HBC abundance, the establishment of other adult HBC populations through translocation, or
502 variation in environmental condition that alter HBC population dynamics (e.g., steady flows at
503 GCD to increase macroinvertebrate production) (Interior 2016). These factors are important
504 when considering the actual implementation of a preferred removal strategy. For example, is it
505 reasonable to assume resource managers would forego removals at high RBT abundance and low
506 adult HBC abundance?

507 The model provides an assessment from a HBC stochastic viability approach that achieves
508 predetermined population goals through an efficient policy. The model framework was
509 developed to incorporate changes in environmental conditions and revised parameter estimates
510 based on continued research of the biological and physical system, and changes in the options
511 and relative prices of management alternatives. Although the model results are presented in
512 specific terms, the intent of the modeling framework is to 1) provide a general framework to
513 identify the most cost-effective approach to enhancing native species population viability via

514 invasive species control, and 2) develop a framework to identify additional tradeoffs in
515 management of RBT and other downstream resources due to dam operations. This general
516 framework could be applied in different systems with management actions that include direct
517 invasive species management, habitat manipulations, or other actions. Managing aquatic invasive
518 species in freshwater ecosystems, especially those species intentionally introduced to provide
519 social and economic value, will undoubtedly continue to present conservation challenges. The
520 scientific investment in estimating parameters for population models of interacting species can
521 be significant; however, the advantage of joint population abundance predictions within a cost-
522 effectiveness analysis framework has the potential to lead to efficient management outcomes.
523 This framework may also be apt at addressing multiple stakeholder objectives or conflicting
524 values that are often present in resource conservation efforts. Our model considers population
525 level dynamics, species interaction and economic cost to provide an effective and efficient
526 solution to long-run management of RBT in Glen and Grand Canyons to improve the probability
527 that HBC population goals are met.

528 **Acknowledgements**

529 We thank Thomas Gushue for the map of the study area; and are grateful for comments provided
530 by Michael Runge, and Scott VanderKooi (all with USGS), as well as Josh Korman, Carl
531 Walters, and four anonyms reviewers. The Glen Canyon Dam Adaptive Management Program
532 financially supported this project. Any use of trade, firm, or product names is for descriptive
533 purposes only and does not imply endorsement by the U.S. Government.

534 **Literature Cited**

535 Adams, D.K. and A.C. Comrie. 1997. The North American monsoon. *Bulletin of the American*
536 *Meteorological Society* 78(10):2197-2213.

537 Bair, L.S., D.L. Rogowski, and C. Neher. 2016. Economic value of angling on the Colorado
538 River at Lees Ferry: Using secondary data to estimate the influence of seasonality. *North*
539 *American Journal of Fisheries Management* 36(6): 1229-1239.

540 Baxter, P.W., J.L. Sabo, C. Wilcox, M.A. McCarthy, and H.P Possingham. 2008. Cost-effective
541 suppression and eradication of invasive predators. *Conserv Biol.* 22(1):89-98.

542 Bureau of Reclamation. 1995. Operation of Glen Canyon Dam, Colorado River storage project,
543 Arizona: Final Environmental Impact Statement. Pages 337 in. U.S. Department of the Interior,
544 Salt Lake City, UT.

545 Coggins, L.G. Jr., M.D. Yard, and W.E. Pine III. 2011 Nonnative fish control in the Colorado
546 River in Grand Canyon, Arizona: an effective program or serendipitous timing? *Transactions of*
547 *the American Fisheries Society* 140(2):456-470.

548 Coulson, T., G.M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population
549 viability analysis. *Trends in Ecology and Evolution* 16(5):219–221.

550 Cross, W. F., and coauthors. 2013. Food-web dynamics in a large river discontinuum. *Ecological*
551 *Monographs* 83(3):311-337.

552 Dodrill, M.J., Yard, M.D., and Pine, W.E. 2016. Assessing predation risks for small fish in a
553 large river ecosystem between contrasting habitats and turbidity conditions. *Am. Midl. Nat.*
554 175:206–221.

555 Dzul, M.C., C.B. Yackulic, D.M. Stone, and D.R. Van Haverbeke. 2016. Survival, growth, and
556 movement of subadult humpback chub, *Gila cypha*, in the Little Colorado River, Arizona. *River*
557 *Research and Applications* 32(3):373–382.

558 Ebbert, S.M. and G.V. Byrd. 2002. Eradications of invasive species to restore natural biological
559 diversity on Alaska Maritime National Wildlife Refuge. In: Veitch, C.R. and M.N. Clout (eds.).

560 Turning the tide: the eradication of invasive species, pp. 102-109. IUCN SSC Invasive Species
561 Specialist Group, Gland, Switzerland and Cambridge, UK

562 Korman J., M.D. Yard, and C.B. Yackulic. 2015. Factors controlling the abundance of rainbow
563 trout in the Colorado River in Grand Canyon in a reach utilized by endangered humpback chub.
564 Can. J. Fish. Aquat. Sci. 73(1):105–124.

565 Korman, J., S.J.D. Martell, C.J. Walters, A.S. Makinster, L.G. Coggins, M.D. Yard, and W.R.
566 Persons. 2012. Estimating recruitment dynamics and movement of rainbow trout (*Oncorhynchus*
567 *mykiss*) in the Colorado River in Grand Canyon using an integrated assessment model. Can. J.
568 Fish. Aquat. Sci. 69: 1827-1849.

569 Korman, J, and M.D. Yard. 2017. Effects of environmental covariates and density on the
570 catchability of fish populations and interpretation of catch per unit effort trends. Fisheries
571 Research 189:18–34.

572 Lampert, A., A. Hastings, E.D. Grosholz, S.L. Jardine, and J.N. Sanchirico. 2014. Optimal
573 approaches for balancing invasive species eradication and endangered species management.
574 Science 344:1028–1031.

575 Moore, M.A., A.E. Boardman, A.R. Vining, D.L. Weimer, D.H. Greenberg. 2004. “Just give me
576 a number!” Practical values for the social discount rate. Journal of Policy Analysis and
577 Management 23(4):789-812.

578 Moran, D., H. Laycock, and P.C.L. White. 2010. The role of cost-effectiveness analysis in
579 conservation decision-making. Biological Conservation 143: 826–827.

580 Murdoch, W., S. Polasky, K.A. Wilson, H.P. Possingham, P. Kareiva, and R. Shaw. 2007.
581 Maximizing return on investment in conservation. Biological Conservation 139:375–388.

582 Naidoo R., A. Balmford, P.J. Ferraro, S. Polasky, T.H. Ricketts, and M. Rouget. 2006.
583 Integrating economic costs into conservation planning. *Trends in Ecology and Evolution* 21:681–
584 687.

585 Polasky, S. 2008. Why conservation planning needs socioeconomic data. *Proceedings National*
586 *Academy of Sciences* 105(18):6505–6506.

587 R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for
588 *Statistical Computing*, Vienna, Austria. <https://www.R-project.org/>.

589 Rose, L.E., G.W. Heard, Y.E. Chee, and B.A. Wintle. 2016. Cost-effective conservation of an
590 endangered frog under uncertainty. *Conservation Biology* 30(2):350–361.

591 Sagoff, M. 2009. Regulatory review and cost-benefit analysis. *Philosophy and Public Policy*
592 *Quarterly* 29(3/4):21–26.

593 Schmidt, J.C., R.H. Webb; R.A. Valdez, G.R. Marzolf, L.E. Stevens. 1989. Science and Values
594 in River Restoration in the Grand Canyon. *BioScience* 48(9):735-747.

595 Schlaepfer, M.A., D.F. Sax, and J.D. Olden. 2011. The Potential Conservation Value of Non-
596 Native Species. *Conservation Biology* 25(3):428–437.

597 U.S. Bureau of Reclamation (Reclamation). 2011. *Environmental Assessment for Non-Native*
598 *Fish Control Downstream from Glen Canyon Dam, Upper Colorado Region, Salt Lake City,*
599 *Utah.*

600 U.S. Department of Interior (Interior). 2016. *Glen Canyon Dam long-term experimental and*
601 *management plan environmental impact statement*. Bureau of Reclamation, National Park
602 *Service.*

603 U.S. Fish and Wildlife Service (USFW). 1994. *Endangered and threatened wildlife and plants;*
604 *determination of critical habitat for the Colorado River endangered fishes: razorback sucker,*

605 Colorado squawfish, humpback chub, and bonytail chub. 59: 54 [1994] 13374-13400. Federal
606 Register.

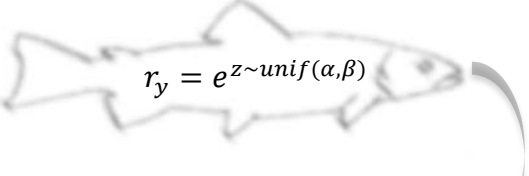
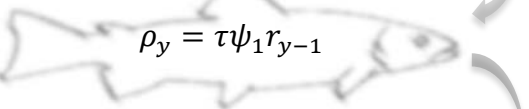
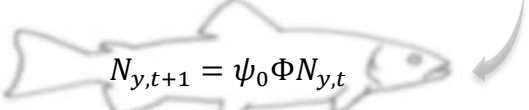
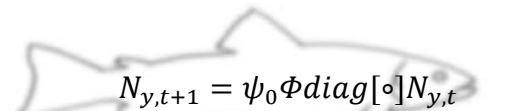
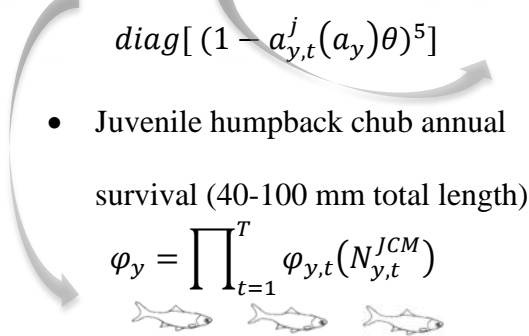

607 Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying Threats to
608 Imperiled Species in the United States. *BioScience* 48(8): 607-615.

609 Yackulic, C.B., Korman, J., Yard, M.D., Dzul, M. *In Press*. Inferring species interactions
610 through joint mark-recapture analysis. *Ecology*.

611 Yackulic, C. B., M.D. Yard, J. Korman, and D.R. Van Haverbeke. 2014. A quantitative life
612 history of endangered humpback chub that spawn in the Little Colorado River: variation in
613 movement, growth, and survival. *Ecology and Evolution* 4(7):1006-1018.

614 Yard, M.D., L.G. Coggins, C.V. Baxter, G.E. Bennett, and J. Korman. 2011. Trout piscivory in
615 the Colorado River, Grand Canyon – effects of turbidity, temperature, and fish prey availability.
616 *Trans. Am. Fish Soc.* 140:471-486.

617 Table 1: Model schematic

Location	Component*	Timeline
Glen Canyon (0 -26.4 km)	Trout recruitment  $r_y = e^{z \sim unif(\alpha, \beta)}$	Annual log recruitment is a function of a random draw from a uniform distribution representing the range of possible age-1 RBT recruiting into Lees Ferry.
Marble Canyon (26.4 km)	Trout outmigration  $\rho_y = \tau \psi_1 r_{y-1}$	Outmigration of age-1 RBT occurs in river-segment 1 (kilometer 26.4) in the year subsequent to recruitment.
Marble and Grand Canyons (26.4 – 267.8 km) <ul style="list-style-type: none"> • Removal reach (116.5 – 147.1 km) • Juvenile Humpback Chub Monitoring reach (127.8 – 130.2 km) 	Trout movement and abundance  $N_{y,t+1} = \psi_0 \Phi N_{y,t}$ <ul style="list-style-type: none"> • Trout removal  $N_{y,t+1} = \psi_0 \Phi \text{diag}[\circ] N_{y,t}$ $\text{diag}[(1 - a_{y,t}^j (a_y) \theta)^5]$ <ul style="list-style-type: none"> • Juvenile humpback chub annual survival (40-100 mm total length)  $\varphi_y = \prod_{t=1}^T \varphi_{y,t}(N_{y,t}^{JCM})$ 	Trout movement is the spatial distribution of outmigrants from Glen Canyon reach and the resident population and abundance is based on survival. <ul style="list-style-type: none"> • Rainbow trout removal level is a choice variable on the abundance of rainbow trout in the JCM reach without removals. • The annual survival of juvenile humpback chub is calculated following management actions to remove rainbow trout in the removal reach.

618 *Table 2 for model parameter description

Table 2: Definition of model variables

Variable	Description	Value or transformation	Citation
RBT recruitment: $r_y = e^{z \sim \text{unif}(\alpha, \beta)}$			
α	Lower recruitment bound specified by historical flow characteristics	11	Korman et al. 2012
β	Upper recruitment bound specified by historical flow characteristics	14	Korman et al. 2012
RBT outmigration: $\rho_y = \tau \psi_1 r_{y-1}$			
τ	Annual out-migration rate from Glen Canyon reach	0.397	Korman et al. 2012
ψ_1	Annual age-1 trout survival rate out-migrating from Glen Canyon reach	0.437	Korman et al. 2012
RBT movement and abundance in each river segment: $\mathbf{N}_{y,t+1} = \psi_0 \Phi \mathbf{N}_{y,t}$			
ψ_0	Monthly trout survival rate	0.96	Korman et al. 2012
Φ	$J \times J$ matrix based on a Cauchy distribution; $J = 1, \dots, 151$ matrix (river reach)	$\chi_0=0, \gamma=3.38$	Interior 2016
t	Months	$\in \{1, 2, \dots, 12\}$	-

Y	Years	$\in\{1,2,\dots,20\}$	Interior 2016
RBT removal: $N_{y,t+1} = \psi_0 \Phi \text{diag}[(1 - a_{y,t}^j(a_y)\theta)^5]N_{y,t}$			
a	Number of removals in a year	$\in \{0,1, \dots,6\}$	Interior 2016
θ	Removal efficacy (proportion of RBT removed)	0.10	Korman et al. 2012
Discounted cost of removal: $E(\sum_{y=1}^Y \delta^y c(a_y))$			
Y	Period in years	20	Interior 2016
c	Removal cost per trip	\$75000	Yard, 2017, <i>pers. comm.</i>
δ	Annual discount rate	(1- 0.03)	Moore et al. 2004
Annual HBC survival: $\varphi_y = \prod_{t=1}^T \varphi_{y,t}(N_{y,t}^{JCM}) = \prod_{t=1}^T 1/(1 + e^{-(\mu_1 + \mu_2 * N_{y,t}^{JCM})})$			
$\mu_{1,2}$	Constant parameters in survival function	4.767, -9.125×10^{-4}	Yackulic, <i>In Press</i>
φ_y^*	Annual average survival target for warm (cold) mainstem temperatures	0.81 (0.89)	Current study

622 Figure 1. Study area map

623

624 Figure 2. Cost-effective rainbow trout removal strategies under warm Colorado River
625 temperatures conditions that on average meet the juvenile humpback chub survival target.
626 Depicted relationships between simulation period (20 year baseline) and average annual
627 expected removals (A) and preferred annual removal strategy (B). Grey box in A is baseline and
628 colored lines (B) show baseline (grey), 25-year (blue), and 15-year (green) simulation. Depicted
629 relationships between probability of on average meeting juvenile humpback chub survival targets
630 and average annual expected removals (C) and preferred annual removal strategy (D). Grey box
631 in B is baseline and colored lines (D) show baseline (grey) results, 85% probability (blue), and
632 95% probability (green) of on average meeting juvenile humpback chub survival target. Depicted
633 relationships between removal reach (upstream is negative) and average annual expected
634 removals (E) and preferred annual removal strategy (F). Grey box in E is baseline and colored
635 lines (F) show baseline (grey) and -8 kilometer removal reach (blue) results. Depicted
636 relationships between rainbow trout recruitment and average annual expected removals (G) and
637 preferred annual removal strategy (H). Grey box in G is baseline and colored lines (H) show
638 baseline (grey) results, 20% decrease (red), and 10% decrease (blue) in rainbow trout
639 recruitment. When the probability of, on average, meeting juvenile humpback chub survival
640 targets is infeasible, boxplot label marked with asterisk (A, C, D, and E).

641

642

643

644

645

646

647

648

649

650

651

652

653

654

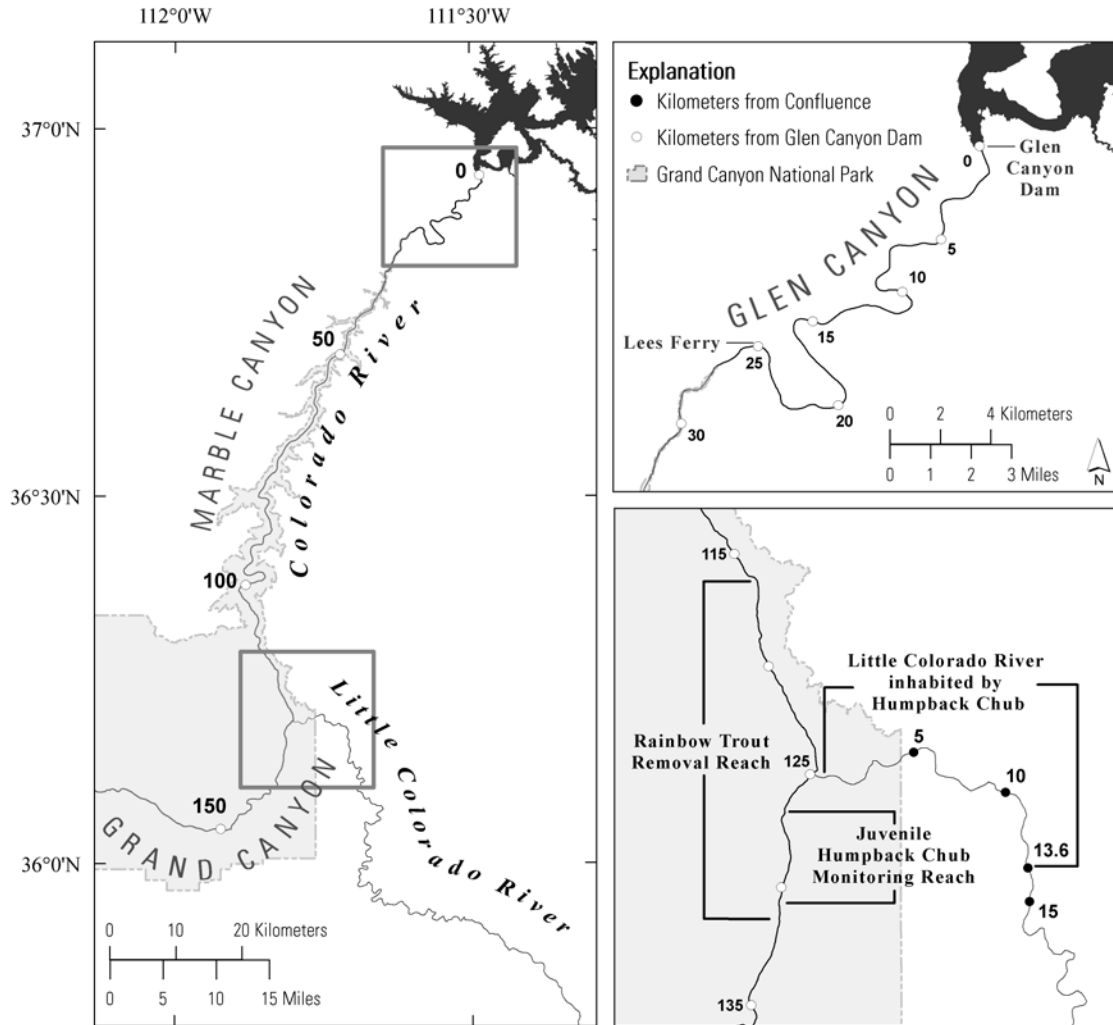


Figure 1

655
 656
 657
 658
 659
 660
 661
 662
 663
 664
 665
 666
 667
 668
 669
 670
 671
 672
 673

674
 675
 676
 677
 678
 679
 680
 681
 682
 683
 684
 685
 686
 687
 688
 689
 690
 691
 692
 693
 694
 695
 696
 697
 698
 699
 700
 701
 702
 703
 704
 705
 706
 707
 708
 709
 710
 711
 712
 713
 714
 715
 716
 717
 718
 719

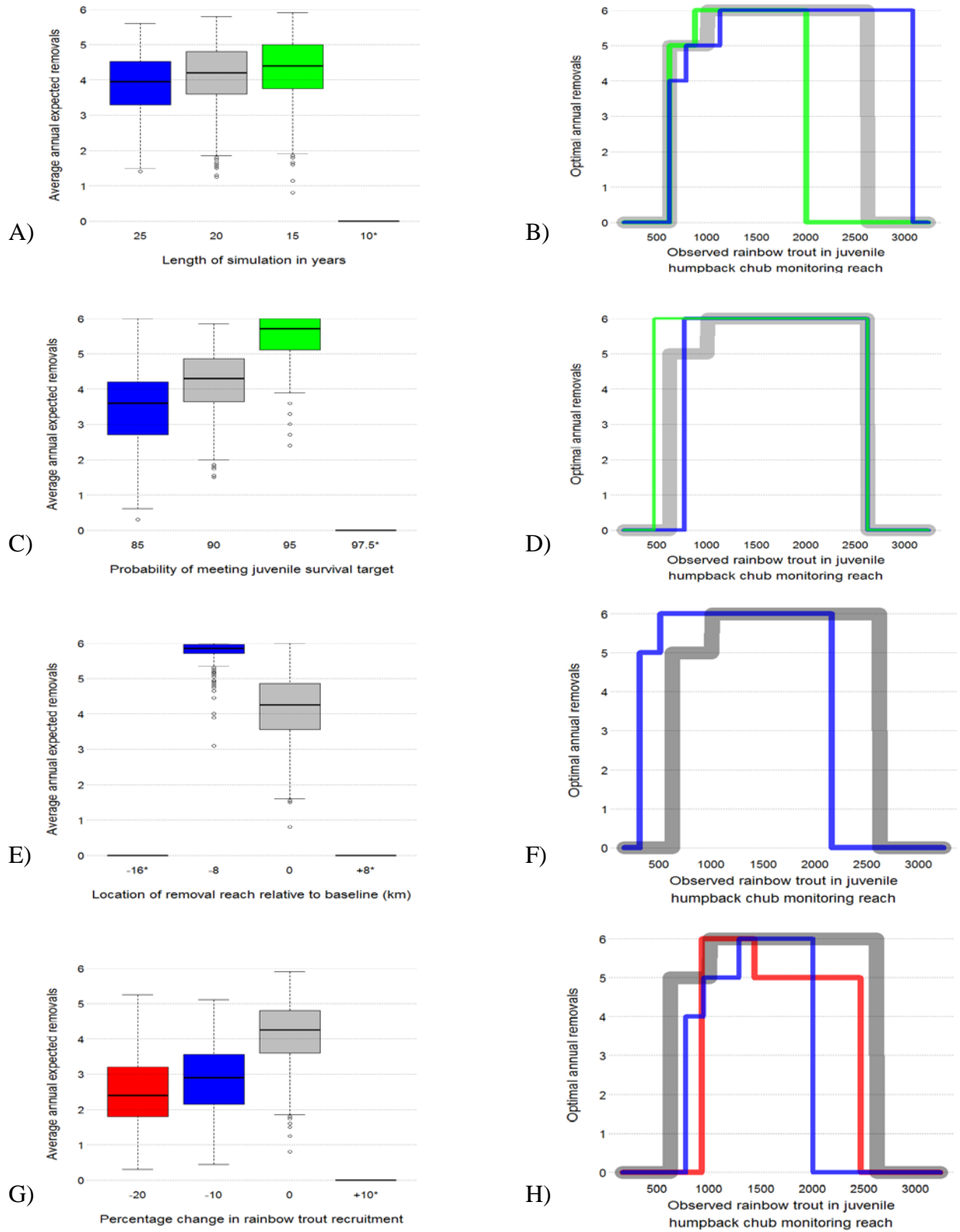


Figure 2