Title

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

Running Head

Cost-effective invasive species control

Authors

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

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

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

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

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

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

[*] Corresponding author: lbair@usgs.gov

Abstract

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

Key Words

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

Introduction

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

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

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

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

In this paper we developed a bioeconomic model to identify the least-cost management strategy to control invasive rainbow trout (*Oncorhynchus mykiss*; hereafter, RBT) subject to achieving juvenile humpback chub (*Gila cypha*; hereafter, HBC) survival targets. We modified established population models for RBT and HBC and utilized management cost information generated from long-term monitoring and research at the Grand Canyon Monitoring and Research Center (GCMRC) (Korman et al. 2012, Yackulic et al. 2014, Yackulic, *In Press*). We identify the least-cost management action given juvenile HBC survival targets, which supports long-run viability of the adult population over time. Further, we explore the sensitivity of the model across assumptions regarding RBT population parameters and risk preferences, and discuss the potential environmental conditions that would affect fundamental model assumptions and results.

Methods

Study Area

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

Glen Canyon, often referred to as Lees Ferry. Rainbow trout recruitment in the tailwater of the GCD (i.e., Glen Canyon reach) is driven by many factors, including within-day, seasonal and annual variation in flows from the GCD, and a proportion of RBT move downstream (Korman et al. 2012, Korman et al. 2015). Rainbow trout that move downstream along the mainstem to the LCR confluence prey on, and compete with, HBC (Yard et al. 2011) and increased RBT abundances are associated with lower survival of juvenile HBC (Yackulic, *In Press*).

In an effort to reverse declining HBC abundance, mechanical removal of RBT was performed from 2003 to 2006 and in 2009 (Interior 2016). Mechanical removal involves boat electrofishing for RBT, which are subsequently processed (e.g., cleaned, frozen) for beneficial use outside of GCNP[1]. Humpback chub abundance appeared to increase following RBT removals; however, these increases coincided with two favorable changes in the environment from the perspective of HBC: warming mainstem temperatures and declining RBT numbers system-wide (Coggins et al. 2011). The GCMRC has continued to monitor and collect data on RBT and HBC, along with environmental conditions, since RBT removals began in the 2000s. Concerted juvenile HBC research beginning in 2009 allowed us to develop an empirically-grounded model to explore the ability of RBT removals to meet HBC long-run population recovery goals under historically demarcated periods of cold and warm mainstem temperatures. The bioeconomic model modified recent approaches to modeling HBC and RBT demographics and utilized existing empirical data to inform parameter estimates, as summarized in the Long-Term Experimental and Management Plan Final Environmental Impact Statement (LTEMP FEIS) (Interior 2016).

Model Framework

[1]Beneficial 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.

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

<u>Population Model</u>

The population model depicts the stylized dynamics, or simplified configuration of empirical findings, of RBT and HBC along a ~130-kilometer reach of the mainstem, from Glen Canyon to just past the LCR confluence (see Table 1). The population model is comprised of the following three components: 1) RBT recruitment in Glen Canyon; 2) outmigration of RBT and their movement and survival in Marble Canyon between Glen Canyon and the JCM reach; and 3) juvenile HBC survival in the JCM reach in response to RBT abundance from September through August of each year.

Rainbow trout recruitment

Rainbow trout recruitment, which largely occurs in the Glen Canyon reach, is highly variable and is determined by factors exogenous to our model. We follow Korman et al. (2012) and model annual RBT recruitment r_y , where *y* denotes year, as density independent according to a stochastic exponential function e^z, where *z* is a random variable that follows a uniform distribution, z~unif(α,β). The parameters α and β are chosen such that all potential recruitment events r_y lie within the range of historical estimates (Korman et al. 2012, Interior 2016). Estimated abundance of RBT in Glen Canyon over the last several decades has ranged from ~0.2 – 1.0 million individuals (Korman and Yard 2017).

Rainbow trout outmigration and movement

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

$$\rho_y = \tau\psi_1 r_{y-1}, \quad (1)$$

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

For the purposes of implementing mechanical removal, we model monthly movement and dispersion of RBT between each of the *J* river segments (approximately 1.6 km in length) of the mainstem between river-kilometer 26.4 and 267.8. We assume that movement is independent of RBT density and follows a Cauchy distribution $f(x; 0, 3.38)$, a continuous distribution with a lower probability than a normal distribution of RBT moving long distances (Interior 2016). Letting $\boldsymbol{N}_{y,t}$ denote a $J \times 1$ vector containing the abundance of RBT within each river-segment along the mainstem in year *y* and month *t*, the movement and survival of RBT can be characterized as:

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

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

Juvenile humpback chub survival

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

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

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

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

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

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

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 abundance in the set of JCM reach river segments (J^{JCM}), i.e., river kilometers 127.8 to 130.2, and T =12 months. See Table 2 for the functional form of φ_y.

Management Model

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

$$c(a_y) = c^T a_y, \tag{4}$$

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

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

$$\boldsymbol{N}_{y,t+1} = \psi_0 \boldsymbol{\Phi} \mathrm{diag}[(1-a_{y,t}^{j}(a_y)\theta)^5]\boldsymbol{N}_{y,t}, \quad (5)$$

where diag[∘] denotes a diagonal matrix whose *j*th diagonal element is $(1-a_{y,t}^{j}(a_y)\theta)^5$. Note that equation (5) implicitly assumes that monthly removal occurs prior to the movement of RBT between river segments of the mainstem. This results in movement of RBT in the mainstem prior to estimating HBC survival, reducing the efficacy of removal. We would multiply equation (2) 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 implement removal following RBT movement.

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

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

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

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

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

over the planning horizon.

The discount factor $\delta < 1$ in equation (6) reflects that costs are given less emphasis the further they lie in the future. The expectation in equation (6) is taken with respect to stochastic annual recruitment of RBT from Glen Canyon, and reflects uncertainty regarding how environmental conditions, exogenous to our model, affect future abundance of RBT. The target survival rate in equation (7) is established to achieve a minimum population abundance with a probability of σ (e.g., 0.90) over a 20-year planning horizon, the same planning horizon specified in recent environmental planning documents (Interior 2016). The probability of meeting a minimum HBC population abundance (σ) was chosen to reflect the fact that RBT abundance in the JCM and mainstem temperature only explain approximately 40 percent of the juvenile HBC survival (Yackulic, *In Press*) and past planning documents have included similar probabilities of recovery (Interior 2016). However, by not specifying $\sigma = 1$ we are diverging from an economically efficient solution[2].

Model Solution Process

The solution to the management model in equation (6) identifies a policy function, which is the approximate optimal number of annual mechanical removals given an observed level of RBT abundance in the JCM reach. Identifying the solution involves searching over an infinite set of 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.

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

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

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

The process for finding the preferred policy function $a^*(N^{JCM+})$ requires finding the parameters $[\alpha^*, \beta^*, \tau^*_{min}, \tau^*_{max}]$ that minimize the objective function in equation (6) while satisfying the probabilistic HBC survival constraint σ in equation (7). We discretize α and β and then examine each feasible pair to identify the preferred policy from the set, over all parameter combinations of a partitioned set of $\tau_{min} \in \{300,450, \dots ,950\}$ and $\tau_{max} \in \{2000,2150, \dots ,3200\}$, the set over which mechanical removals are impactful. Specifically, we consider $\alpha \in \{0,1, \dots ,6\}$—this intercept parameter determines removals at the lowest RBT abundance, motivating the use of integers. The second parameter determines the rate over RBT abundance at which removals increase ($\beta > 0$) or decrease ($\beta < 0$) as the expected RBT population increase. We consider $\beta \in \{-10, -9 \dots ,0, \dots 9, 10\}$. For each unique pair of these two parameters—i.e. for each candidate policy function—we evaluate costs and population outcomes using 1000 Monte Carlo simulations. From the set of candidate policy functions, we first exclude those that do not meet the population abundance constraint. Then from the set remaining, we identify the preferred policy function as the one with the lowest expected present value of management costs. The preferred policy is described in the results as annual removal effort over a defined range of RBT abundance in the JCM reach. The sensitivity of the preferred policy to risk preferences or management strategies was tested along with RBT population parameters. This included variation in the length of the simulation period, probability of successfully meeting juvenile HBC survival targets, and the location of RBT removal actions. We also investigated the influence of RBT abundance over the simulation period.

Results

Model results indicated that the most cost-effective strategy to achieve an average annual juvenile HBC survival target of 81% (median estimated target) under warm mainstem temperature conditions, with a likelihood of 90%, required considerable levels of RBT removal at moderate RBT abundances. Under cold mainstem temperature conditions, the average annual survival target of juvenile HBC required to achieve long-run population goals increased to 89% (median estimated target). An average 89% juvenile HBC survival over a 20-year period was not achieved in any base model simulation, under any set of parameter assumptions, even with the most intensive removal strategy (6 annual removals regardless of RBT abundance). This is a result of a change in the annual probability of transition of juvenile HBC out of size class (40 – 100 mm) from 30 to 22 percent in warm and cold mainstem temperatures, respectively The expected present value of management costs that met the average annual juvenile HBC survival target under warm mainstem temperatures were lowest with a policy function where removals started moderately high (5), then increased to 6 with increasing RBT abundance (Fig. 2). Additionally, the preferred policy function was constrained by lower and upper RBT abundance bounds. Specifically, delaying removal until RBT abundance exceeded ~600 individuals and then implementing five annual removals, followed by increasing annual removals with increasing RBT abundance, until RBT abundance exceeded ~2600 individuals, at which point removals ceased, led to the lowest expected present value of management costs over the 20-year planning horizon ($4.6 million). Given the expected recruitment of RBT and the relatively prompt response of RBT abundance to it, removals did not occur at low RBT abundances, when the juvenile HBC survival target was met. Similarly, these population characteristics led to removals over the upper RBT abundance trigger being ineffective. Conditional on initial parameter values, the expected number of annual removals with this preferred policy function was 4.2. However, removals were typically zero and then jumped to between four and six removals following larger RBT recruitment events. Absent RBT removal, achieving an average annual juvenile HBC survival target of 81% over a 20-year simulation only occurred 6% of the time.

Model Sensitivity

We assessed the sensitivity of model results under different parameter assumptions. Parameters were organized into three categories (discussed further below) including policy criteria, juvenile HBC survival targets, and RBT abundance. In general, variation of these parameters lead to a similar removal strategy (e.g., four or five initial removals, increasing with increasing RBT abundance) but with variation in the starting and ending RBT abundances over which this removal strategy was applied. This variation in preferred policy functions under different parameter assumptions led to differences in the average annual expected removals that occurred when varying model parameters (Fig. 2). For example, we made several policy criteria assumptions when specifying parameters in the base model: we set the simulation period to 20 years (Interior 2016), specified the risk tolerance (the required probability of staying above the average juvenile HBC survival target) at 90%, and located the RBT removal reach at the confluence of the LCR and mainstem (river kilometers 116.5 – 147.1). When decreasing or increasing the planning horizon from 20 years, we found that average annual expected removals either increased or decreased with shorter or longer planning horizons, respectively, and that the preferred removal strategies became more or less intensive to meet these requirements (Fig. 2A-B). The solution was sensitive to starting RBT abundance in the mainstem when reducing the planning horizon. Using recent average RBT abundance in the mainstem (Interior 2016), reducing the planning horizon to 10-years made meeting average annual juvenile HBC survival target 90% of the time unattainable even with the most intensive removal strategy.

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

The policy assumption with the largest impact on the effectiveness of RBT removal required to achieve the average juvenile HBC survival target was the location of RBT removal. Relocating the removal reach upriver from river kilometers 113.5 – 147.1 made meeting average annual juvenile HBC survival target 90% of the time unattainable (Fig. 2E-F). Relocating removals upstream from the LCR confluence takes less advantage of the slow dispersion of RBT from Glen Canyon and the natural rainbow trout mortality during the interval it takes for the trout to move downstream. Relocating the removal reach downstream approximately 8 kilometers, increased the average annual expected removals significantly (Fig. 2E-F).

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

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

Discussion

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

The model demonstrated that considerable levels of RBT removal would be needed to cost-effectively achieve annual juvenile HBC survival targets under the present condition of warm mainstem temperatures. A considerable level of removals is required due to monthly RBT movement following a removal trip, reducing the efficacy of removals. Under cold mainstem temperature removals were unable to achieve annual juvenile HBC survival targets. The preferred RBT removal policy was dependent on model parameter specification but was insensitive to higher-order approximation of the policy function. We evaluated model sensitivity by varying parameters associated with policy criteria, RBT abundance and juvenile HBC survival targets. In general, variation in parameter estimates led to similar preferred policy functions with variation in RBT "trigger" bounds. These 'trigger' bounds are defined by RBT recruitment and movement parameters and the juvenile HBC survival function. Over the simulation period, the frequency of large RBT recruitment events and the time it takes RBT to populate the JCM govern the bioeconomic model solution. For example, implementing removals following RBT movement, increasing the efficacy of removals, narrows the 'trigger' bounds of the preferred removal strategy. 'Trigger' bounds are further defined by the reverse 'S-curve' shape of the juvenile HBC survival function, resulting in limited marginal benefit of removal at low and high RBT abundance.

Increasing the probability of meeting a juvenile HBC survival target or decreasing the simulated planning horizon required a higher expected number of removals. In addition, higher abundance of RBT from upstream sources made the likelihood of achieving a juvenile HBC survival target infeasible. For context, the largest recruitment event (2011) in the last 15 years led to RBT abundance in the vicinity of the JCM reach of ~400 RBT per 1.5 km (Korman and Yard 2017). Relocating removal upriver of the removal reach also resulted in infeasible model solution. Given a constant proportion of RBT removed in any removal reach and the Cauchy-distributed movement of RBT, removals that occurred upriver from the LCR (greater RBT abundance) were less useful at reducing long-run abundance in the JCM reach. Removal of RBT at locations distant to the JCM reach is further complicated by the location of RBT abundance that triggers removal. Bifurcating removal and the location of the RBT abundance trigger results in less effective removals. These model characteristics highlighting the tradeoffs between variation in removal location and the difference in removal effort required to achieve long-run HBC population goals. The confluence has cultural significance to Native American tribes tied to Glen and Grand Canyons, therefore the location of the removal reach is an important aspect of the model structure and consideration in exploring the preferred management strategy.

Because several assumptions were made in development of this model, an important consideration in model implementation is the ability to accurately predict changes in estimated parameters (Coulson et al. 2001). Several of the parameters used in this study could be influenced by environmental conditions that were exogenous to our model, including turbidity and food base conditions in the tailwater and mainstem. As Lake Powell changes and climate influences the Colorado River Basin hydrology, characteristics of the tailwater are likely to change, affecting RBT recruitment. Increasing mainstem temperature as a result of decreasing reservoir levels has been identified as an environmental condition that may increase RBT recruitment (Dibble, 2017, written comm.). In addition, long-term changes in mainstem turbidity or the food base due to environmental or management perturbations are factors that would affect RBT and HBC populations or further constrain the number of annual removals (Cross et al. 2013, Dodrill et al. 2016; Dzul et al., 2016; Yackulic, *In Press*). Another significant model assumption concerning RBT population dynamics is that no local recruitment occurred in Marble Canyon (Korman et al. 2015). The dynamic between RBT abundance and characteristics of removal (timing, intensity and location) could be increased if this condition changed. It is also important to recognize that HBC recruitment and movement is predicated on historical hydrologic conditions in the LCR (Interior 2016). If historical flooding patterns change, in the winter or during monsoon season, HBC recruitment and movement (i.e., dispersal into the mainstem) parameters could be altered significantly.[3] This in turn would affect target rates of survival, influencing the preferred RBT removal strategy. Continued monitoring and research of RBT and HBC populations would allow for the identification of any departure from the estimated population parameters as a result of changing environmental conditions.

Future development of this bioeconomic model could include alternative RBT control options and/or RBT and HBC population triggers that prompt management actions. An example is the tradeoff between managing RBT recruitment in Glen Canyon, immediately below Glen Canyon Dam, and RBT removals at the confluence of the LCR. The LTEMP FEIS (Interior 2016) has 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).

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

The model provides an assessment from a HBC stochastic viability approach that achieves predetermined population goals through an efficient policy. The model framework was developed to incorporate changes in environmental conditions and revised parameter estimates based on continued research of the biological and physical system, and changes in the options and relative prices of management alternatives. Although the model results are presented in specific terms, the intent of the modeling framework is to 1) provide a general framework to identify the most cost-effective approach to enhancing native species population viability via invasive species control, and 2) develop a framework to identify additional tradeoffs in management of RBT and other downstream resources due to dam operations. This general framework could be applied in different systems with management actions that include direct invasive species management, habitat manipulations, or other actions. Managing aquatic invasive species in freshwater ecosystems, especially those species intentionally introduced to provide social and economic value, will undoubtedly continue to present conservation challenges. The scientific investment in estimating parameters for population models of interacting species can be significant; however, the advantage of joint population abundance predictions within a cost-effectiveness analysis framework has the potential to lead to efficient management outcomes. This framework may also be apt at addressing multiple stakeholder objectives or conflicting values that are often present in resource conservation efforts. Our model considers population level dynamics, species interaction and economic cost to provide an effective and efficient solution to long-run management of RBT in Glen and Grand Canyons to improve the probability that HBC population goals are met.

Acknowledgements

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

Literature Cited

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

U.S. Fish and Wildlife Service (USFW). 1994. Endangered and threatened wildlife and plants; determination of critical habitat for the Colorado River endangered fishes: razorback sucker, Colorado squawfish, humpback chub, and bonytail chub. 59: 54 [1994] 13374-13400. Federal Register.

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

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

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

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

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) • Removal reach (116.5 – 147.1 km) • Juvenile Humpback Chub Monitoring reach (127.8 – 130.2 km)	Trout movement and abundance $N_{y,t+1} = \psi_0 \Phi N_{y,t}$ • Trout removal $N_{y,t+1} = \psi_0 \Phi diag[\circ] N_{y,t}$ $diag[\,(1 - a_{y,t}^{j}(a_y)\theta)^5]$ • 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. • 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.

*Table 2 for model parameter description

Table 2: Definition of model variables

Variable	Description	Value or transformation	Citation
RBT recruitment: $r_y = e^{z \sim unif(\alpha,\beta)}$			
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: $\boldsymbol{N}_{y,t+1} = \psi_0 \boldsymbol{\Phi} \boldsymbol{N}_{y,t}$			
ψ_0	Monthly trout survival rate	0.96	Korman et al. 2012
Φ	$J \times J$ matrix based on a Cauchy distribution; $J = 1, \ldots, 151$ matrix (river reach)	$\chi0=0$, $\gamma=3.38$	Interior 2016
t	Months	$\in\{1,2,\ldots,12\}$	-

Y	Years	∈{1,2,...,20}	Interior 2016
RBT removal: $\boldsymbol{N}_{y,t+1} = \psi_0 \boldsymbol{\Phi} \mathrm{diag}[(1 - a^{j}_{y,t}(a_y)\theta)^5]\boldsymbol{N}_{y,t}$			
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: $E\left(\sum_{y=1}^{Y} \delta^{y} c\left(a_y\right)\right)$			
Y	Period in years	20	Interior 2016
c	Removal cost per trip	$75000	Yard, 2017, *pers. comm.*
δ	Annual discount rate	(1- 0.03)	Moore et al. 2004
Annual HBC survival: $\varphi_y = \prod_{t=1}^{T} \varphi_{y,t}\left(N^{JCM}_{y,t}\right) = \prod_{t=1}^{T} 1/(1 + e^{-\left(\mu_1 + \mu_2 * N^{JCM}_{y,t}\right)})$			
$\mu_{1,2}$	Constant parameters in survival function	$4.767, -9.125 \times 10^{-4}$	Yackulic, *In Press*
φ^{*}_{y}	Annual average survival target for warm (cold) mainstem temperatures	0.81 (0.89)	Current study

Figure 1. Study area map

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

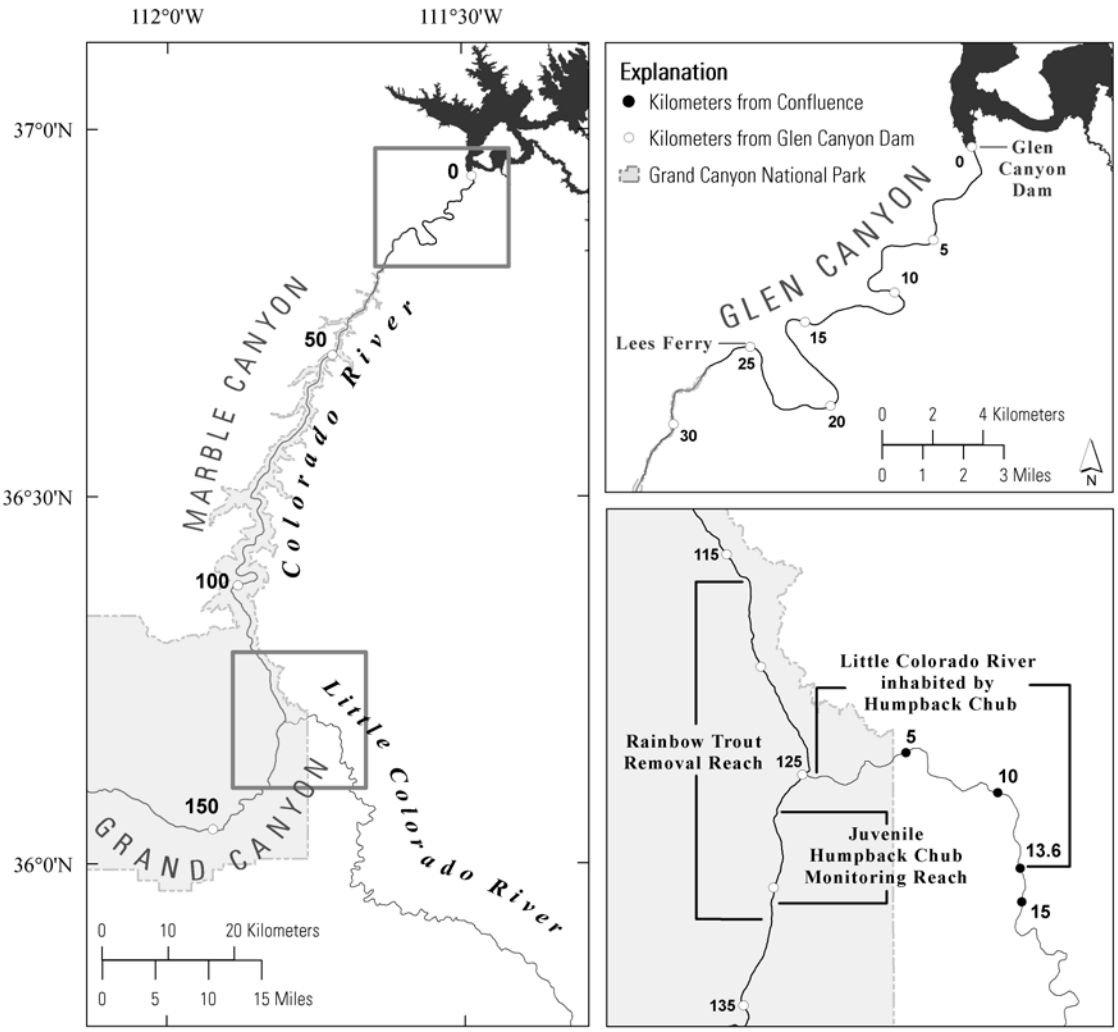
112°0'W
111°30'W
37°0'N
36°30'N
36°0'N
MARBLE CANYON
Colorado River
Little Colorado River
GRAND CANYON
0
50
100
150
0 10 20 Kilometers
0 5 10 15 Miles
Explanation
Kilometers from Confluence
Kilometers from Glen Canyon Dam
Grand Canyon National Park
GLEN CANYON
Glen Canyon Dam
Lees Ferry
0
5
10
15
20
25
30
0 2 4 Kilometers
0 1 2 3 Miles
N
115
125
135
Rainbow Trout Removal Reach
Little Colorado River inhabited by Humpback Chub
Juvenile Humpback Chub Monitoring Reach
5
10
13.6
15

Figure 1

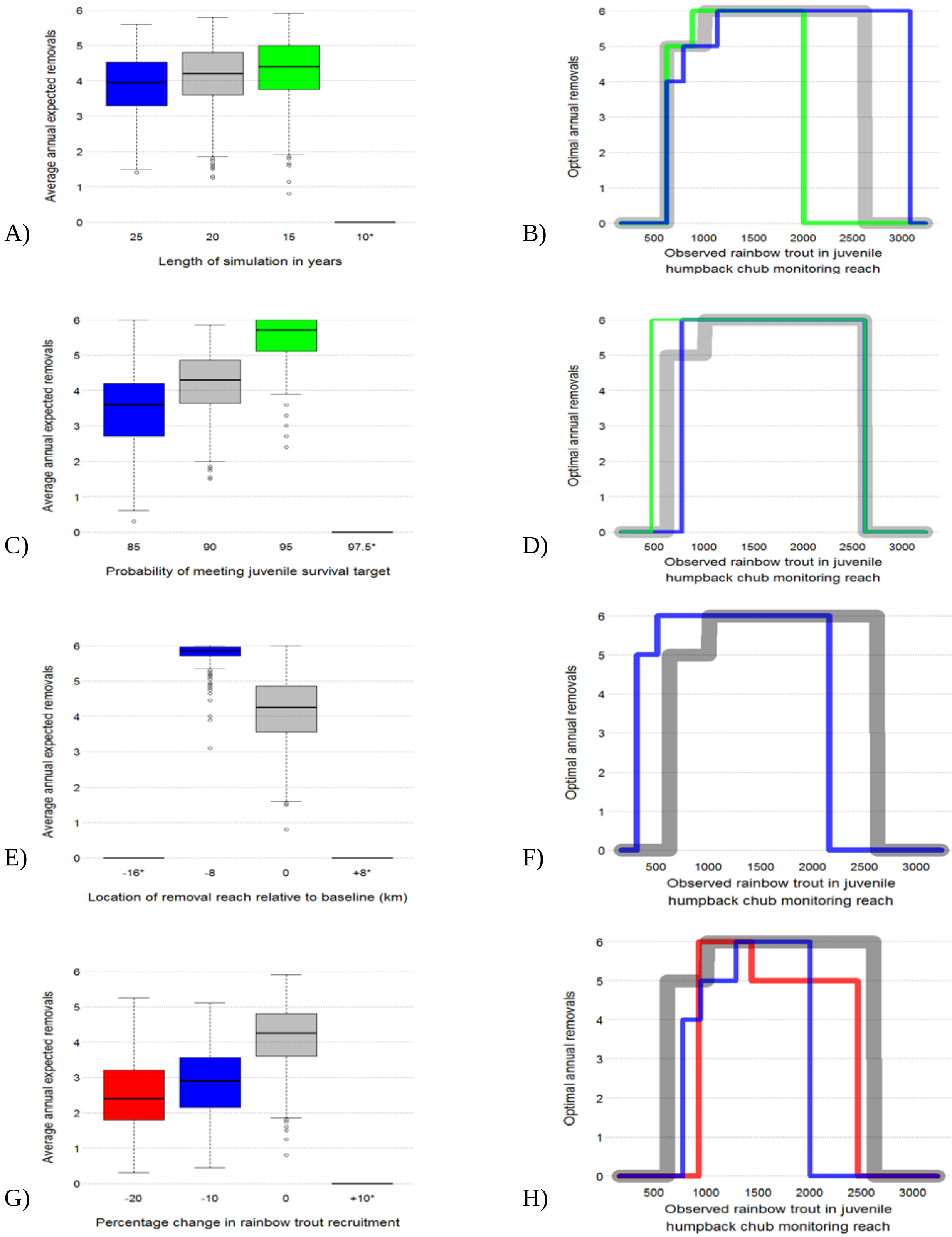
A)
Average annual expected removals
25
20
15
10*
Length of simulation in years
B)
Optimal annual removals
Observed rainbow trout in juvenile humpback chub monitoring reach
C)
Average annual expected removals
85
90
95
97.5*
Probability of meeting juvenile survival target
D)
Optimal annual removals
Observed rainbow trout in juvenile humpback chub monitoring reach
E)
Average annual expected removals
-16*
-8
0
+8*
Location of removal reach relative to baseline (km)
F)
Optimal annual removals
Observed rainbow trout in juvenile humpback chub monitoring reach
G)
Average annual expected removals
-20
-10
0
+10*
Percentage change in rainbow trout recruitment
H)
Optimal annual removals
Observed rainbow trout in juvenile humpback chub monitoring reach

Figure 2