POPULATION DYNAMICS MODELING OF INTRODUCED
SMALLMOUTH BASS IN THE UPPER COLORADO RIVER BASIN


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POPULATION DYNAMICS MODELING OF INTRODUCED
SMALLMOUTH BASS IN THE UPPER COLORADO RIVER BASIN

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Executive Summary

In response to the predatory threat posed by non-native smallmouth bass *Micropterus dolomieu*, the Upper Colorado River Endangered Fish Recovery Program (Recovery Program) initiated efforts to control smallmouth bass via mechanical removal in affected stream reaches. To date, substantial information has been collected on distribution, population abundance, size structure, and movements of smallmouth bass concurrent with removal actions throughout the upper Colorado River basin. A comprehensive synthesis of this information suggested that the density of smallmouth bass has either declined or stabilized throughout the upper basin in recent years, demonstrating that removal has been at least partially successful. Nonetheless, considerable uncertainty remains concerning the most efficient and effective strategy for further reducing smallmouth bass density to foster recovery of the four endangered fish species in the upper Colorado River basin. To address potential management alternatives, we developed a stage-structured population model to simulate smallmouth bass population dynamics under a suite of management alternatives (See Appendix II for Users Guide).

Model simulations focused on sub-adult and adult smallmouth bass density (hereafter density or bass density that includes all life stages) in Little Yampa Canyon, a 24 mile (39 km) reach on the Yampa River. We focused on Little Yampa Canyon because it may be the epicenter of the Yampa River smallmouth bass population. Additionally, a long-term dataset from this reach was available including published early life history data. Despite our focus on smallmouth bass population dynamics in Little Yampa Canyon, insights from our projection results are applicable to reaches throughout the upper Colorado River basin by parameterizing the model with estimates of controlling factors from other reaches. We performed two types of analyses with our model: (1) an assessment of anticipated changes to the smallmouth bass population
under several management scenarios, and (2) a sensitivity analysis to assess the performance of the model with respect to population parameters that were not well known.

Management Scenarios

The purpose of assessing management scenarios was twofold. First, we sought to evaluate if standard spring electrofishing mechanical removal efforts were effective in reducing smallmouth bass densities. Second, we evaluated efficacy of additional control strategies that could further reduce smallmouth bass densities from current levels. We focused on parameters in the model that managers could manipulate by management actions. We evaluated reduction of spring electrofishing effort, reallocation of removal effort to other seasons, the disruption of reproduction, and reduction of immigration into the Yampa River.

We found that spring electrofishing removal was essential for maintaining the current baseline smallmouth bass density in Little Yampa Canyon. When we simulated a reduction of spring electrofishing exploitation below that of the 2010 removal rate, the result was a dramatic and non-linear increase in bass density in just a few years in Little Yampa Canyon. Higher smallmouth bass densities would place additional predation pressure on native fishes, increase emigration of young smallmouth bass from Little Yampa Canyon to other reaches, lead to higher densities in adjacent reaches, and increase bass densities throughout the basin. Thus, reductions in smallmouth bass removal effort are not recommended. Additional removal effort in spring by itself may not be the most effective way to further reduce smallmouth bass density in Little Yampa Canyon.

Disrupting reproduction greatly diminished bass density depending on when the disruption occurred. The largest reductions in density were realized by disturbing early season nests (Cohort 1) followed by middle season nests (Cohort 2). Given the large effect of disturbing
Cohort 1 and 2 in our simulations, we recommend that any means of inducing early season nest failure (disturbance) should be investigated by the Recovery Program.

We evaluated two scenarios for reallocating removal effort. The first was concentrating removal effort during smallmouth bass spawning and the second was fall exploitation of Age-0 individuals. Simulations showed removal effort during spawning effectively removed nearshore spawning adult smallmouth bass and had the added benefit of inducing nest failure when guarding males were removed. Our modeling indicated that a modest 20% level of Cohort 1 disturbance along with 10, 20 and 30% increases in removal rates (over 2010 levels) produced some of lowest densities of smallmouth bass in our management scenarios. In our simulations using minimal removal effort, the autumn exploitation of Age-0 bass had a small impact on densities.

We simulated how smallmouth bass densities were affected by immigration of smallmouth bass, including escapees from Elkhead Reservoir, and how precluding that escapement reduced densities in Little Yampa Canyon. Our simulations showed that the greater the number of escapees, resident or otherwise, the higher the immigration rate of bass into Little Yampa Canyon, which greatly reduced effects of mechanical removal. The escapement analysis demonstrated the potential significance of Elkhead Reservoir as a source of adult smallmouth bass escaping to the Yampa River and highlighted the importance of understanding the abundance and escapement dynamics of the resident reservoir smallmouth bass population. It is important to remember that immigrants are probably produced in the river as well as the reservoir so understanding the relative proportions of each and the effects of reduced reservoir escapement on modeled bass densities should be investigated.
Eliminating immigration was the only means to reduce smallmouth bass populations to zero in Little Yampa Canyon in our simulations. This result demonstrates the critical importance of immigration into Little Yampa Canyon, and perhaps other reaches as well, and suggests the smallmouth bass population in Little Yampa Canyon would likely be eradicated in a few years under the present level of exploitation by eliminating immigration. Immigration into Little Yampa Canyon is affected by electrofishing removal effectiveness in adjacent and other reaches upstream and downstream. It is also impacted by escapement from Elkhead Reservoir. Improving electrofishing effectiveness and increasing effort in upstream and downstream reaches and precluding escapement should be considered valuable options for significantly reducing immigration into Little Yampa Canyon. Immigration will continue to be a source of population recovery for smallmouth bass even when bass densities have been pushed below the threshold of recruitment failure in a particular reach.

Model Sensitivity Analyses

Several parameters in our model have not been estimated for the Upper Colorado River Basin or were not well known in general. Due to our uncertainty in these parameters, we conducted a sensitivity analysis to estimate their influence on model predictions of smallmouth bass density. The parameters with largest effect were the survival of Age 1-2 bass, the alpha stock-recruitment parameter, and the proportion of breeding adults. However, each parameter’s effect is much reduced after applying a realistic range of values. Whether or not it would be cost effective to acquire better estimates of these parameters may be a worthwhile discussion point for Recovery Program managers, but we are not convinced that the need to improve parameter estimates outweighs foreseeable research costs and diversion of resources from removal efforts.
Recommendations

Based on our modeling efforts, we make the following recommendations.

1. Maintain the exploitation rate represented by our baseline model (Little Yampa Canyon 2010 level).
2. Reallocate effort during ineffective removal periods such as early spring sampling in Little Yampa Canyon, to periods in later spring or early summer that overlap with smallmouth bass reproduction (a primary goal of the surge).
3. Make removal during spawning (the surge) a core component of the electrofishing removal effort on the Yampa River and other reaches.
4. Consider other management options such as flow management, in addition to electrofishing, to further disrupt smallmouth bass reproduction and recruitment.
5. Permanently discontinue translocation of smallmouth bass to Elkhead Reservoir and other locations in the upper Colorado River basin.
6. Prevent escapement of resident and remaining non-resident smallmouth bass and other fishes from Elkhead Reservoir and other sources into streams of the upper Colorado River basin.
7. Re-evaluate simulated predictions as new data becomes available to better parameterize the smallmouth bass population dynamics model.
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List of Key Words
Invasive species, stocking, \(Micropterus dolomieu\), Little Yampa Canyon, projection, simulator, Recovery Program, endangered species
Introduction

Introduction and establishment of non-native fish in rivers of the western United States is a major threat to conservation of native fish assemblages (Minckley and Deacon 1968, Stanford and Ward 1986, Moyle et al. 1986, Carlson and Muth 1989, Minckley and Deacon 1991, Olden et al. 2006). In the upper Colorado River basin, non-native fish invasions began over 100 years ago, with the introduction of channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, and salmonids for sport fishery purposes. In the 1970s, small-bodied species such as red shiner expanded rapidly (Vanicek et al. 1970, Holden and Stalnaker 1975a and 1975b) with negative consequences for the native fish fauna (Haines and Tyus 1990, Dunsmoor 1993, Ruppert et al. 1993, Muth and Snyder 1995, Bestgen et al. 2006a). More recently, piscivores such as smallmouth bass *Micropterus dolomieu* and northern pike *Esox lucius* have established and are common in the Yampa River, the upper and middle Green River basins, and the upper Colorado River (Wick et al. 1985, Anderson 2002, 2005, Bestgen et al. 2006b, Burdick 2008, Breton et al. 2014).

The predatory threat of large-bodied piscivorous taxa such as northern pike and smallmouth bass is substantial. For example, based on results of a bioenergetics model, Johnson et al. (2008) ranked smallmouth bass as the most problematic invasive species because of their high abundance, habitat use that overlaps with most native fishes, and ability to consume a wide variety of life stages of native fishes in the Colorado River Basin. Increasing populations of piscivores such as smallmouth bass are a major impediment to conservation actions aimed at recovery efforts for the four endangered fishes in the Upper Colorado River Basin: Colorado pikeminnow *Ptychocheilus lucius*, razorback sucker *Xyrauchen texanus*, humpback chub *Gila cypha*, and bonnytail *Gila elegans* (U.S. Fish and Wildlife Service 2002a, b, c, d). In response to
the predatory threat posed by non-native smallmouth bass, the Upper Colorado River Endangered Fish Recovery Program (Recovery Program) initiated efforts to control such species via mechanical removal in affected stream reaches. Interim goals for removal actions have also been established for the Yampa River and include reduction of smallmouth bass to <30 adult bass/mile in the Yampa River and increasing the composition the small-bodied fish community to 10–30% native fishes. To date, substantial information has been collected on distribution, population abundance, size structure, and movements of smallmouth bass concurrent with removal actions throughout the Upper Colorado River Basin. Removal efforts implemented vary in intensity and effectiveness across stream reaches where invasive piscivores exist, but in only a few reaches are thought to approach levels of removal needed to enhance survival prospects for native fishes (Badame et al. 2008, Burdick 2008, Hawkins et al. 2009, Breton et al. 2014).

A comprehensive synthesis of available information has recently clarified population-level effects of removal actions in six focal reaches to aid in formulation of a comprehensive control strategy that will effectively reduce populations of smallmouth bass and enhance prospects for recovery of native fish populations (Breton et al. 2014). That analysis showed that the density of smallmouth bass has either declined or stabilized in all six reaches (Breton et al. 2014). This change in the trajectory of smallmouth bass density demonstrated that the removal of smallmouth bass in the basin has been at least partially successful. Nonetheless, considerable uncertainty remains concerning the most efficient and effective strategy for further reducing smallmouth bass density to foster recovery of the four endangered fish species in the upper Colorado River basin (Bestgen et al. 2007a).

We integrated estimates of smallmouth bass density and exploitation from Breton et al. (2014), Elkhead Reservoir escapement rates from Breton et al. (2013), and published early life
history and environmental data into a population dynamics model to predict smallmouth bass density under a variety of management scenarios. We focused on projections of sub-adult and adult smallmouth bass density within Little Yampa Canyon, a 24 mile (39 km) reach on the Yampa River. We assessed the sensitivity of our population dynamics model to poorly known components such as the stock-recruitment relationship, and then assessed population dynamics under many management scenarios.

Based on a review by Hawkins et al. (2009) and density estimates of smallmouth bass from the upper Colorado River basin (Breton et al. 2014), Little Yampa Canyon appears to represent the epicenter of the Yampa River population. In addition, a long-term dataset from this reach was available to integrate into the projections including published early life history data (Hill and Bestgen 2014, Bestgen and Hill 2015a). Despite our focus on smallmouth bass population dynamics in Little Yampa Canyon, insights from our simulation results are applicable to reaches throughout the upper Colorado River basin.

Methods

Smallmouth Bass Life History

Smallmouth bass are a widely distributed piscivore in North America and a popular game fish (Brown et al. 2009). Smallmouth bass spawn at water temperatures of about 15–16°C, are most active (feeding) when water temperatures are in the 20–28°C range, and are inactive when water temperatures are below about 12°C (Peterson and Rabeni 1996; see also Coble 1967, Webster 1954, Bennett and Childers 1957, Coutant 1975, Brown et al. 2009). Smallmouth bass are typically sedentary in summer, with net movement over this period <0.62 miles (1 km), but may migrate more than 47 miles (75 km) to reach winter refuges (Wallas and Simon 2008).
Smallmouth bass establish home ranges of several hundred meters (Etnier and Starnes 1993) and displaced fish display a strong homing instinct (Ridgway and Shuter 1996), even for fish that were experimentally moved up to three times (Larimore 1952). Smallmouth bass prefer rock substrates as well as submerged woody debris including logs (Miller 1975, Etnier and Starnes 1993). In streams, smallmouth bass show a preference for slack water below substrate or flow edges and are not associated with strong currents (Coble 1975). Other important life history events critical to the population modeling are described below.

Study Area

The section of the Yampa River referred to as Little Yampa Canyon is a 24 river mile (39 river kilometers) reach 100 miles (161 km) upstream of the Yampa River-Green River confluence in Dinosaur National Monument at Echo Park (Figure 1). Estimates of hectares of Yampa River habitat per river kilometer and total hectares in Little Yampa Canyon are 6.8 and 262.65, respectively, based on average channel width (68 meters) from the Duffy study site reported by Anderson and Stewart (2007; Table II-4, pg. II-19).

The Model

We developed a stage-structured population model with a user-friendly interface to simulate smallmouth bass population dynamics under a suite of management alternatives. Our model accommodates eleven ages, Age-0 through Age-10 years (Table 1; Figures 2-3) and projects the density of Age-0, sub-adult, and adult smallmouth bass annually after exploitation. In our model, Age-0 are young-of-year; Age-1 and 2 are sub-adults; and Ages 4–10 are adults. Age-3 smallmouth bass ranged from 171–246 mm total length (TL) and could be sub-adults or adults. In our assessment we considered Age-3 fish ≥200 mm TL as adults and those below 200 mm TL sub-adults (Breton et al. 2014). The 200-mm threshold was based on reproductive condition of
smallmouth bass from Little Yampa Canyon (JAH unpubl. data). Minimum and maximum total lengths for fish of each age (Table 1) were based on data from Little Yampa Canyon (JAH unpubl. data).

The model begins with ages 1-10 present in the population (Figure 2). The order of events in the model are (1) spring emigration and immigration of Age 1+ cohorts (Figure 2a), (2) spring electrofishing removal (Figure 2b), (3) summer reproduction and recruitment of Age-0 smallmouth bass through a density-dependent stock-recruitment function (Figure 2c), (4) splitting of Age-0 fish into three cohorts, Cohort 1, Cohort 2, and Cohort 3 (Figure 2d), (5) growth of Age-0 bass as a function of Yampa River discharge and water temperature (Figure 2e), and (6) over-summer survival (Figure 2f). The summer events determine the number of fish in each age class that enter the winter model (Figure 3). The winter model consists of (1) exploitation of Age-0 fish (Figure 3a), and (2) over-winter survival (Figure 3b and 3c). Age-0 over-winter survival is a function of winter duration as a function of water temperature and smallmouth bass length (Figure 3b). The details for each of the events in both the winter and summer sub-models are explained below. General equations for each step in the model are given in Appendix I. Appendix II contains a User’s Manual with examples to assist with model simulations. We used 2010 post-exploitation density estimates from Little Yampa Canyon, the most recent that were available (Breton et al. 2014), as initial starting densities for all of our projections.

Summer Sub-Model

We estimated the number of spring immigrants (Figure 2a) using our estimates of smallmouth bass abundances and electrofishing removals in Little Yampa Canyon from 2004–2010 (Breton et al. 2014). Electrofishing crews removed about 1000 (42 per river mile) adult smallmouth bass (≥200 mm TL) annually from Little Yampa Canyon since 2004 (see Breton et
al. 2014 for more details). In recent years, between 1000 and 1500 (42 and 63 per river mile) sub-adults (100–200 mm TL) were removed (see Breton et al. 2014 for more details). Despite these removals, the adult population has been stable at about 2000 individuals. Although recruitment from sub-adult to adult age classes within the reach explains some of the recovery of the population after removal the previous year, the balance of the population increase must be due to smallmouth bass that immigrated into Little Yampa Canyon from other reaches. In our projections, we assumed that 750 adults and 750 sub-adults immigrated into Little Yampa Canyon annually (each time-step) and the remaining 250 fish were recruited within the reach.

For immigration and recruitment, Age-3 was treated as sub-adults. No adjustments were made for emigration because we assumed that fish were unlikely to emigrate from the high quality habitat and forage base found in Little Yampa Canyon (Martinez 2011).

Consistent with electrofishing removal protocol for Little Yampa Canyon, we modeled removal (exploitation) of smallmouth bass in the summer sub-model immediately after immigration (Figure 2b). To aid in understanding the contribution of exploitation to population dynamics, we kept exploitation separate from summer and winter survival probabilities (more below). We also assume that there is no density-dependent compensation in summer and winter survival probabilities as a result of population reductions due to removal. We assumed that Age-1 and older smallmouth bass were susceptible to capture and removal by boat-based electrofishing. We adopted 2010, age-specific, exploitation rates from Little Yampa Canyon estimated by Breton et al. (2014). An exploitation rate estimate for Age-1 was not available from field data, so we assumed this was 10% annually. Ten percent exploitation was an arbitrary starting point but seemed reasonable given that smaller (i.e. younger) smallmouth bass are harder to capture with electrofishing gear (Breton et al. 2013). Due to the uncertainty in this parameter
it was included in our sensitivity analysis to determine its effect on our predictions. Exploitation rate for Age-9 adults was also not available and we assumed this was identical to Age-10 exploitation rate (79%). In our baseline model, exploitation rates were kept at 2010 levels for all time-steps.

The summer sub-model is flexible because it can accommodate user-specified estimates of reproduction to the egg stage as well as various survival rates of fry and Age-0 (Figure 2c). In lieu of information on egg and fry survival for smallmouth bass, the model can also predict recruitment directly to Age-0 through several stock-recruit functions including Ricker and Beverton-Holt models. We did not have sufficient data from the upper Colorado River basin to reliably model the relationship between smallmouth bass stock and recruitment so we used a Ricker stock-recruitment function (Ricker 1954; Hilborn and Walters 1992). The Ricker stock-recruitment function has been used in other population assessments of smallmouth bass and fits empirical data on those populations; therefore we felt it would be an appropriate baseline assumption (Peterson and Kwak 1999). We used the necessary parameters from Peterson and Kwak (1999). We also did not have estimates from the Yampa River of the effect of flow and temperature on recruitment and removed those from the Peterson and Kwak (1999) stock-recruitment function leaving,

\[
R_t = S_t \exp(\ln(\alpha) - \beta S_t)
\]

where \(R_t\) are recruits and \(S_t\) is the stock size at time \(t\), \(\alpha\) is recruitment per unit stock at low stock densities, and \(\beta\) is the strength of the negative effect of density on recruitment. We do include flow and water temperature into relationships for timing of smallmouth bass spawning and Age-0 growth, which ultimately affects their survival during the winter period. Density of adults (stock) per hectare (\(S_t\)) was calculated at each time-step and then integrated into the stock-
recruitment function to estimate recruit density per hectare ($R_t$). We adopted stock-recruitment function estimates from Peterson and Kwak (1999) of $\alpha$ (6.9872) and $\beta$ (0.0437).

Reproduction can also be influenced by physical disturbance of all stages of reproduction (Figure 2) and by the proportion of adults that breed (Figure 2). In our baseline model, we set disturbance to zero (no nests disturbed). We set the proportion of adults that breed to 0.75 at all time-steps. Reproductive studies on smallmouth bass suggest that the proportion of males that spawn within a season is quite variable, ranging from 17-55% (Raffetto et al. 1990; Baylis et al. 1991, 1993). Therefore, we felt that it was reasonable to assume that not all individuals spawned. However, we also set the spawning proportion (0.75) higher than published reports because we felt it was more conservative to consider high levels of recruitment initially.

Additionally, Age-3 individuals may or may not reproduce, because reproduction is length dependent at that age. Generally we considered the adult threshold for Age-3 and older fish to be 200 mm; however, the proportion of Age-3 breeders was calculated by using a normal distribution with Age-3 mean size estimated by averaging the Age-3 and Age-4 minimum lengths (mean = 208.5). We estimated the standard deviation by taking the Age-3 mean length minus the Age-3 minimum length divided by three (= 1 STD), assuming that six standard deviations (± 3) encompasses most (>99%) of the data in a normal distribution (Ott 1988). After the number of Age-0 recruitment was predicted, recruits were split into three numerically equal cohorts (Figure 2d) for modeling convenience, recognizing that in a dome-shaped normal distribution of recruit lengths that more fish will be in the center of the distribution and fewer on the margins. These represent the offspring of early, middle, and late season smallmouth bass reproduction in Little Yampa Canyon based on modes in the distribution of hatching dates.
determined by aging using otolith daily increments (Hill and Bestgen 2014; Bestgen and Hill 2015a.

Discharge and temperature were used to predict timing of spawning of smallmouth bass and growth of Age-0 fish so their length can be predicted at the end of the growing season in mid-September (Figure 2e). The mean total length for each cohort at the end of summer was determined using the equation,

\[ TL(mm) = 101.4 - (days \times 0.66) + (temp \times 2.82) + cohort. \]

where \( days \) is a proxy for bass hatch initiation, \( temp \) is a proxy for growing conditions and cohort is an offset for cohorts 1 and 2; Cohort 3 is represented by the intercept. These (estimated) offsets were 32.7 and 16.1, respectively. To determine \( days \) at each time-step we solved the equation,

\[ days = 164.19 + (count \times 0.6254) \]

where \( count \) is the count of days when mean daily flow of the Yampa River was \( \geq 8000 \text{ cfs} \) between 1 April and 30 September (equation is from Hill and Bestgen 2015a). We used flow data from 1998–2011 measured at the U.S. Geological Survey Gauge (#09251000) at Maybell, Colorado, which is just downstream of our study area (Figure 1). Average 1 July to 15 August water temperature data from 1998–2011 were also from the same location. At each time-step, we drew a random variable from normal distributions with mean and standard deviation estimated from these flow and temperature data (Table 2). These values were redrawn if they did not meet environmental condition requirements (good vs. poor years, more below). Once a value for each environmental variable was selected we solved the equation for \( days \) and then \( TL (mm) \) for each cohort. We assumed that TL of each Age-0 cohort was normally distributed with a mean specific
for each cohort (see equation above) and a standard deviation of 10 mm. The standard deviation was estimated based on the range of lengths for those fish (Ott 1988).

Over-summer survival for all stages can be modeled and represents mortality due to sources other than electrofishing removal (Figure 2f). We assume that over-summer survival is independent of removal and that there are no compensatory effects of removal on over-summer survival rates. It is important to note that over-summer survival is within age classes and that individuals do not change age class during the summer. In our baseline model, we assume that over-summer survival is one (i.e. no mortality occurs, except removal).

**Winter Sub-Model**

The first event in the winter sub-model is electrofishing removal of Age-0 cohorts (Figure 3a). The timing of Age-0 exploitation was based on established field protocols (Bestgen et al. 2007b). In the absence of electric seine exploitation rates of Age-0 fish in Little Yampa Canyon, we assumed 10% were removed annually by this method at all time-steps.

After electrofishing removal, over-winter survival estimation is modeled (Figure 3b and c). Over-winter survival for Age-0 fish (recruits) has been demonstrated the period most limiting for smallmouth bass recruitment (Shuter et al. 1980, Shuter and Post 1990). Age-0 over-winter survival is influenced by their body size at the end of the summer growing season and the temperature and duration of winter (Figure 3b). The Age-0 over-winter survival component was integrated into our sub-model using relationships and insights published by Shuter et al. (1980) and Shuter and Post (1990) making the assumptions: (1) the critical period for smallmouth bass recruitment is over-winter survival; (2), over-winter survival is determined by body condition and winter severity; and (3) over-winter survival is density independent. At each time-step, we
determined fish total length at which 20% (L20) and 80% (L80) of individuals in these length categories survived. From Shuter and Post (1990),

\[
L20 = (-3.31 + (0.032 \times \text{sdays})) \times 10 \times 1.05
\]

\[
L80 = (-3.27 + (0.044 \times \text{sdays})) \times 10 \times 1.05
\]

where \text{sdays} (starvation days) is a proxy of winter severity. The last two terms in the equations are adjustments for converting from centimeters to millimeters and fork length to total length, respectively. Conversion from fork length to total length is an average of three values (page 153 in Carlander 1977). Consistent with Shuter and Post (1990), we used \leq 10^\circ \text{C} as the threshold below which fish stopped feeding, lived off of their body reserves, and hence, began to starve.

We used mean daily water temperature data over the 1 June to 1 May period (1997–2011) from the Maybell Gauge to estimate a mean and standard deviation of starvation days to create a distribution (Table 2). At each time-step, we drew a random variable from this distribution and then solved the L20 and L80 equations. These values were redrawn if they did not meet environmental condition requirements (good vs. poor years, more below). Over the winter period, all Age-0 fish \leq L20 survived with probability 0.20 and those \geq L80 survived with probability 0.80. Survival probabilities for Age-0 bass cohorts with total lengths between L20 and L80 were determined by linear interpolation (Shuter and Post 1990). Rather than determine survival for each length between L20 and L80, we determined survival for 10 mm size categories and applied the survival to all fish in that size category.

Age-0 fish surviving the winter were allocated to the Age-1 sub-adult cohort in the spring prior to exploitation by boat-based electrofishing. Although we drew random values from the distributions describing environmental covariates affecting Age-0 growth and over-winter mortality, the randomness was constrained by probabilities of poor conditions in summer and
winter. Observations suggested that environmental conditions allowed for successful smallmouth bass recruitment year classes in about two out of the last 10 years (20%). By “successful” we refer to those cohorts that were easily detected throughout the recruitment process (Age-0 to Age-1, Age-1 to Age-2, etc) such as the 2007 smallmouth bass cohort. Consistent with ‘about two successful cohorts per decade’, in our baseline model, we forced environmental conditions for about 8 out of every 10 time-steps to be poor for Age-0 rearing (spring, summer) and Age-0 over-winter survival. This was accomplished by taking a random value between 1 and 10 at each time-step, if the value was ≤8 then conditions on that time-step were forced to be below user provided thresholds (poor conditions; Table 2); if above 8, then conditions were forced to be above these thresholds (conditions favoring bass growth and survival).

Over-winter survival for Age 1 bass and older are annual survival rates and describe the survival from one age class to the next (Figure 3c). For the Age-1+ over-winter survival components of our baseline model, we used published estimates of annual survival from Age-1 to Age-2 (0.25 ± 0.14 SD), Age-2 to Age-3 (0.66 ± 0.21) and Age-3+ (0.9 ± 0.2) from Peterson and Kwak (1999). Given that these were estimates of annual survival, we set summer survival probabilities for Age-1+ fish to 1.0 in our baseline model. Consistent with Peterson and Kwak (1999), we implemented environmental stochasticity into Age-1 and Age-2 survival probabilities by drawing a random variable from normal distributions (mean, SD) at each time-step. These values were redrawn if they did not meet environmental condition requirements (good vs. poor years, more below). Age-3+ survival probabilities were held constant at 0.90 at all time-steps. Also consistent with Peterson and Kwak (1999), we assumed that survival of Age 1+ fish was not density-dependent and that electrofishing removals did not result in compensatory changes in over-summer survival. Unlike projections from Peterson and Kwak (1999) and Haines and
Modde (2007), a terminal age was not implemented in our model: Age-10+ fish survive according to the annual adult survival probability (0.90; more below).

*Performance of the Baseline Model*

To assess the performance of our baseline model, we ran 50 replicate projections over 50 time-steps each, taking the average of these at each time-step and comparing post-exploitation predictions of bass densities to recent post-exploitation density estimates from Little Yampa Canyon (Breton *et al.* 2014). Comparison of the model predictions to actual smallmouth bass densities revealed how well our baseline model performed at simulating smallmouth bass density in the Yampa River reach. Although it was not our objective to predict the exact number of bass in Little Yampa Canyon in the future, this assessment provided assurance that our baseline model was performing well relative to what was observed in Little Yampa Canyon from 2004–2010.

*Overview of Sensitivity and Management Projections*

For all projections described below, we first set each parameter to the highest assessed value and then reduced (decremented) each parameter by 5% or 10% intervals. All other parameters were set to our baseline model values and we compared the simulations to the baseline. For each interval, we ran 50 replicates over 50 time-steps. In our results we provide the average densities per hectare of Yampa River surface area across time-steps and replicates for each interval. We also report the lower and upper hectare density extremes, their difference, and then convert these from hectare density to river mile and reach densities. Reach density is equivalent to density derived from an estimate of the population abundance of bass within Little Yampa Canyon.
Baseline Model Sensitivity Analysis

We assessed the sensitivity of our baseline model predictions to changes in the following parameters: the stock-recruitment parameters ($\alpha$, $\beta$); the proportion of stock that breeds; the length threshold at which smallmouth bass initiate breeding; and Age 1–2, 2–3, 3-adult, and adult survival probabilities. These parameters were drawn from the literature but selected for sensitivity analyses because of uncertainty in their estimates. For the $\alpha$ (alpha) parameter in the Ricker stock-recruitment function we decremented from 10 to 1. For the $\beta$ (beta) parameter we held $\alpha$ at 6.9872 (baseline) and decremented $\beta$ from 0.1 to 0. We decremented breeding proportion and survival probabilities from 1 to 0 by 0.1 intervals. The length threshold was decremented from 250 to 150 mm TL. Length threshold and survival probabilities were decremented by 5% intervals; all others were decremented by 10% intervals.

Management Scenarios

As part of our management scenarios, we used parameters that could be manipulated by managers: cohort-specific disturbance; spring immigrants; spring (Age-1+) exploitation rates; and the fall (Age-0) exploitation rate. All of these parameters were decremented by 10% intervals. We decremented the proportion of nests disturbed from Age-0 cohorts 1, 2 and 3 (early, middle and late nesting, respectively), from 1 to 0 by 0.1 intervals. For the remaining parameters, we decremented all age values (Table 1) using a rate. For spring immigrants we assumed our baseline represented the maximum number of immigrants that could move into Little Yampa Canyon so we set the maximum rate to 1 and decremented by 0.1 intervals. For exploitation parameters we set the maximum rate to 3, i.e., three times the values shown in Table 1, and then decremented this rate by 0.1 intervals down to 0. Regardless of the rate adjustment, exploitation was never allowed to be greater than 1 for any age cohort.
In addition to decrementing parameters that managers could manipulate, we projected smallmouth bass abundance under two more complex management scenarios. These scenarios were motivated by discussions with Recovery Program staff and collaborators: (1) reduction of adult smallmouth bass escapement from Elkhead Reservoir to zero; and (2), a shift to less exploitation in the spring and more in mid-summer during the bass reproductive period, an effort referred to as "the surge". With all other parameters set at baseline levels, we implemented the first scenario by decreasing the density per river mile of adult immigrants by 4.87 on each time-step. The estimate, 4.87, is the maximum density across post-reconstruction Elkhead Reservoir translocation cohorts (2006–2009) that escaped from the reservoir and migrated to Little Yampa Canyon (Breton et al. 2013). This estimated density per river mile provides a worst case scenario for translocated (non-resident of Elkhead Reservoir) smallmouth bass migration into Little Yampa Canyon from Elkhead Reservoir. To account for escapement by non-translocated (resident) adult smallmouth bass from Elkhead Reservoir, we assumed equal escapement, thereby doubling the number of fish leaving the reservoir and resulting in immigration of 9.74 fish per river mile (rmi) into Little Yampa Canyon. To simulate the elimination of migration from Elkhead Reservoir, we decreased the density per river mile of adult immigrants by 9.74 for each time-step of our simulations. It is likely that the non-translocated (resident) adult smallmouth bass population in the reservoir was larger than the translocated adult population; therefore, we ran five more simulations increasing the density of non-translocated adult smallmouth bass that escaped from Elkhead Reservoir and immigrated to Little Yampa Canyon by 2x, 3x, 4x, 5x, and 6x. For example, the highest level of escapement included 4.87 non-resident fish and 29.22 resident fish (6X resident density; for a total of 34.09 fish/rmi) escaping from Elkhead Reservoir and immigrating into Little Yampa Canyon. When we simulated
excluding these immigrants from Little Yampa Canyon, it suggested that nearly all of the adult immigrants into Little Yampa Canyon could be attributed to escapees from Elkhead Reservoir. However, we make the assumption in this analysis that all immigrants are coming from Elkhead Reservoir and managers should remember that immigration of smallmouth bass into Little Yampa Canyon is likely affected immigration from other river reaches.

To simulate effects of removal during the surge we increased exploitation rates by 10%, 20%, and 30% to reflect increased capture probability that occur during under conditions of lower flows (relative to spring) and increased disturbance of Cohort 1 from 0 to 0.20 (20% of nests are disturbed. The range of increased capture probabilities were used to functionally increase exploitation rate and seemed reasonable given higher concentration of bass in near shore spawning areas during lower late spring flows.

**Results**

*Performance of the Baseline Model*

The average density of smallmouth bass predicted by our baseline model was 9.14 fish per hectare (ha), 100/rmi and 2401 fish for the Yampa River study reach over 50 years (Figure 4). These estimates are very similar to the average over the period 2004–2010 estimated by Breton *et al.* (2014) using capture-mark-recapture models: 8.4 fish/ha, 92 fish/rmi and 2206 fish for the reach.

*Baseline Model Sensitivity Analysis*

We refer to sensitivity as shifts in density from our baseline projections following a change in a particular parameter in the population model. Bass density was most sensitive to the probability of Age 1–2 survival followed by the alpha ($\alpha$) stock-recruitment parameter and the proportion of
adult stock that breeds (Table 3; Figure 5). The differences in density from the lowest to highest value assessed for these parameters were 133, 77 and 75 bass/rmi in Little Yampa Canyon, respectively. Density was moderately sensitive to changes in the probability of Age 2–3 survival followed by breeding length threshold and then the probability of Age 3-adult survival. The differences in density from the lowest to highest value assessed for these parameters were 43, 27 and 25 bass/rmi, respectively. Density was least sensitive to adult survival followed by the beta ($\beta$) stock-recruitment parameter; the differences in density from the lowest to highest value assessed for these parameters were 16 and 11 bass/rmi, respectively. The relationship between predicted density and breeding length threshold was non-linear, all others were approximately linear across the parameter ranges we assessed.

Management Scenarios

The difference in density of smallmouth bass when no nests were disturbed versus all nests disturbed (0-100%) was 23 bass/rmi for Cohort 2 and 37 for Cohort 1 (Table 3, Figure 6). Thus, the greatest impact of disturbance on bass density was achieved by disturbing Cohort 1 followed by Cohort 2. There was effectively no change in bass density when Cohort 3 (age-0 recruits) was disturbed, even when the proportion of nests disturbed was 1 (all Cohort 3 nests fail).

With no immigration, bass density declined to 11 fish/rmi. (average of 50 replicate projections). For 20 of these projections, the population was eradicated before reaching the 50th time-step. Reducing immigration to zero was the only condition that caused eradication in any replicate. At 20%, 40%, 60% and 80% of the baseline immigration rate (Table 1), average densities were 26, 45, 64 and 82/rmi, respectively.

Changes in fall exploitation of Age-0 bass had very little impact on bass densities (Figure 6), the impact was slightly less than the Cohort 2 breeding proportion but note that fall
exploitation was simulated over a much greater range (0 to 3 versus 0 to 1). An adjustment of three times the baseline fall exploitation rate is an exploitation rate of 0.30 for Age-0 smallmouth bass. Even though it might be possible to exploit Age-0 fish in the fall at a higher rate, a decline of only 0.65 bass/ha for each 0.1 unit increase in fall exploitation suggests that not much would be gained relative to other parameters assessed in our analysis.

When spring exploitation rates were reduced (by decrementing from 0.9 to 0; Table 1), the density per river mile of bass increased dramatically from 126 to 870. Above the baseline model exploitation rates, the change in density was gradual relative to decreasing exploitation reflecting the non-linear relationship between density/ha and spring exploitation rate. Despite increasing exploitation to three times the current rates none of the 50 replicate projections experienced population eradication before reaching the 50th time-step. Nonetheless, mean density under these conditions was just 14 bass/rmi over 50 years.

When escapement of translocated (non-resident) smallmouth bass from Elkhead Reservoir was precluded, spring immigration into Little Yampa Canyon was reduced by 4.87 adult bass/rmi annually, and simulations showed average density of smallmouth bass in Little Yampa Canyon declined from a baseline of 100 to 93 bass/rmi. Assuming non-translocated smallmouth bass escaped at the same rate as translocated adult bass (4.87 bass/rmi) and population sizes of translocated and non-translocated adult bass in Elkhead Reservoir were identical, preventing escapement of bass from Elkhead Reservoir resulted in a decline in density in Little Yampa Canyon from a baseline of 100 to 89 bass/rmi. When simulations assumed that resident bass outnumbered translocated smallmouth bass in Elkhead Reservoir by increments of 2x, 3x, 4x, 5x, and 6x, smallmouth bass densities in LYC declined proportionally from 100 to 82, 76, 70, 63, and 57 bass/rmi, respectively.
Densities of smallmouth bass per river mile were 74, 61 and 50 when 20% of Cohort 1 nests were disturbed and spring exploitation was increased by 10, 20 and 30%, respectively, over baseline (Table 1). These simulations of the increased exploitation during the surge produced some of lowest densities of bass in our management scenarios (compare these densities to the lower river mile density column in Table 3 for management scenario parameters).

**Discussion**

Our population dynamics model was developed primarily to assess changes in smallmouth bass populations in the Upper Colorado River Basin to management scenarios that could be implemented by agencies attempting to limit the distribution and abundance of the species. Simulations showed that mechanical removal coupled with reduced immigration and lower survival of early hatching cohorts was effective to reduce populations over the long term. We also performed a sensitivity analysis to assess the performance of the model with respect to population parameters that were not well known. We discuss management scenarios, model sensitivity, and make recommendations relative to both below.

**Management Scenarios**

The purpose of assessing management scenarios was twofold. First, we sought to evaluate if standard spring electrofishing mechanical removal efforts were effective in reducing smallmouth bass densities. Second, we evaluated efficacy of additional control strategies that could further reduce smallmouth bass densities from current levels (Breton et al. 2014). We focused on parameters in the model that managers could manipulate by management actions.

We found that spring electrofishing removal was essential for maintaining the current baseline smallmouth bass density in Little Yampa Canyon. When we simulated a reduction of
spring electrofishing exploitation below that of the 2010 removal rate, the result was a dramatic and non-linear increase in bass density in just a few years in Little Yampa Canyon (Table 3; Figure 6). Higher smallmouth bass densities would place additional predation pressure on native fishes, increase emigration of young smallmouth bass from Little Yampa Canyon to other reaches, lead to higher densities in adjacent reaches, and increase bass densities throughout the upper basin. Thus, reductions in smallmouth bass removal effort are not recommended. Additional removal effort in spring removal effort by itself may not be the most effective way to further reduce smallmouth bass in Little Yampa Canyon.

Additional control strategies that we evaluated through model simulations were the disruption of reproduction, reallocation of removal effort to other seasons, and reduction of immigration into the Yampa River. By removing adult male smallmouth bass from nests in early summer, production of eggs and fry was greatly diminished, with largest reductions in density realized by disturbing early season nests (Cohort 1) followed by middle season nests (Cohort 2). Nest disturbance was more effective during hatching times for Cohorts 1 and 2 because those fish hatched earlier, grew faster, and achieved larger lengths at the end of the growing season than late hatching fish (Bestgen and Hill 2015a). Because larger fish survive at higher rates overwinter, reductions in abundance of early hatching smallmouth bass resulted in the greatest population declines. Disturbance of late season nests (Cohort 3) would likely have a smaller effect on bass density because most or all individuals from the late season cohort succumb to over-winter mortality due to their small body size and inability to withstand starvation.

Given the large effect of disturbing Cohort 1 and 2 in our simulations, we recommend that any means of inducing early season nest failure (disturbance) should be investigated by the Recovery Program. In some cases, disturbance can be accomplished via flow releases timed with
smallmouth bass reproduction. For example, releases from Flaming Gorge Reservoir that flush downstream Green River spawning areas at the correct time may displace eggs and weak-swimming larvae in any spawning cohort and encourage nest abandonment by males (see Bestgen and Hill 2015a and 2015b for further discussion). This strategy could be useful in Lodore Canyon of the Green River, and under certain, relatively low flow years, in the Green River downstream of the Yampa River. Although this is another demand on water resources in Flaming Gorge Reservoir, a strategy to accomplish flow releases to enhance razorback sucker survival as described in the Larval Trigger Study Plan, higher summer flows for Age-0 Colorado pikeminnow recruitment, as well as flow to disadvantage reproductive success of smallmouth bass was discussed in Bestgen and Hill (2015a and 2015b, draft reports).

We evaluated two scenarios for reallocating removal effort. The first was concentrating removal effort during smallmouth bass spawning and the second was fall exploitation of Age-0 individuals. Removal during spawning effectively removed nearshore spawning adult smallmouth bass and had the added benefit of inducing nest failure when guarding males were removed. Our modeling indicated that a modest 20% level of Cohort 1 disturbance along with 10, 20 and 30% increases in removal rates (over 2010 levels) produced some of lowest densities of smallmouth bass in our management scenarios. There are several reasons managers should consider additional electrofishing removal during the spawning period. First, adult smallmouth bass may be more susceptible to electrofishing during this period because they occupy shallow nearshore nesting areas for extended times and are highly territorial during nest building and guarding, which increases capture vulnerability. Second, spawning locations may be limited and new spawning adults will eventually attempt to nest in areas in which other males have been removed, making them more susceptible to removal. Simulations showed that higher adult
removal rates combined with increased mortality of eggs and fry on nests should reduce populations, but timing of such efforts is key, and should begin when smallmouth bass reproduction begins, typically when water temperatures reach 16°C (Hill and Bestgen 2014, Bestgen and Hill 2015a).

We also assessed autumn electrofishing removal of Age-0 smallmouth bass. In our simulations, the relatively low autumn exploitation rate of Age-0 bass had a small impact on densities, inducing a decline of only 0.65 bass/rmi for each 0.1 unit increase in fall exploitation. Therefore, the direct effect of removing abundant Age-0 individuals in autumn does not appear to be an effective management option. However, removal of Age-0 smallmouth bass may have other benefits, such as reducing local predation on early life stages of native fishes.

We simulated how smallmouth bass densities were affected by immigration of smallmouth bass, including escapees from Elkhead Reservoir, and how precluding that escapement reduced densities in Little Yampa Canyon. Data on escapement rates of non-tagged, resident bass in Elkhead Reservoir were lacking, but there was data on escapement rates of tagged bass translocated into the reservoir (Breton et al. 2013). Thus, we simulated effects of various abundances of resident smallmouth bass in Elkhead Reservoir. Our simulations showed that the greater the number of escapees, resident or otherwise, the higher the immigration rate of bass into Little Yampa Canyon, which greatly reduced effects of mechanical removal. If only translocated (non-resident Elkhead Reservoir fish) adult smallmouth bass were precluded from escaping, our simulations showed only a small decline in densities relative to the baseline. Similarly, when we assumed translocated and non-translocated adults escaped at the same rate and their populations were the same size, and the escapement of both populations was precluded, the decline in baseline density remained small (100 to 89 bass/rmi). However, as the population
size of non-translocated adult smallmouth bass was increased by 2x, 3x, 4x, 5x, and 6x compared to the translocated adult smallmouth bass population size in Elkhead Reservoir, precluding escapement had a much greater effect and bass density in Little Yampa Canyon decreased dramatically from a baseline of 100 to 82, 76, 70, 63, and 57 bass/rmi, respectively. In other words, as the Elkhead Reservoir resident smallmouth bass population increased relative to the non-resident population, precluding escapement from the reservoir resulted in larger declines in bass density in Little Yampa Canyon. For instance, if resident bass densities were much greater than non-resident (6X or more), then precluding escapement from Elkhead Reservoir would account for the majority of adult immigration into Little Yampa Canyon.

The escapement analysis demonstrated the potential significance of Elkhead Reservoir as a source of adult smallmouth bass escaping to the Yampa River and highlighted the importance of understanding the abundance and dynamics of the resident reservoir smallmouth bass population. Precluding smallmouth bass escapement from Elkhead Reservoir was also considered essential given that propagule pressure, represented by escapees, was more than sufficient to re-establish a fully depleted Yampa River bass population (Baylis et al. 1991, 1993, Gross and Kapuscinski 1997) even when only a fraction of the adult smallmouth bass in our simulations continue to escape. Considering the documented contribution of Elkhead Reservoir smallmouth bass escapement to immigration into the Yampa River, and the potential for escapees to re-establish populations through reproduction, we echo the recommendation made by Breton et al. (2013) to permanently discontinue translocation of smallmouth bass to Elkhead Reservoir. We add that smallmouth bass escapement would be precluded from Elkhead Reservoir by removal of that fishery or by effective screening, which would also prevent escapement by resident, non-translocated bass and other invasive fishes such as northern pike.
The only simulation conditions that drove smallmouth bass populations to zero in Little Yampa Canyon was reducing immigration to zero (from all sources including riverine and reservoir stocks) while continuing removal efforts. This demonstrated how important immigration was in maintaining the smallmouth bass population in Little Yampa Canyon, and perhaps other reaches as well, and further suggested that the smallmouth bass population in Little Yampa Canyon would likely be eradicated in a few years under the present level of exploitation if immigration was curtailed. However, managers should remember that immigration of smallmouth bass into Little Yampa Canyon was affected by electrofishing removal effectiveness in other reaches, as well as escapement from Elkhead Reservoir (Breton et al. 2013). Increasing effort, improving electrofishing effectiveness in adjacent reaches and precluding reservoir escapement should be considered necessary steps for significantly reducing immigration and decreasing bass density in the Little Yampa Canyon reach of the Yampa River. Until immigration is reduced, the likelihood of substantial and permanent reductions in smallmouth bass density in Little Yampa Canyon is low.

Sensitivity Analyses

Several parameters in our model have not been estimated for the Upper Colorado River Basin or were not well known in general. Due to our uncertainty in these parameters, we conducted a sensitivity analysis to estimate their influence on model predictions of smallmouth bass density. Results of this analysis were intended to determine if better parameter estimates were needed to improve the precision of our baseline model. The largest variation in bass abundance in our sensitivity analysis was caused by changes in the probability of Age 1–2 survival (over the range 0-1), followed by the alpha stock-recruitment parameter and the proportion of adult stock that breed.
In our baseline model, we used the Age 1–2 survival probability from Peterson and Kwak (1999) of 0.25 ± 0.14 SD. When Age 1-2 survival was set to zero (i.e. total mortality), the model predicted 78 bass/rmi and if it was set to 1 (i.e. no mortality), the model predicted 211 bass/rmi (Table 3); the population was not reduced to zero under 100% mortality because of immigration. The difference in density over the entire range was 133 bass/rmi, and indicated the model was sensitive to Age1-2 survival. However, it was likely that the range of Age 1-2 survival was much more constrained. If we constrained the survival variation to three standard deviations from 0.25, we have a survival range from 0-0.67 and the difference in predicted bass density dropped to 73 bass/rmi. Even this constrained range was probably higher than actually encountered in the field. It may be feasible to estimate Age 1-2 survival with a targeted mark/recapture study but would require the Recovery Program to preclude removal in a section for several years.

The 2nd-most sensitive parameter in our analysis was alpha, the parameter that described recruitment per unit stock (number of small bass produced per adult female) at low stock densities in the Ricker function. Over the range 0–10, bass/rmi increased by 77 individuals. However, a more plausible range, given the similarities between our system and the system studied by Peterson and Kwak (1999), may be closer to 4–8 for the alpha parameter. Across this narrower range the difference dropped from 77 to 35 bass/rmi. Despite model sensitivity to alpha, it is unlikely that better estimates will be available in the near future. System-specific estimates would require the Recovery Program or other agencies to manipulate adult (stock) densities at many low and high values to estimate how recruit abundance is affected, a difficult and time-consuming task. Therefore, we recommend that users of the model recognize that the alpha parameter may influence their inferences and conduct model simulations across a range of
alpha. Additionally, other density dependent recruitment functions are available in the model software and could be used in place of the Ricker function. However, the Ricker function has been used in other modeling of smallmouth bass populations and makes reasonable biological sense, so we suggest continued use of that function (Peterson and Kwak 1999).

We assessed breeding proportion of smallmouth bass over its full range of possible values (0–1) in our sensitivity analysis. The difference in bass density between 0 (no adults reproducing) and 1 (all individuals reproducing) was 75 bass/rmi. We adopted a baseline value of 0.75 adults breeding even though smallmouth bass studies outside of the upper basin have suggested that this proportion could be less than 0.75 (Baylis et al. 1991, 1993, Gross and Kapusciniski 1997). However, we feel the assumption of 0.75 is reasonable given information from other studies and is conservative from a conservation perspective because it likely overestimates reproduction. In other words, the model may be predicting higher bass densities than are being realized but we feel that overestimating reproduction at this juncture in the removal program is better for resource conservation than underestimating it. Estimating this particular parameter from field data is especially problematic and published studies on closed populations indicate it can be highly temporally variable. Therefore, we recommend inferences regarding modeled smallmouth bass densities be tempered by understanding the uncertainty regarding the proportion of adults reproducing. Regardless of aforementioned parameter uncertainty, model simulations of bass abundance were similar to actual abundances, so parameter uncertainty may in fact, be minimal.

Other parameters such as Age 2-3 survival, Age 3 survival, and breeding length threshold had more moderate effects on simulation model predictions. Letting these variables vary across their entire range resulted in modest differences in baseline bass density (43, 25, and 27 bass/rmi,
respectively). The model was least sensitive to adult survival and the beta parameter from the Ricker function. These parameters caused a change of 16 and 11 bass/rmi across the range of variation modeled. Similar to the more sensitive parameters, the actual variation in these parameters was probably more constrained and likely had relatively small effects on modeled bass densities.

In conclusion, the parameters with largest effect remain, the survival of Age1-2, alpha stock-recruitment parameter, and the proportion of breeding adults. However, each parameter’s effect is much reduced after applying a more realistic range of values. Whether or not it would be cost effective to acquire better estimates of these parameters may be a worthwhile discussion point for Recovery Program managers, but we are not convinced that the need to improve parameter estimates outweighs foreseeable research costs and diversion of resources from removal efforts.

Future Model Uses

There are many other uses of the population dynamics simulation model that could be implemented to assist with evaluation of potential management actions. For example, if additional early life stage smallmouth bass information was available, such data could be modeled directly rather than through the use of the stock-recruitment functions. The simulation model also has options to explore time (in years) to achieve a management goal for smallmouth bass densities, given a level of removal and other user inputs. Some of those uses and other model options are outlined in the user’s guide.

Another use of the model may be to simulate effects of climate change on smallmouth bass populations in streams of the Colorado River basin. We ran preliminary simulations that assumed less overall stream discharge, fewer days of maximum daily flow > 8,000 (45 d in
baseline model vs. 10 in climate change simulations), and higher stream temperatures (19°C mean summer water temperature vs. 23°C in climate change simulations), all of which promoted earlier smallmouth bass spawning a longer growing season, and faster growth of young bass. This ultimately led to higher over-winter survival and increased abundance of adult bass. The time to achieve the management goal of smallmouth bass population reduction to 30 fish/river mile, assuming a 60% annual removal rate, more than doubled from 16 to 35 years, a substantial change under the climate change scenario. The preliminary simulation results discussed here showed the potential effects of flow reductions and increased water temperatures in the Yampa River, from climate change or other effects, and also illustrated the flexibility of the simulation model to explore other questions of management concern.

Based on our simulations and results reported by Breton et al. (2013, 2014), we recommend the following as the most effective and efficient strategy for further reducing abundance of smallmouth bass in the upper Colorado River basin: (1) in all reaches, maintain, as a minimum, the electrofishing intensity as represented by our baseline model (2010 effort); (2) reallocate ineffective removal periods such as those in early spring to the spawning period (a primary goal of the surge) in reaches where reproduction occurs; (3) make the surge a core component of the electrofishing removal effort on the Yampa River; (4) implement the surge strategy to area(s) of smallmouth bass reproduction responsible for recruitment in the Echo-Split reach and the adjacent downstream Middle Green reach; (5) consider other management options, in addition to electrofishing to further disrupt smallmouth bass reproduction or recruitment; (6) maintain the management strategy to not translocate smallmouth bass to Elkhead Reservoir and other locations in the upper Colorado River basin; and (7) prevent escapement of resident and
remaining non-resident smallmouth bass and other fishes from Elkhead Reservoir and other sources into streams of the upper Colorado River basin.

These management recommendations can be applied in the field with the funding that is available and are based on the best available information to date (see related discussion and suggestions in Coggins et al. 2011 and Loppnow et al. 2013). We believe that their full implementation will result in another major reduction in the density of smallmouth bass in the upper Colorado River basin, compounding reductions that followed recommendations made by Haines and Modde (2007) and reported by Breton et al. (2014). We recommend periodic re-evaluations of the control program based on a minimum of revised estimates of (1) escapement from Elkhead Reservoir to Little Yampa Canyon (Breton et al. 2013); (2) smallmouth bass abundance and density estimates for Little Yampa Canyon from a mark-recapture analysis (Breton et al. 2014); and (3), projected densities under management scenarios from this contribution. These re-evaluations should be integrated into a carefully designed adaptive management strategy to recover the four endangered fish species in the upper Colorado River basin.

Conclusions

1. Simulation modeling was useful to explore factors controlling abundance dynamics of smallmouth bass in the Yampa River in Little Yampa Canyon.

2. Model simulations indicate that maintaining removal rates at levels similar to those of the 2010 Little Yampa Canyon baseline rate is important for holding bass densities in check. A decrease in removal intensity would result in smallmouth bass rebounding to high densities in a short time and would also increase emigration to adjacent reaches.
3. Increasing Little Yampa Canyon early spring exploitation rates above the 2010 level has only a small effect on reducing smallmouth bass density.

4. Intensive removal during the late spring and early summer spawning period (the surge) should be a core component of any future smallmouth bass management strategy in the upper basin. A modest 20% level of Cohort 1 nest disturbance along with 10, 20 and 30% increases in removal rates (over 2010 levels) produced some of lowest densities of bass in our management scenarios. This approach has been adopted in the upper Yampa River and the Green River just downstream of the Yampa River and could be implemented elsewhere.

5. Large reductions in density were realized by disturbing early season nests (Cohort 1) followed by middle season nests (Cohort 2). Manipulating flows, particularly in the regulated Green River, may be an effective way to reduce smallmouth bass reproductive success. Disturbance of late season nests (Cohort 3) would have only a small or no effect on smallmouth bass density.

6. Simulations showed reducing immigration to zero, while continuing removal efforts, was the only condition that forced smallmouth bass populations to zero in Little Yampa Canyon. In other words, the bass population in Little Yampa Canyon would likely be eradicated in a few years under the present level of exploitation if immigration was curtailed. This result demonstrates the critical role of immigration in supporting the Little Yampa Canyon smallmouth bass population, and perhaps other reaches as well, and also demonstrates the value of bass removal. Improving electrofishing effectiveness in adjacent reaches to Little Yampa Canyon and precluding escapement from Elkhead Reservoir are valuable options for significantly reducing immigration into Little Yampa Canyon.
7. Changes in fall exploitation of Age-0 smallmouth bass had little impact on bass densities over the limited level of removal that was simulated.

Recommendations

1. Maintain the exploitation rate represented by our baseline model (Little Yampa Canyon 2010 level).

2. Reallocate effort during ineffective removal periods such as early spring sampling in Little Yampa Canyon, to periods in later spring or early summer that overlap with smallmouth bass reproduction (a primary goal of the surge).

3. Make removal during spawning (the surge) a core component of the electrofishing removal effort on the Yampa River and other reaches.

4. Consider other management options such as flow management, in addition to electrofishing, to further disrupt smallmouth bass reproduction and recruitment.

5. Permanently discontinue translocation of smallmouth bass to Elkhead Reservoir and other locations in the upper Colorado River basin.

6. Prevent escapement of resident and remaining non-resident smallmouth bass and other fishes from Elkhead Reservoir and other sources into streams of the upper Colorado River basin.

7. Re-evaluate simulated predictions as new data becomes available to better parameterize the smallmouth bass population dynamics model.
Literature cited


Larimore, R. W. 1952. Home pools and homing behavior of smallmouth black bass in Jordan Creek, Biological Notes, No. 29.


Table 1. Smallmouth bass (*Micropterus dolomieu*) age structure, initial starting densities for projections, spring immigrants at each time-step, age-specific lengths (mm) and exploitation rates integrated into our baseline model. Values were estimated using data from Little Yampa Canyon, and starting densities are post-exploitation densities. Age-3 fish include both sub-adults (<200 mm TL) and adults ≥ 200 mm TL; those adults are included in the breeding stock, but sub-adults are not.

<table>
<thead>
<tr>
<th>Age By Class</th>
<th>By Year</th>
<th>Starting Densities</th>
<th>Spring Immigrants</th>
<th>Exploitation Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>fish/ha</td>
<td>fish/rkm</td>
<td>fish/ha</td>
</tr>
<tr>
<td>Young-of-Year</td>
<td>Age-0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sub-adult</td>
<td>Age-1</td>
<td>4.10</td>
<td>27.85</td>
<td>44.81</td>
</tr>
<tr>
<td>Sub-adult</td>
<td>Age-2</td>
<td>1.81</td>
<td>12.33</td>
<td>19.84</td>
</tr>
<tr>
<td>Sub-adult/Adult</td>
<td>Age-3</td>
<td>5.03</td>
<td>34.19</td>
<td>55.03</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-4</td>
<td>0.65</td>
<td>4.40</td>
<td>7.08</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-5</td>
<td>0.28</td>
<td>1.91</td>
<td>3.07</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-6</td>
<td>0.05</td>
<td>0.35</td>
<td>0.57</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-7</td>
<td>0.01</td>
<td>0.06</td>
<td>0.10</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-8</td>
<td>0.00</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-9</td>
<td>0.02</td>
<td>0.14</td>
<td>0.22</td>
</tr>
<tr>
<td>Adult</td>
<td>Age-10</td>
<td>0.02</td>
<td>0.13</td>
<td>0.21</td>
</tr>
</tbody>
</table>

† These rates are approximations, they are not based on estimates from field data, see text for more details.
Table 2. Summary statistics and coverage (year, period) for three environmental covariates integrated into our baseline model. Data were from the U.S. Geological Survey, gauge #09251000 (Maybell, Colorado). Covariates describing thresholds for poor conditions for Age-0 smallmouth bass growth (spring, summer) and over-winter survival are also presented.

<table>
<thead>
<tr>
<th>Units</th>
<th>Mean</th>
<th>SD</th>
<th>Years</th>
<th>Period</th>
<th>Poor Conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rearing Flow days</td>
<td>23.05</td>
<td>22.53</td>
<td>1998–2011</td>
<td>1 April to 30 September</td>
<td>≥25 days</td>
</tr>
<tr>
<td>Rearing Water temperature C</td>
<td>21.75</td>
<td>1.36</td>
<td>1998–2011</td>
<td>1 July to 15 August</td>
<td>≤20º C</td>
</tr>
<tr>
<td>Winter Starvation Days days</td>
<td>199.5</td>
<td>16.01</td>
<td>1997–2011</td>
<td>1 June to 1 June</td>
<td>≥190 days</td>
</tr>
</tbody>
</table>
Table 3 a-b. Mean sub-adult and adult smallmouth bass density per hectare, river mile and reach (Little Yampa Canyon) from our (a) sensitivity and (b) management scenarios. For comparison, hectare, river mile, and reach densities from our baseline model projections were 9.14, 100 and 2401, respectively. All fish densities are based on averages from 50 replicate projections over 50 time-steps (years).

(a)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter Range &amp; Units</th>
<th>Hectare Density</th>
<th>River Mile Density</th>
<th>Reach Density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lower       Upper       Unit</td>
<td>Lower   Upper  Diff†</td>
<td>Lower   Upper  Diff†</td>
<td>Lower   Upper  Diff†</td>
</tr>
<tr>
<td>Breeding Proportion</td>
<td>0           1            proportion</td>
<td>4.14     11.01   6.87</td>
<td>45       120     75</td>
<td>1087    2892   1804</td>
</tr>
<tr>
<td>Breeding Length Threshold</td>
<td>150         250           mm TL</td>
<td>7.25     9.74    2.49</td>
<td>79       107     27</td>
<td>1904    2558   654</td>
</tr>
<tr>
<td>Stock-recruitment (α)</td>
<td>1           10           fish/ha</td>
<td>4.72     11.78   7.06</td>
<td>52       129     77</td>
<td>1240    3094   1854</td>
</tr>
<tr>
<td>Stock-recruitment (β)</td>
<td>0           0.1          fish/ha</td>
<td>8.64     9.68    1.04</td>
<td>95       106     11</td>
<td>2269    2542   273</td>
</tr>
<tr>
<td>Age 1–2 Survival</td>
<td>0           1            probability</td>
<td>7.12     19.29   12.17</td>
<td>78       211     133</td>
<td>1870    5066   3196</td>
</tr>
<tr>
<td>Age 2–3 Survival</td>
<td>0           1            probability</td>
<td>6.92     10.82   3.9</td>
<td>76       118     43</td>
<td>1818    2842   1024</td>
</tr>
<tr>
<td>Age 3-adult Survival</td>
<td>0           1            probability</td>
<td>7.09     9.41    2.32</td>
<td>78       103     25</td>
<td>1862    2471   609</td>
</tr>
<tr>
<td>Adult Survival</td>
<td>0           1            probability</td>
<td>7.89     9.35    1.46</td>
<td>86       102     16</td>
<td>2072    2456   383</td>
</tr>
</tbody>
</table>

†Difference between upper and lower densities.
### Parameter Range & Units

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter Range &amp; Units</th>
<th>Hectare Density</th>
<th>River Mile Density</th>
<th>Reach Density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lower</td>
<td>Upper</td>
<td>Unit</td>
<td>Lower</td>
</tr>
<tr>
<td>Cohort 1</td>
<td>0</td>
<td>1</td>
<td>proportion</td>
<td>5.78</td>
</tr>
<tr>
<td>Cohort 2</td>
<td>0</td>
<td>1</td>
<td>proportion</td>
<td>7.1</td>
</tr>
<tr>
<td>Cohort 3</td>
<td>0</td>
<td>1</td>
<td>proportion</td>
<td>9.09</td>
</tr>
<tr>
<td>Immigration Rate</td>
<td>0</td>
<td>1</td>
<td>Rate</td>
<td>1.04</td>
</tr>
<tr>
<td>Spring Exploitation</td>
<td>0</td>
<td>3</td>
<td>Rate</td>
<td>1.26</td>
</tr>
<tr>
<td>Fall Exploitation</td>
<td>0</td>
<td>3</td>
<td>Rate</td>
<td>7.91</td>
</tr>
<tr>
<td>Poor Rearing Conditions</td>
<td>0</td>
<td>1</td>
<td>probability</td>
<td>8.58</td>
</tr>
<tr>
<td>Poor Over-winter Conditions</td>
<td>0</td>
<td>1</td>
<td>probability</td>
<td>8.71</td>
</tr>
</tbody>
</table>

†Difference between upper and lower densities.
Figure 1. The Yampa River subbasin of the upper Colorado River basin including the confluence of the Yampa River-Green River confluence at Echo Park in Dinosaur National Monument. The towns of Hayden, Craig and Maybell, Colorado are provided as references.
Figure 2. The summer sub-model for smallmouth bass. The sub-model begins with the number of fish in age classes 1-10 (Adult age group is Age-3 ≥ 200 mm TL and all fish in age classes 4-10) surviving the winter. The model consists of the following components or processes: a. immigration and emigration occur; b. Each age class are subjected to exploitation; and c. Reproduction occurs, which is influenced by the proportion of adults that spawn. Reproduction can result in eggs, fry, or Age-0 fish depending on user input. The number of surviving offspring can also be influence by disturbance of any early life stage including eggs, fry, and Age-0 fish. After Age-0 abundance is predicted, d. equal-sized cohorts (Cohort 1-3) are defined, and e. Age-0 oversummer growth occurs and is influenced by discharge and temperature. After Age-0 growth is predicted then all age classes undergo oversummer survival (f) and this predicts the number of fish in each age class that proceed to the winter submodel.
Figure 3. The winter sub-model for smallmouth bass includes: a. Age-0 smallmouth bass are removed using electric seines ($\mu_0$) and then subjected to over-winter mortality through equations that integrate body size and starvation days as a function of water temperature; and b. Age-0 fish that survive are allocated to the Age-1 population cohort at the next time-step (spring). Age-1 and Age-2 sub-adult ($S_{1,2}$) survive by probabilities that are drawn from distributions providing random variation in survival for these ages. All other rates are assumed to be constant (age-3+).
Figure 4. Estimated density/ha of sub-adult and adult smallmouth bass in Little Yampa Canyon predicted by our baseline model. Points along the line are averages at each time-step from 50 simulations. The average density across time-steps was 9.14 sub-adults and adults/ha, which is similar to the average density in Little Yampa Canyon from Breton et al. (2014) over the period 2004–2010 of 8.4 sub-adults and adults /ha.
Figure 5. Average sub-adult and adult smallmouth bass density/ha from all replicates and time-steps from the sensitivity component of our analysis while decrementing the target parameter by 5% or 10% intervals. In all plots, the horizontal dashed line is the baseline model density (9.14 fish/ha).

Note that the y-axis scale is 0–25 for Age 1–2 survival and 0–12 for all other parameters.
Figure 6. Average sub-adult and adult smallmouth bass (*Micropterus dolomieu*) density/ha from all replicates and time-steps from our management scenario simulations. The horizontal dashed line shown in most plots is the baseline model density (9.14 fish/ha). In the spring and fall exploitation panel (lower middle), the left y-axis plots spring removal densities (open circles) and the right y-axis are autumn removal densities (open triangles). The y-axis scale is 0–100 for spring exploitation and 0–12 for all other parameters.
Appendix I

Summer Equations

Immigration (Figure 2a)

\[ N_{a,t+1} = N_{a,t} + I_a \]

Where \( a \)= age class (1-10), \( t \)= end of winter, \( t+1 \)= after immigration, and \( I \)= the number of immigrants.

Electrofishing removal (Figure 2b)

\[ N_{a,t+1} = N_{a,t} - u_a N_{a,t} \]

Where \( a \)= age class (1-10), \( t \)= after immigration, \( t+1 \)= after removal, and \( u \)= the proportion of fish removed in each age class.

Reproduction/Recruitment (Figure 2c)

\[ S = P_b \times N_{\text{adult}} \]

Where \( S \) is the number of spawning fish (spawning stock), \( P_b \) is the proportion of adults breeding, and \( N_{\text{adult}} \) is the total number of adult fish. \( P_b \) was 0.75 in the baseline model. The user can specify several stock recruit relationships but our baseline model used a standard Ricker Function that predicted the number of recruits (\( R \)). Where \( S_t \)= spawning stock, \( \alpha \) is recruitment per unit stock at low stock densities, and \( \beta \) is the strength of the negative effect of density on recruitment. In our baseline model, we set egg and fry survival a 1 and are predicting the number of Age-0 produced (using the Ricker function). In the baseline model, \( \alpha = 6.9872 \) and \( \beta = 0.0437 \).
\[ R = S \exp(\ln(\alpha) - \beta S) \]

**Disturbance (Figure 2)**

Disturbance can be implemented on three life stages (eggs, fry, or Age-0). It is the proportion of total reproduction experiencing total mortality due to disturbance.

\[ N_{0,t+1} = N_{0,t} - P_d N_{0,t} \]

Where \( N_0 \)= the number of Age-0 individuals, \( P_d \)= the proportion disturbed, \( t \)= time prior to disturbance, and \( t+1 \)= time immediately after disturbance. In our baseline model, \( P_d = 0 \).

**Cohorts (Figure 2d)**

After reproduction and disturbance, the total number of Age-0 individuals are divided into three equal cohorts. For instance, if 900 Age-0 fish were produced, each cohort would have 300 individuals.

**Age-0 Growth (Figure 2e)**

The mean total length for each cohort at the end of summer was determined using the equation,

\[ TL(mm) = 101.4 - (days \times 0.66) + (temp \times 2.82) + \text{cohort}. \]

where \( days \) is a proxy for bass hatch initiation, \( temp \) is a proxy for growing conditions and cohort is an offset for cohorts 1 and 2; Cohort 3 is represented by the intercept. These (estimated) offsets were 32.7 and 16.1, respectively. To determine \( days \) at each time-step we solved the equation,

\[ days = 164.19 + (count \times 0.6254) \]

where \( count \) is the count of days when mean daily flow of the Yampa River was \( \geq 8000 \) cfs between 1 April and 30 September (equation is from Hill and Bestgen 2015a). We used flow data from 1998–2011 measured at the U.S. Geological Survey Gauge (#09251000) at Maybell, Colorado, which is just downstream of our study area (Figure 1). Average 1 July to 15 August
water temperature data from 1998–2011 were also from the same location. At each time-step, we
drew a random variable from normal distributions with mean and standard deviation estimated
from these flow and temperature data (Table 2). These values were redrawn if they did not meet
environmental condition requirements (good vs. poor years, more below).
Once the mean TL of each Age-0 cohort was calculated, we assumed that the lengths were
normally with a standard deviation of 10 mm. The standard deviation was estimated based on
the range of lengths for those fish (Ott 1988).

**Over-summer Survival (Figure 2f)**

\[
N_{a,t+1} = s_s N_{a,t}
\]

Where \(a=\) age class (0-10), \(t=\) end of summer (after Age-0 growth occurs), \(t+1=\) after exploitation,
and \(s_s=\) oversummer survival. \(S_s=1\) for all age classes in the baseline model. That assumes there
is no natural mortality in the summer.

**Winter Equations**

**Age-0 Removal (Figure 3a)**

\[
N_{0,c,t+1} = N_{0,c,t} - \mu_0 N_{0,c,t}
\]

Where \(N_0=\) number of Age-0 fish, \(c=\) cohort number (1-3), \(t=\) after summer survival, \(t+1=\) after
removal, and \(\mu_0=\) the proportion of fish removed.

**Over-winter Age-0 survival (Figure 3b)**

At each time-step, we determined fish total length at which 20% (L20) and 80% (L80) of
individuals in these length categories survived. From Shuter and Post (1990),

\[
L20 = (-3.31 + (0.032 \times s\text{days})) \times 10 \times 1.05
\]
\[ L_{80} = \left( -3.27 + (0.044 \times s\text{days}) \right) \times 10 \times 1.05 \]

where \textit{sdays} (starvation days) is a proxy of winter severity. The last two terms in the equations are adjustments for converting from centimeters to millimeters and fork length to total length, respectively. We used \( \leq 10^\circ \text{C} \) as the threshold below which fish stopped feeding, lived off of their body reserves, and hence, began to starve. We used mean daily water temperature data over the 1 June to 1 May period (1997–2011) from the Maybell Gauge to estimate a mean and standard deviation of starvation days to create a distribution (Table 2). At each time-step, we drew a random variable from this distribution and then solved the \( L_{20} \) and \( L_{80} \) equations. Over the winter period, all Age-0 fish \( \leq L_{20} \) survived with probability 0.20 and those \( \geq L_{80} \) survived with probability 0.80. Survival probabilities for Age-0 bass cohorts with total lengths between \( L_{20} \) and \( L_{80} \) were determined by linear interpolation (Shuter and Post 1990). Rather than determine survival for each length between \( L_{20} \) and \( L_{80} \), we determined survival for 10 mm size categories and applied the survival to all fish in that size category.

**Over-winter Survival for Other Age Classes (Figure 3c)**

\[ N_{a,t+1} = s_{w,a} N_{a,t} \]

Where \( a = \text{age class (1-10)} \), \( t = \text{end of summer (after Age-0 growth occurs)} \), \( t+1 = \text{end of winter} \), and \( s_{w,a} = \text{overwinter survival for each age class} \).
Appendix II

Users guide
A user manual for running population dynamics simulations in the projection tool developed for smallmouth bass (*Micropterus dolomieu*) in the upper Colorado River basin


February 2014

Upper Colorado River Endangered Fish Recovery Program, Project 161

Bureau of Reclamation Agreement # 9-FC-81-0143 09FC402885
A USER MANUAL FOR RUNNING POPULATION DYNAMICS SIMULATIONS IN
THE PROJECTION TOOL DEVELOPED FOR SMALLMOUTH BASS
(MICROPTERUS DOLOMIEU) IN THE UPPER COLORADO RIVER BASIN

Prepared by,
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For,

Colorado River Recovery Implementation Program
U. S. Department of Interior, Fish and Wildlife Service
Lakewood, Colorado 80225

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Larval Fish Laboratory Contribution 180
February 2014
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Disclaimer: Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the authors, the Fish and Wildlife Service, U.S. Department of Interior, or members of the Recovery Implementation Program.
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Executive Summary

The population projection tool described in this User’s Guide provides an opportunity to Recovery Program managers, and other stakeholders in the effort to recover non-native fish species in the upper Colorado River basin, to specify and compare scenarios (population models) through estimates of population densities projected through time. Given uncertainty in the values that are integrated into any population model, estimates from a single projection (or averages of identical projections) may be of limited value. For this reason, the strengths of the projection tool described here are its option to store projections and decrement a parameter. The former, e.g., allows managers to estimate and visualize the effect of a management action such as increasing exploitation over some baseline by 10%, 20% and 30%; or reducing fecundity, through nest disturbance or some other method, by a similar set of percentages. And by decrementing a parameter from a maximum to minimum value, such as over-winter adult survival from 0-1 (full range), managers can not only estimate the effect of a potential management action but they can also judge the sensitivity of density estimates from their population model to changes in the decremented parameter. This feature of the projection tool was utilized extensively by Breton et al. (2015) in their sensitivity analysis, as well as their assessment of management scenarios. Just like the seminal work provided by Haines and Modde (2007) contributed to and has been overshadowed by recent advances and insights (Breton et al. 2015), this projection tool will hopefully inform another advance and so will likely not be the final contribution to the effort to manage smallmouth bass in the upper Colorado River basin. Nonetheless, the projection tool exceeds all the expectations outlined in the proposal to the Recovery Program authored by Winkelman et al. (2009) and so should be a much valued aid to managers for the coming years.
We recommend that Recovery Program managers become adept at running projections and that they integrate estimates, with caution, from these projections as evidence in future management decision making contexts. These users should be comfortable with the strengths of the projection tool, the options to store projections and decrement a parameter. From these exercises we expect that recommendations for projection tool updates will be forthcoming, eventually leading to a new advance in projection capabilities.
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Figure 2. The spring and summer life cycle components of our population model for smallmouth bass (*Micropterus dolomieu*). Adults and sub-adults immigrate to or emigrate from the population in the spring. Subsequently, these age classes can be subjected to exploitation (removal) through any method such as boat-based electrofishing ($\mu_{1,2,3,a}$). Following exploitation, adult stock produce age-0 recruits through a user-specified density-dependent stock-recruitment function. Remaining parameters, all assumed to be constant rates, are survival probabilities: egg ($S_e$); fry ($S_f$); age-0 ($S_0$); sub-adult ($S_{1,2,3}$) and adult ($S_a$). After reproduction, a proportion of the recruits can be removed by nest disturbance. Spring and summer growth of age-0 smallmouth bass can be a function of spring and summer river discharge and water temperature (rearing conditions).......... 149

Figure 3. The fall and winter life cycle components of our population model for smallmouth bass (*Micropterus dolomieu*). Prior to entering the winter, age-0 smallmouth bass can be exploited (removed) by electric seines ($\mu_0$) or any other method prior to over-winter mortality through equations that can accommodate body size and starvation days. Age-0 fish that survive are allocated to the age-1 component of the population at the next time-step (spring). Age-1 and age-2 sub-adult ($S_{1,2}$) survive by probabilities that can be drawn from distributions providing random variation in survival for these ages. All other sub-adult and adult rates are assumed to be constant (age-3+).............................................. 150

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List of Key Words

projection, simulation, modeling, population dynamics, smallmouth bass, Micropterus dolomieu,
Colorado River, northern pike, Esox lucius, fisheries management, exploitation
Introduction and Modus Operandi. The smallmouth bass (*Micropterus dolomieu*) population projection tool described in this report was developed to fulfill one of many objectives outlined in Winkelman *et al.* (2009, pg. 7), "One essential element of the [population projection tool] would allow users to change life history parameters, environmental relationships, and forms of density dependence." Winkelman *et al.* (2009) also provided the basic summer and winter smallmouth bass life history models, parameters, and equations. These initial ideas were supplemented and modified during development of the projection tool. Application of the projection tool begins with a user specifying a population model using the options provided. Subsequently, that population model is used to calculate population projections over user-specified time-steps and replicas. We suggest the following *modus operandi* (manner of operating) when deploying the projection tool to gain insights into any scenario: think critically about the structure and parameter values of the population model before running projections; and respect that projection results are only estimates based on a finite model of an infinitely complex process (truth).

We recommend that users familiarize themselves with the examples provided in the section Saved Parameter Values (Examples) before attempting to specify and run a population model on their own. With over 300 parameters that can be modified by the user, many (infinite) population models could be implemented, including (special cases) those proposed by Haines and Modde (2007) and Peterson and Kwak (1999). Although the tool was developed to model smallmouth bass dynamics, any species population with similar life history characteristics could be investigated including northern pike (*Esox lucius*). The density of recruits (age-0), sub-adults and adults are projected over annual time-steps based on the population model specified by the
user. Projected population densities provided in various outputs (plots, spreadsheets) are hectare and river mile densities\(^2\) after (optional) spring exploitation.

*Age Structure, Timeline, and Parameters.* The projection tool is age-structured. Parameters, such as exploitation, can be set by the user for each age 0-10 year class. For older age classes, age-10+ fish can survive at the adult survival rate or be removed from the projection using options provided (see *Survival Options* section). Each annual projection steps through an ordered series of events (Figure 1), many of these are optional such as exploitation (removal) of age-0 fish in the fall. The order of these events was based on the life history of smallmouth bass and the timing of spring exploitation (typically boat electrofishing) and fall exploitation (typically electric seine) conducted by Recovery Program collaborators in the upper Colorado River basin (Breton *et al.* 2014, 2015): (1) spring emigration and immigration followed by; (2) spring exploitation; (3) recruitment of age-0 fish through a user-specified density-dependent stock-recruitment function; (4) growth of age-0 fish as a function of spring and summer environmental conditions; (5) losses due to over-summer mortality (all ages); (6) fall exploitation of age-0 fish; and lastly, (7) over-winter survival. For convenience, we've summarized events in the annual time-line (Figure 1) into Spring & Summer (Figure 2) and Fall & Winter components (Figure 3). To these summaries (Figures 2-3) we've also added many of the demographic parameters and environmental effects that users will encounter when specifying their population model. Figures 1-3 have been conveniently integrated into the projection tool to aid model formulation and building (see tabs on the projection form). There are 309 check-, text- and combo-box options

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\(^2\) All outputs provide hectare density, some outputs provide both river mile and hectare density. A convenient *Convert* option is provided on the bottom left hand side of the projection form, users can easily convert ha, rmi and rkm densities using this option.
that can be manipulated by the user to specify their population model, the majority of these are population and management parameters that will affect the projection results.

*Saved Parameter Values (Examples)*. It may be beneficial, before getting into the many details of the projection tool, to introduce a few examples. These examples will provide an opportunity to introduce many of the core features of the projection tool, such as projection and plotting options. The projection tool was initially integrated into the Non-native Fish Database developed by Colorado State University, the Larval Fish Laboratory, and the Colorado Cooperative Fish and Wildlife Research Unit (US Geological Survey). To access the projection tool, users opened the database and then click on the **Population Projection Tool** option on the Main Switchboard.

This option opens a form (hereafter, "projection form") with tabs across the top.
In the stand-alone version of the projection tool, the Projection Form is the default form (there is no switchboard in the stand-alone version).

**Haines and Modde (2007).** All of the projection results reported in the main section of the seminal report by Haines and Modde (2007) can be re-calculated/re-output by this projection tool by setting parameters to the values specified by Haines and Modde (2007), i.e., by specifying the population model they developed for each of their figures. We'll start by reproducing the Ricker stock-recruitment projection from Figure 3.
In Figure 3 from Haines and Modde (2007), the blue line projects the sub-adult and adult smallmouth bass population (numbers per ha) in Yampa Canyon through the period of very low density (1990s), onset of population growth (early 2000s) and subsequent fluctuations (blue line). Also shown in their Figure 3 (pink squares), are estimates from field data of smallmouth bass density in Yampa Canyon (Modde et al. 2006). To reproduce this figure using the population projection tool, click the View option on the bottom right hand corner of the projection form. The form that pops-up provides users access to previously saved parameter values.

Each set of saved parameter values includes a name, date and notes. The Save feature, on the projection form, was used to save these sets of parameter values (see section Other Options for more details). Use the Move To option on the bottom of this form to select the set of parameter values named HM07_Figure_3 and then click Apply.
Be patient as the projection tool transfers all of the saved parameter values (309 values) from the saved parameters form to the projection form. The small black and red \textit{Processing} form will close when the task has been completed.

Once the processing form closes, close the saved parameters form and spend a few minutes reviewing the parameter values under the tabs on the projection form. Your goal at this point is to become familiar with the projection form and parameters, full disclosure of each parameter is provided in the \textbf{Options} sections below (one section for each tab). Note, for example, that Haines and Modde (2007) integrated an environmental covariate (environ.) into their stock-recruitment function, \textit{Mean June Flow (cfs)}. The mean, standard deviation and effect size ($c$) used by Haines and Modde (2007) for \textit{Mean June Flow} are also integrated and can be revised by the user.

When you're done reviewing the parameter values, select the \textbf{Run} tab and then click the option \textit{Project Population to Zero (P0)}. This option terminates each replicate projection when the population declines to zero density \textit{or} the projection reaches the end of the time-steps requested by the user under the \textbf{Simulation} tab. Review your request and then click \textit{Yes} to initiate the projection which will consist of 10 replicas each projected over 25 time-steps. The small black
and red form will inform you of progress, the following figure\(^3\) opens automatically when the projection has completed.

![Graph showing fish density over time](image)

By clicking the *Show 1993-2006 Yampa Canyon Density Estimates* option (not shown above) the user can add black triangles (equivalent to pink squares used by Haines and Modde 2007, Figure 3) representing estimates from field data of smallmouth bass density in Yampa Canyon (Modde *et al.* 2006).

![Graph with added triangles](image)

Given that each projection will be unique, and plots are averages at each time-step from all replicas, plots produced by the projection tool will not exactly match Figure 3 from Haines and Modde (2007) but they'll be very similar. Note, also, that Haines and Modde (2007) based their Figures 3-4 on single projections (not averages of projections).

\(^3\) Not shown is a plot summarizing changes in the population growth rate (lambda) over time.
If the plot(s) are closed for any reason, then they can be reopened by clicking on the *Projection Plots* option to the right of *Project Population to Zero* under the **Run** tab.

Users can also use the *Export Results* options to export all projection results or an average of the results over all replicas and time-steps. The *AVG Across Replicas (Figure)* option provides the data used for the Project to Zero plots. Another plotting option is the *Fall & Spring Recruits Plots*. Users can click this option at any time to view the following plots.
Alternatively, they can check the box to the right of the option and this plot will open automatically at the end of a projection. Detailed legends are available by clicking on either plot.

The top plot provides the density of age-0 fish over the summer and age-1 fish (same cohort) in the spring before and after spring exploitation. SR Density (pink line) is the density of age-0 bass provided by the stock-recruitment function, in this case Ricker. Fall Density (yellow line) provides age-0 density after losses due to fall exploitation and other effects that occur after stock-recruitment and before onset of winter (such as random error in recruitment when requested). Spring Density is provided both before and after spring exploitation - they're the same here because Haines and Modde (2007) did not exploit age-1 fish in their population model. The solid blue line and right y-axis in the top plot describes the density of breeder stock.

The lower plot provides post-exploitation spring densities (D) by age (2, 3, 4 and 5-10 combined); D5-10 are plotted on the right y-axis.

The following Diagnostic Plots option were developed for debugging the Visual Basic Code underlying the projection tool but users might also find these plots useful.
Mean spring flow is integrated into the form of the Ricker function implemented by Haines and Modde (2007) — the top left plot confirms that the effect was applied in the projection. Depensation mortality and random error in recruitment, other features of the Haines and Modde (2007) population model, were also integrated as is confirmed in the top right and bottom left plots, respectively. The bottom right plot shows the relationship between recruitment and stock, note the consistency with the Ricker stock-recruitment function. These diagnostics demonstrate that the model is performing as expected.

Close any pop-up forms (plots, etc) that remain open, and click the View option. This time choose **HM_07_Figure_4** from the Move To option and then click Apply. Once the parameter values have been applied, close the pop-up form and click Project Population to Zero. For this projection, we'll project 10 replicas out to 50 time-steps and deploy the Ricker stock-recruitment function. Here is an example set of results.
Compare the projection results to the top projection (blue line) from Haines and Modde (2007), this projection deployed the Ricker stock-recruitment function (Ricker 85). Recall that Haines and Modde (2007) based these projection results on a single replica (not averages of replicas), hence the projection tool results are dampened (by averaging over replicas we removed variation inherent in individual projections) relative to the plot from Haines and Modde (2007). The purpose of this seminal plot from Haines and Modde (2007) was to project, based on their population model, smallmouth bass over 50 years in the absence of exploitation by electrofishing or any other method available to managers.

Close any pop-up forms (plots, etc.) that remain open, and click the View option. This time choose HM_07_Figure_5 from the Move To option and then click Apply. Once the
parameter values have been applied, close the pop-up form and click *Project Population To Management Goal* under the **Run** tab. For this projection, the management goal will be 4.2 sub-adult and adult bass/ha (equivalent to 20/rmi in Yampa Canyon⁴), we'll project 10 replicas out to 100 time-steps each and deploy the Ricker stock-recruitment function. In addition, we'll vary the spring exploitation rate, a management parameter, between 0.45 and 0.85 incrementing by 0.05 units. Here is an example set of results.

And the same plot from Haines and Modde (2007).

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⁴ To translate this into, e.g., fish/rmi, use the *Convert* option on the bottom left-hand side of the projection form. To convert from fish/ha to fish/rmi you'll need to provide reach ha/rkm.
The predictions are very similar but not identical because they're based on different sets of projection results. Despite this variation, both plots suggest, based on the population model proposed by Haines and Modde (2007) that included the Ricker stock-recruitment function (Ricker 85, blue line), that at an exploitation rate of 60% the management goal (4.2 sub-adult and adult bass/ha, 20/rmi) would be achieved in Yampa Canyon in just under 20 years.

**Breton et al. (2015).** In their prospective assessment of smallmouth bass dynamics in the upper Colorado River basin, Breton et al. (2015) used the projection tool to specify a baseline population model for Little Yampa Canyon and then run a suite of projections to judge the sensitivity of projected smallmouth bass abundances to changes in certain demographic parameters (e.g., adult survival) and the relative effectiveness of a set of management scenarios for reducing bass numbers in this reach. Their baseline population model and parameter values can easily be loaded onto the projection form using the View option. The form that pops-up provides users access to saved parameter values. Use the Move To option on the bottom of this form to select the set of parameter values named **LYC_2010_Baseline** and then click Apply. Be patient as the projection tool transfers all of the saved parameter values (309 values) from the saved parameters form to the (tabbed) projection form. The small black and red Processing form will close when the task has been completed.

Once the processing form closes, close the saved parameters form and return to the projection form. Select the Run tab and then click the option **Project Population to Zero (P0)**. This option terminates each replicate projection when the population declines to zero density or the projection reaches the end of the time-steps requested by the user. Review your request and then click Yes to initiate the projection which will consist of 5 replicas each projected over 50 time-steps. Note, in the projection report 50 replicas over 50 time-steps were conducted for each
projection; 5 is used in place of 50 in this user manual to save users time but they can always change number of replicates (and time-steps) on their own under the Simulation tab. The small black and red form will inform you of progress, the following Figure opens automatically when the projection has completed.

The results closely resemble Figure 4 from Breton et al. (2015).

Both plots provide estimated density per ha of sub-adult and adult smallmouth bass (*Micropterus dolomieu*) in Little Yampa Canyon, points along the line are averages at each time-step from the 5 (top plot) or 50 (lower plot) projections.

Much of analysis reported by Breton et al. (2015) made use of the projection tool's Decrement option.
The idea is to specify a range for a parameter, such as the proportion of adults that breed, and then repeat the projection across this range while maintaining all other aspects of the population model constant. Here are the results of this process for the proportion of adults that breed from Breton et al. (2015; Figure 5).

As this plot implies, Breton et al. (2015) varied the proportion that breed from 0-1, the full range of the parameter. At the lowest value, 0.0, there were just over 4 sub-adults and adults/ha (44/rmi, 27/rkm<sup>5</sup>) on average in Little Yampa Canyon over 50 time-steps (years). At the other extreme, all adults breed, this number increased to 11/ha (120/rmi, 75/rkm). Baseline condition (proportion of adults that breed set to 0.75; Breton et al. 2015) is shown by the dashed line.

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<sup>5</sup> Use the Convert tool on the bottom left-hand side of the projection form to convert from fish/ha to fish/rmi and fish/rkm. Set ha/rkm to 6.8 (Little Yampa Canyon) and then change fish/ha from 4.2 (default) to 4 and press the tab or enter key.
The steps for reproducing this figure are the same for all parameters. If necessary, re-apply the baseline model parameter values (LYC_2010_Baseline) used by Breton et al. (2015) as described above. Next, click on the Recruitment tab and find the Proportion of Potential Breeder Stock that Breed (BP) parameter. Set this to the highest value to be considered by the decrement procedure, in this case we'll set it to 1.0 consistent with Breton et al. (2015). Now click the Decrement tab. Under the label Decrement Parameter? check the box to identify to the projection tool that you want to decrement a parameter.

Next, click the Choose Parameter option and click the box to the right of Proportion of Breeder Stock that Breed.

Close the pop-up form. Lastly, we'll Set Analysis Parameters. If the default parameters were left as-is, Decrementing By 25% Down To 0%, then five sets of projection results would be
calculated, a set with the proportion that breed at 1, 0.75 (baseline), 0.50, 0.25 and 0. To produce the figure shown above, Breton et al. (2015) decremented by 5% intervals down to 0. Intuitively, these parameters will affect projection run time. With this in mind, consider maintaining the default Decrement By to 25 and Down To to 0 for now (you can always run it later with any specifications you desire). Now click the P0 option near the bottom right of the projection form, a convenience that is equivalent to clicking the Run tab and then Project Population to Zero. By clicking Yes to the message that pops-up, you'll be requesting 5 replicas per level of the decremented parameter, each replica will be projected out to 50 years. The Processing form will keep the user informed of progress, please be patient. For example,

at this stage the projection tool is on the 4th replicate and 43rd time-step with breeding proportion (BP) set to 25% of the maximum value (1.0).

Here are the results of the projection (Decrement Plot).
Average sub-adult and adult density (fish/ha) across replicas for each time-step and breeder proportion are provided. The light blue line provides average sub-adult and adult density under baseline conditions (breeding proportion 0.75). Increasing the proportion of adults that breed to 100% (1.0) increases the population size relative to baseline; decrementing to 50%, 25% and 0% results in reductions relative to baseline. This convenient summary, and the decrement feature in general, was designed to help managers estimate the effect of management actions, such as reducing the proportion of adults that breed.

The inset plots shown in Figure 5 from Breton et al. (2015) are not available from the projection tool. To reproduce these, close the figure shown above, click the Run tab and then Export Results: AVG Across Replicates (Figure).

In your preferred graphing software, plot the average ha_density or RM_Density (your choice) across time-steps (t) for each Parameter_Value (1, 0.75, 0.50, 0.25, 0 in this example). That’ll produce something that looks similar to the following plot without the baseline (dashed) line.

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6 The plot can always be reopened by clicking the Decrement Plot option closest to Project Population to Zero under the Run tab.
Multiple Projections in a Single Plot. Breton et al. (2015) reported densities of sub-adult and adult smallmouth bass per river mile of (average of 50 replicates) 74, 61 and 50 when 20% of cohort one nests were disturbed and spring exploitation was increased by 10, 20 and 30%, respectively, over baseline. These surge simulations produced some of lowest densities of bass in their analysis (Breton et al. 2015). Although they chose to report averages (74, 61 and 50), they could have combined projections from each spring exploitation scenario into a single plot, and the resulting plot would have been very similar to the breeding proportion plot that was automatically outputted (above) using the decrement feature. In this example, we'll demonstrate the Mult. Proj. Plot, Store Projections, and Purge options.

If necessary, re-apply the baseline model parameter values (LYC_2010_Baseline) used by Breton et al. (2015) as described above. Next, check the Store Projections box under the Run tab, a message informs the user that all previously stored projection results have been purged (deleted). Now we're ready to set up our first population model and project sub-adult and adult densities out to 50 time-steps. Under the Recruitment tab find the Proportion of Nests Disturbed. Below this option, locate the proportion that is specific for Cohort 1, the earliest hatching nests in the population (Breton et al. 2015). Change the default value from 0 to 0.20 (equivalent to 20%).
Next, we want to increase spring exploitation by 10%. In a moment, we'll repeat our steps and increase spring exploitation by 20% and 30% and then combine all three sets of projection results in a single plot. To increase spring exploitation by 10%, click on the Density tab and locate the Rate Adjustment (Spring) option (see red arrow below).

The default rate is 1, which is equivalent to 100% of the exploitation rates shown in the last column (labeled Exploit?). Note that each age-class has its own (user-specified) exploitation rate. To increase these baseline rates by 10%, all we need to do is change the Rate Adjustment (Spring) option from 1 to 1.10. Alternatively, users could manually increase all exploitation rates in the Exploit? column by 10%, but that would get tedious. All of the Rate Adjustment options under this tab were implemented to make percentage adjustments to baseline densities (starting densities, spring immigrants, spring emigrants) and exploitation rates easy to apply.

Now click the P0 option near the bottom right of the projection form, a convenience that is equivalent to clicking the Run tab and then Project Population to Zero. By clicking Yes to the message that pops-up, you'll be requesting 50 replicas, each replica will be projected out to 50
years. The *Processing* form will keep the user informed of progress, please be patient. For example,

![Replicate 4 of 50, Timestep 30...](image)

at this stage the projection tool is on the 4th replicate out of 50 and 30th time-step. Here are the results of the projection provided by the projection tool.

![Population Projection To Zero Density: Plot Multiple Projections](image)

As always, what we see here is the average across replicas calculated for each time-step. Recall that this initial projection was based on 20% nest disturbance of cohort 1 and a 10% increase in spring exploitation over baseline conditions (Breton *et al.* 2015).

Close the plot\(^7\) and then change the *Rate Adjustment (Spring)* option from 1.10 to 1.20. This scenario provides a spring exploitation rate that is 20% over baseline. Note, exploitation rate for each age-class is not allowed to exceed 1 regardless of the value set by the user in the

\(^7\) The plot can always be reopened by clicking the *Mult. Proj. Plot* option under the *Run* tab.
Rate Adjustment (Spring) and Rate Adjustment (Fall)\(^8\) options. Now click the \(P0\) option near the bottom right of the projection form, here is the Mult. Proj. Plot that pops-up at the end of the projection.

As soon as more than one projection has been saved, a legend appears on the top of the figure.

The blue line labeled #1 is the first projection that we ran, exploitation at 10% over baseline. The pink line, labeled #2, is the 20% spring exploitation scenario. Given all of the possible scenarios that a user might combine in a single plot it wouldn't be practical to make the legend more detailed. We suggest that users keep a record of the projections that they run and number them 1, 2, 3 ... etc.

We'll add one more series to this plot. Close the plot\(^9\) and then change the Rate Adjustment (Spring) option from 1.20 to 1.30. This scenario provides a spring exploitation rate

\(^8\) When requested by the user, spring exploitation affects age 1+ fish and fall exploitation affects age-0 fish.

\(^9\) The plot can always be reopened by clicking the Mult. Proj. Plot option under the Run tab.
30% over baseline. Click the P0 option near the bottom right of the projection form, here is the plot that pops-up at the end of the projection.

![Population Projection To Zero Density Plot Multiple Projections](image)

The final plot, based on averages across replicas and time-steps for three population models (or scenarios), provides a very convenient summary for informing managers. To produce the averages for the three scenarios (74, 61 and 50 sub-adults and adults/rmi) reported by Breton et al. (2015), click the Run tab and then the Export Results: AVG Across Replicas option below Project Population to Zero. In your preferred spreadsheet, take the average over all time-steps from the output for each projection (they'll be numbered just like the legend).

A nice extension would be to add a fourth series to this plot, one that predicts sub-adult and adult densities under baseline exploitation rates (Breton et al. 2015). Close the plot and return to the Density tab, return Rate Adjustment (Spring) to its default value, 1.0. Now re-run the projection.
The series labeled #4 (light blue line) provides predicted sub-adult and adult density/ha at baseline exploitation rates (those shown in the column labeled *Exploit?* under the **Density** tab).

Let's say we forgot to change the baseline exploitation rate, and the result was two identical series #3 and #4? We could salvage our mistake by clicking the **Run** tab and **Export Results: All Replicates** under **Project Population to Zero**. Scroll through the list, find the **Projection Number** that you want to delete, and delete all rows that include this reference number. Once deleted, a new (correct) series could be projected. Alternatively, your mistake might require that you start from the beginning. In this case, click the **Purge** option to the right of **Store Projections** under the **Run** tab. Of course, you could also open the **All Results** spreadsheet and delete every record, it's your choice.

**Projection, Plotting, and Export Options.** There are two projection options, **Project to Zero** (P0) and **Project to Management Goal** (PMG). Associated with each of these are a set of plots and options for exporting results of the projections. The **Project to Zero** option also allows users to combine projections (as series) in a single plot using the **Store Projection(s)** option.
**Project to Zero (P0) or End of Time-steps.** The option to **Project to Zero** terminates the projection either when the projection completes the number of time-steps requested by the user (set under the **Simulation** tab) or the population goes extinct. Users can initiate a **Project to Zero** simulation by either clicking the option under the **Run** tab or by clicking the **P0** option to the bottom right hand side of the projection form, this convenient option is always accessible despite which tab has focus. Here are the options associated with the **Project to Zero** option under the **Run** tab.

To the right of the **Project Population to Zero** option is a button labeled with a question mark. Click on this option to review the projection steps that are carried-out when the user requests to **Project Population to Zero** (or end of time steps, whichever comes first). This feature also sets focus to the **Fall & Winter Model** tab. This is a reminder to users that projection steps and other projection details are summarized under the **Spring & Summer Model**, **Fall & Winter Model**, and **Events Timeline** tabs.

Below the **Project Population to Zero** option are two options for exporting results of a projection(s) in spreadsheet format. As their labels imply, the **Export Results: All Replicates** provides the data from all replicates and time-steps. The **Export Results: AVG Across Replicates (Figure)** option provides the data from all time-steps after averaging across replicates. If only one replicate is projected, then the two export options will give identical results. The **AVG Results** option provides the data underlying many of the figures associated with the **Project to**
**Zero** option. Use the External Data > Export on the Microsoft Access Menu to export these data to Microsoft Excel and other formats.

Results of a single projection with no decrementing (more below) are conveniently summarized (including population growth rate) by the *Projection Plots* option.

Typically, this is the default plot that opens whenever a **Project to Zero** projection is run and neither the *Store Projections* nor *Decrement* options have been selected. By clicking the
unlabeled check-box to the right of the option *Fall & Spring Recruits Plots* users can select this plot as the default over the (less detail) *Projection Plots*.

Detailed legends for the *Fall & Spring Recruits Plots* are available by clicking on either plot.

The *Mult. Proj. Plot* option is used in combination with the *Store Projection* and *Purge* options. When users want to combine results from multiple (mult.) projections (proj.) into a single plot they should start by checking the *Store Projections* box. The projection tool will respond by erasing all previous projection results. All subsequent projections will be numbered sequentially, starting at #1, and each will be stored so that they can be added as series to the *Mult. Proj. Plot*. Here is an example where the interest was the effect of reducing, through
management, immigration on the density of sub-adult and adult smallmouth bass. The light blue line provides densities under baseline conditions for the population model used to produce the projections. When immigration was reduced to zero (dark blue line), the projected population went extinct in about 21 years.

One more example, managers asked what benefits might they expect from an increase in removal (exploitation) rates?
Predictions from the baseline population model are provided by the dark blue line. Percentages refer to increases, over baseline, in the exploitation rate of sub-adult and adult smallmouth bass. A 30% increase in exploitation results in about a 50% reduction in the number of sub-adult and adult bass in the population projections.

Whenever users check the Store Projections option the Mult. Proj. Plot will be the default plot (opens automatically following a projection). Note, the Projection Plots option will always plot the series with the lowest reference number, it will not plot all series in the cue when the Store Projections option has been selected.

The option labeled Diagnostic Plots were developed for debugging purposes.

The projection tool, despite its appearance as a Microsoft Access form, it driven by over 4,000 lines of Visual Basic Code that are hidden from the user. The diagnostic plots were developed to debug parts of this code. Nonetheless, users might find the plots useful, e.g., the lower right plot
can be used to demonstrate the relationship between recruitment and stock under different stock-recruitment functions (Beverton-Holt, Ricker). Note, the Diagnostic Plots option will always plot the projection series with the lowest number, it will not plot all series in the cue when the Store Projections option has been selected.

The Decrement Plot is the default plot whenever the Decrement option (Decrement tab) is selected by the user. Users should avoid other plotting options when the Decrement option has been selected. Details on how to use the Decrement option are provided in the next section.

Adding Decrement Option to P0. The idea is to specify a range for a parameter, such as the proportion of adults that breed, and then repeat the projection across this range while maintaining all other aspects of the population model constant. This procedure was used to produce all of the results in Figures 5-6 in Breton et al. (2015). We'll assume that the user has specified their population model, i.e., provided values for all demographic and management parameters under the tabs on the projection form. Next, we'll assume that they're interested in estimating the sensitivity of projected densities to the proportion of adults that breed. Click on the Recruitment tab and find the Proportion of Potential Breeder Stock that Breed (BP) parameter. Set this to the highest value allowed for this parameter, 1.0, we'll decrement the parameter from 1 to 0 in a moment. Now click the Decrement tab. Under the label Decrement Parameter? check the box to identify to the projection tool that you want to decrement a parameter. Next, click the Choose Parameter option and click the box to the right of Proportion of Breeder Stock that Breed.
This form will only allow you to select one parameter at a time, i.e., you cannot decrement >1 parameter simultaneously. Close the pop-up form. Lastly, we'll Set Analysis Parameters. By **Decrementing By 25% Down To 0%** we'll build five sets of projection results, a set with the proportion that breed at 1, 0.75, 0.50, 0.25 and 0. Now click the **P0** option. By clicking **Yes** to the message that pops-up, you'll be requesting $j$ replicas per level of the decremented parameter, each replica will be projected out to $i$ time-steps (the user specifies $i$ and $j$). The **Processing** form will keep the user informed of progress. For example,

![Project Population & Decrement Parameter (Parameter, Percentage): BP, 25](image)

at this stage the projection tool is on the 4$^\text{th}$ replicate and 43$^\text{rd}$ time-step with breeding proportion (BP) set to 25% of the maximum value (1.0).

Here are the results in the **Decrement Plot**.
Average sub-adult and adult density (fish/ha) across replicas for each time-step and breeder proportion are provided. This convenient summary, and the decrement feature in general, was designed to help managers estimate the effect of management actions, such as reducing the proportion of adults that breed.

**Project to Management Goal (PMG).** Rather than project to zero this projection option projects to the number of years required to reach the management goal set by the user. Note that the number of time-steps specified by the user (see Simulation tab) still affect this projection option. If the management goal is not reached within the user-specified time-steps then no prediction will be made and part of the resulting Projection Plot or Decrement Plot will be blank. Keep this in mind when specifying the number of time-steps for Project to Management Goal analyses.

Users can initiate a Project to Management Goal simulation by either clicking the option under the Run tab or by clicking the PMG option to the bottom right hand side of the projection form, this convenient option is always accessible despite which tab has focus. Here are the options associated with the Project to Management Goal option under the Run tab.
To the right of the *Project Population to Management Goal* option is a button labeled with a question mark. Click on this option to review the projection steps that are carried-out when the user requests to *Project Population to Management Goal*. This feature also sets focus to the **Fall & Winter Model** tab. This is a reminder to users that projections steps and other projection details are summarized under the **Spring & Summer Model**, **Fall & Winter Model**, and **Events Timeline** tabs.

Below the *Project Population to Management Goal* option are two options for exporting results of a projection(s) in spreadsheet format. As their labels imply, the **Export Results: All Replicates** provides the data from all replicates and time-steps. The **Export Results: AVG Across Replicates (Figure)** option provides the data from all time-steps after averaging across replicates. If only one replicate is projected, then the two export options will give identical results. The **AVG Results** option provides the data underlying many of the figures associated with the *Project to Management Goal* option. Use the External Data > Export on the Microsoft Access Menu to export these data to Microsoft Excel and other formats.
Results of a single projection with no decrementing (more below) are conveniently summarized by the *Projection Plot* option.

This is the default plot that opens whenever a **Project to Management Goal** projection is run when the *Decrement* option has not been selected. Note that the management goal set by the user is included with other information about the population model across the top of the form.
The *Decrement Plot* is the default plot whenever the *Decrement* option (Decrement tab) is selected by the user. Users should avoid other plotting options when the *Decrement* option has been selected. Details on how to use the *Decrement* option are provided in the next section.

**Adding Decrement Option to PMG.** The idea is to specify a range for a parameter, such as the proportion of adults that breed, and then repeat the projection across this range while maintaining all other aspects of the population model constant. This procedure was used to produce all of the results in Figures 5-6 in Breton *et al.* (2015). We'll assume that the user has specified their population model, i.e., provided values for all demographic and management parameters under the tabs on the projection form. Next, we'll assume that they're interested in estimating the sensitivity of projected densities to the proportion of adults that breed. Click on the Recruitment tab and find the *Proportion of Potential Breeder Stock that Breed (BP)* parameter. Set this to the highest value allowed for this parameter, 1.0, we'll decrement the parameter from 1 to 0 in a moment. Now click the Decrement tab. Under the label *Decrement Parameter?* check the box to identify to the projection tool that you want to decrement a parameter. Next, click the Choose Parameter option and click the box to the right of *Proportion of Breeder Stock that Breed.*
This form will only allow you to select one parameter at a time, i.e., you cannot decrement >1 parameter simultaneously. Close the pop-up form. Lastly, we'll Set Analysis Parameters. By Decrementing By 25% Down To 0% we'll build five sets of projection results, a set with the proportion that breed at 1, 0.75, 0.50, 0.25 and 0. Now click the PMG option. By clicking Yes to the message that pops-up, you'll be requesting $j$ replicas per level of the decremented parameter, each replica will be projected out to $i$ time-steps or the point at which the management goal has been met (the user specifies $i$ and $j$). The Processing form will keep the user informed of progress. For example,

![Projection Tool](image)

at this stage the projection tool is on the 4th replicate and 43rd time-step with breeding proportion (BP) set to 25% of the maximum value (1.0).

Here are the results using the population model from Figure 5, Haines and Modde (2007), in the **Project to Management Goal Decrement Plot**.
The number of years to reach the management goal of 4.2 sub-adult and adult bass/ha are provided for each level of breeding proportion (1, 0.75, 0.5, 0.25, 0) and each exploitation rate requested by the user. This convenient summary, and the decrement feature in general, was designed to help managers estimate the effect of management actions, in this case on the number of years that it may take to reach a specific management goal.

Here's another example of the decrement feature combined with the Project to Management Goal option.

The interest in this plot is the effect of different levels of nest disturbance on the estimated years to reach a management goal of 4.2 sub-adult and adult fish/ha. When 0% of nests are disturbed (dark blue line), exploitation rates below 40% failed to drive the population to 4.2 fish/ha even after 80 years (hence no blue line below 40% exploitation). As nest disturbance is increased, lower exploitation rates are effective but years to reach the management goal are often above 50. Let's say that a feasible exploitation rate might be 35%, dashed lines highlight two scenarios that
might be useful to managers. At 25% nest disturbance and 35% exploitation, the management goal might be reached in 30 years. However, increase nest disturbance to 50% and years to management declines to nine. Many more insights could be extracted from this and similar decrement plots.

Decrement Options. Details are provided above, to apply the decrement feature to Project to Zero projections go to section Adding Decrement Option to P0; for application to Project to Management Goal projections go to section Adding Decrement Option to PMG.

Recruitment Options. Here users encounter various formulae and parameters for specifying the stock-recruitment component of their population model. Users should begin by choosing a stock-recruitment function.

Note that users can decline a density-dependent stock-recruitment option by unchecking the box directly to the left of the combo box.

Otherwise, choose one of the two stock-recruitment functions (Ricker, Beverton-Holt) and up to three arguments (biomass or stock, fecundity, environment). Users also set values for the alpha and beta parameters, if the Ricker model is selected then K (carrying capacity) will be automatically calculated. Formulae at the bottom of the recruitment options are updated each time the user makes a selection from the list of stock-recruitment functions.
Users can click on the formula, a small pop-up will provide reference source and other details.

New users should start by clicking the Info option (right of Formulae label), this options provides definitions for $R'_t$, $P_t$ and $R_t$ among other details.

Associated with the stock-recruitment function are Plotting Options that will be helpful for visualizing the form of the stock-recruitment function specified by the user-provided alpha and beta parameters. For example, choose the Ricker (Stock) function and set alpha to 6.98 and beta to 0.04, the values integrated in the baseline model used by Breton et al. (2015). Under Plotting Options set the Max Stock Size/ha to 100 and then click Plot.

This feature also allows users to combine stock-recruitment functions into a single plot (similar to the mult. proj. plot option described above). To access this feature, check the Store option.
Then click *Plot*. Close the plot, change alpha from 6.98 to 7.98 and click *Plot* again.

![Graph showing stock-recruitment relationship](image)

Each series is given a sequential number in the legend, series #1 alpha was 6.98 and series #2 alpha was 7.98. Users should keep notes on the different parameter values associated with each series. Click the *Data* option to gain access to the stock-recruitment predictions, *View* opens the plot and the data simultaneously, use *Purge* to delete stored data. When plotting just a single series, users should ignore the legend (if shown). A *Spring Flow Differential* can be set when stock-recruitment functions include the *Environ* argument. Click on this option (label) to view more details.

The biomass and fecundity arguments are always combined, these provide an alternative to using stock in the stock-recruitment function, such as was used by Haines and Modde (2007). Biomass is calculated using stock size and the length/weight conversion formula and parameters shown under the *Density* tab.

![Length to Weight Conversion Formula and Parameters](image)

Length and weight have been calculated for many of the reaches in the upper Colorado River
basin. A pop-up message provides all necessary details (source, data) after users select a reach.

For example, if the user selects Yampa Canyon-HM07 the following message pops-up.

![Pop-up message showing source information](image)

Fecundity is set by the user.

![Fecundity input field](image)

Users can click on the $F$ to the right of the fecundity text box to recall details of this parameter.

![Fecundity details](image)

As should be clear by now, whenever questions arise about a parameter or equation users can typically access information by clicking on a button or a label.

The $Environment$ (Environ.) argument can integrate up to two environmental covariates, mean flow (cfs) and water temperature (C) in June. To select an environmental covariate check the box to the left of the option, such as is shown here for $Mean$ $June$ $Flow$. 
These options will have no effect on the projection unless the stock-recruitment option selected by the user includes the *environ* argument. The same is true for *Fecundity*, etc. As elsewhere, data for specific reaches may have already been calculated, information is provided when users select a reach or when they click the buttons to the right of each text box (e.g., \( \begin{bmatrix} 7233 \\ \end{bmatrix} \)).

Users can also request to *Use Historical Yampa Canyon (YC) Flow Data* (see red arrow above) by checking the box to the left of the label. The *Data* option associated with this feature provides the source of the data and a summary in spreadsheet format\(^{10}\).

As with other recruitment options, users can select *Random Variation in Recruitment* by checking the box to the left of the text box associated with this parameter.

The button to the right of the text box provides all necessary details.

And the same is true for *Depensation*,

\(^{10}\) Data can be added to this historical summary, please inquire with the database manager.
which specifies losses due to cannibalism at low population densities. Users can click on the \( M, c \) and \( e \) parameter labels to remind themselves of the definitions of each of these parameters. \( P_t \), at the bottom of the form, provides the depensation equation applied by the projection tool when requested.

\[
P_t = \frac{McR_t^t}{(e + R_t^t)}
\]

Parameters associated with the *Proportion of Nests Disturbed* vary according to selections made under the **Survival** tab. The *Cohort*-specific options are only available when users choose the *Bestgen & Shuter Cohorts* option for age-0 fish — see the **Survival Options** section for more details.

Each text box works the same way, values should be proportions of nests disturbed (destroyed) so should be between 0 and 1. For example, to disturb 20% of nests on each time-step in a projection involving just one cohort.

In a projection where age-0 recruits have been partitioned into cohorts\(^{11}\) of early, middle and late season nests, the following parameterization would disturb 10% of each cohort at each time-step.

The *Proportion of Breeder Stock that Breed* is also a proportion so should take values between 0 and 1.

---

\(^{11}\) *Bestgen & Shuter Cohorts* option for age-0 fish must be selected under the **Survival** tab.
For example, to reduce the breeder stock by half on each time-step set the value in the text box to 0.5.

And click on the BP label to access information about this parameter.

By clicking on labels, column headings and buttons, throughout the projection form (all tabs), users can conveniently access descriptions of parameters, formulae and other helpful information.

**Survival Options.** In this version of the projection tool, users can specify the mean of the over-summer survival probabilities.

At each time-step, these means will be applied, without variation (i.e., as constant rates). In future versions of the projection tool, users may be able to request random variation in these parameters, such as was implemented by Peterson and Kwak (1999) for many of their over-winter survival probabilities. Over-summer survival parameters are abbreviated $S$ (survival) followed by $e$ (egg), $f$ (fry), $0-3$ (age 0-3) and $a$ (adult). Users should think carefully about the
product of the stock-recruitment function and $Se$, $Sf$ and $S0$ over-summer survival probabilities. If, e.g., the user visualizes the stock-recruitment function as producing age-0 fish as a function of environmental covariates then it might not make sense to apply mortality to egg and fry through $Se$ and $Sf$. In this case, the user should leave $Se$ and $Sf$ set at one (no mortality).

For all but the adult age-class, many more options are available for specifying the over-winter survival components of the user’s population model.

![Table of winter survival options](image)

Users can only select a constant adult ($Sa$) rate for all time-steps. Three options are available for ages 1-3 over-winter survival ($S1$, $S2$, $S3$): constant; PK 99 random; and time-varying. Users make their selection by clicking on the box just below the column label. For example, to choose PK 99 Random for age-3.

![Options for age-3](image)

This option specifies a distribution based on the mean and standard deviation ($sd$) provided by the user, and then at each time-step draws a random value from this distribution as the survival probability. This feature of the projection tool has its origins in Peterson and Kwak (1999). The time varying option allows users the ability to specify annual survival rates over a 50 year period. When this option is selected for any of the over-winter parameters, users should limit their projections to 50 time-steps (years). When users click the time varying option the following form pops up.
Scroll down to view all 50 rows, one row for each time-step. Intuitively, since ages 0-3 all include the *time varying* option, there are columns labeled *S0*-S3 on this form. Users can modify all of the probabilities on this form, however they'll only be applied to an age class (0-3) when the *time varying* option is selection. For example, to apply this option to age-3 over-winter survival.

Using the time varying option, managers could implement effects of management actions that, e.g., lowered age-0, -1, -2 or -3 survival every other year or every five years. Many other scenarios could be imagined.

Two unique options are available for the age-0 over-winter survival parameter (*S0*): HM 07; and *Bestgen & Shuter Cohorts*. The *HM 07* option comes from Haines and Modde (2007). When users select this option, *S0* will be affected by the coefficient of variation (CV) of winter flow, an environmental covariate, through the logit link function. The CV and its standard

<table>
<thead>
<tr>
<th>Time step</th>
<th>S0</th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
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</tr>
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<td>0.25</td>
<td>0.66</td>
<td>0.9</td>
</tr>
<tr>
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<td>0.25</td>
<td>0.66</td>
<td>0.9</td>
</tr>
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<td>0.66</td>
<td>0.9</td>
</tr>
<tr>
<td>5</td>
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<td>0.25</td>
<td>0.66</td>
<td>0.9</td>
</tr>
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<td>0.66</td>
<td>0.9</td>
</tr>
<tr>
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<td>0.66</td>
<td>0.9</td>
</tr>
<tr>
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<td>0.9</td>
</tr>
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<td>0.9</td>
</tr>
<tr>
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<tr>
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<td>0.66</td>
<td>0.9</td>
</tr>
<tr>
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<td>0.7</td>
<td>0.25</td>
<td>0.66</td>
<td>0.9</td>
</tr>
</tbody>
</table>

*The SAVE feature on the main form will not save parameters on this form.*
deviation can be manipulated by users under *Distributions including Random Variation in Survival*.

CV and *sd* Estimates from Haines and Modde (2007) are provided when users select *Yampa Canyon-HM07*. In this version of the projection tool, this environmental effect has not been estimated for any other reach or updated for Yampa Canyon (*Yampa Canyon-new*). The *Logit* option below the column label *Visualize Effect Size* can be used to explore the relationship between age-0 over-winter survival and the CV of winter flow.

The last over-winter survival option, *Bestgen & Shuter Cohorts*, is described in some detail in Breton *et al.* (2015) including all of the equations mentioned below. Only details that are needed for implementation in the projection tool will be provided here. When a user selects this option for age-0 fish (does not apply to any other age class) the following message pops-up.
As described in this pop-up, the *Bestgen & Shuter Cohorts* option begins by splitting recruits from whatever stock-recruitment function was selected under the **Recruitment** tab into three equally sized cohorts representing age-0 fish from nests initiated early, middle and late season. The idea is that age-0 fish from the earliest nests will attain a greater length and mass prior to onset of winter with positive consequences for their over-winter survival.

After splitting recruitment into three cohorts, using equations from Bestgen *et al.* (*unpubl.*) a mean total length (mm) is estimated for each cohort with standard deviation assumed to be 10 mm (Breton *et al.* 2015). Equations for estimating the mean of each cohort integrate spring and summer environmental conditions through *count of days ≥8000 cfs* between 1 April and 30 September and *mean water temp C* between 1 July and 15 August. These covariates have been estimated for several reaches in the upper basin and can be modified by the user under **Distributions including Random Variation in Survival**. For example, options for *count of days ≥8000 cfs*,

after the user makes a selection a pop-up box provides the source of the data for all reaches.
At each time-step, values for these environmental covariates are drawn from normal distributions specified by their mean and standard deviations. Assuming for the moment that no poor condition thresholds have been requested for count of days ≥8000 cfs and mean water temp C under the Threshold tab, then the first random draws from the distributions of these environmental covariates are used to estimates the mean fish length (mm) of each of the three cohorts.

Next, the total fish length (mm) at which 20% (L20) and 80% (L80) of individuals survive is determined from equations provided by Shuter and Post (1990). Their equations integrate number of starvation days from 1 June to 1 June, a proxy of winter severity. Consistent with Shuter and Post (1990), we defined a starvation day as any day with average water temperature ≤10º C. Based on seminal work by Shuter et al. (1980), below 10º C temperate fresh-water species such as smallmouth bass stop feeding, live off of their body reserves, and hence, begin to starve. The mean and standard deviation of Count of Days < 10 C (starvation days) for many reaches in the upper basin can be selected below Distributions including Random Variation in Survival.
Assuming for the moment that no poor condition thresholds have been requested for

*Count of Days < 10 C* under the **Threshold** tab, then the first random draw from the distribution of this environmental covariate is used to estimate the total fish length (mm) at which 20% (L20) and 80% (L80) of individuals survive (see Breton et al. 2015). These probabilities are then applied to each of the three cohort distributions in the following way to determine the number of survivors: all age-0 fish \( \leq \) L20 survive with probability 0.20 and those \( \geq \) L80 survive with probability 0.80; survival probabilities for age-0 fish with total lengths between L20 and L80 are determined by linear interpolation. Rather than determine survival for each length between L20 and L80, average survival is determined for each 10 mm length bin and then applied to the entire bin frequency. The sum, across cohorts, of surviving age-0 fish are then allocated to the age-1 sub-adult component in the spring prior to exploitation by boat-based electrofishing.

Options under the **Thresholds** tab can be used to force environmental conditions to be poor over a proportion of time-steps determined by a probability. This feature begins by setting the **Probability (P) of Poor Environmental Conditions: Spring & Summer, Winter** under the **Threshold** tab.

![Thresholds tab](image)

In this example, the user set the probability of poor environmental conditions in spring, summer and winter to 0.8, under these settings the projection tool will force about 8 out of every 10 time steps to be poor for growth (spring & summer) and survival (winter). The user defines *poor* by providing poor condition thresholds. Those affecting the *Bestgen & Shuter Cohorts* feature are thresholds associate with (spring and summer) *mean water temp C, count of days \( \geq 8000 \text{ cfs} \)* and (winter) *count of days \( < 10 \text{ C} \) (starvation days).*
In the example above, poor conditions in spring and summer are those where mean water temp $C$ and count of days $\geq 8000$ cfs are $\leq 20^\circ C$ and $\geq 25$ days, respectively; and poor conditions in winter are those where count of days $< 10^\circ C$ is $\geq 190$ days.

The Info button under the Thresholds tab describes how the probability of poor conditions and thresholds are combined and applied by the projection tool. A random value between 1 and 10 is drawn and then divided by 10 to arrive at a probability, this is done separately for Spring-Summer and Winter at each time step. These probabilities are compared to the Probability of Poor Environmental Conditions in the Spring, Summer and Winter. When the former probability is less than the latter, then environmental covariates selected under the Threshold tab will be repeatedly drawn from their distributions until the draw is above/below the poor condition thresholds provided by the user. Assuming the user specified 0.8 for both poor condition probabilities,

12 As these text imply, in this version of the projection tool, poor conditions in winter and spring/summer are not correlated.
then about 8 time-steps out of 10 would experience poor environmental conditions in Spring, Summer and Winter.

Motivated by the population models developed by Peterson and Kwak (1999) and Haines and Modde (2007), the last option under the **Survival** tab allows users the option to introduce random variation (error) into the over-winter survival process. Below the column labeled *Apply Random Variation?*, all over-winter age classes (*S*0-*S*a) can be affected. Random variation is applied by drawing a random value from the inverse normal distribution at each time step and then applying this, through multiplication, to survivors. The mean of the distribution is set to 0, the standard deviation of the inverse normal distribution is provided by the user.

![Random Variation in Survival: Es](image)

Error is drawn only one time, not separately for each age class.

**Density Options.** The first eleven rows on this form are specific to an age class. For example, changes made to the following row will only affect projection density (D) of the two-year-old age class.

![Density Options](image)

The **Density** tab, at first glance, may seem overwhelming (many parameters) but most of the options can be ignored once the user determines their preferred fish density metric. *Starting Densities, Spring Immigrants* and *Spring Emigrants* can be entered by the user in *fish/ha*, *fish/rkm*, or *fish/rmi*. Any time the user makes changes to any of these columns the projection tool will update, using equations provided under *Other Formulae*,

\[
\text{fish/rkm} = \text{fish/ha} \times \text{ha/rkm}, \quad \text{fish/rmi} = \text{fish/rkm} \times 1.608344
\]

the other two columns and the column **Totals**.
User must provide the age-specific densities that will be used to initiate the population projections.

<table>
<thead>
<tr>
<th>Age-class</th>
<th>Starting Densities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>fah/ha</td>
</tr>
<tr>
<td>D0, Age-0</td>
<td>0</td>
</tr>
<tr>
<td>D1, Age-1</td>
<td>4.09 5</td>
</tr>
<tr>
<td>D2, Age-2</td>
<td>1.81 3</td>
</tr>
<tr>
<td>D3, Age-3</td>
<td>3.08 6</td>
</tr>
<tr>
<td>D4, Age-4</td>
<td>0.68 6</td>
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<td>D5, Age-5</td>
<td>0.28 0</td>
</tr>
<tr>
<td>D6, Age-6</td>
<td>0.02 0</td>
</tr>
<tr>
<td>D7, Age-7</td>
<td>0.00 1</td>
</tr>
<tr>
<td>D8, Age-8</td>
<td>0.01 0</td>
</tr>
<tr>
<td>D9, Age-9</td>
<td>0.10 0</td>
</tr>
<tr>
<td>D10, Age-10</td>
<td>0.01 7</td>
</tr>
<tr>
<td>Total</td>
<td>11.96 5</td>
</tr>
<tr>
<td>Rate Adjustment</td>
<td>0.75</td>
</tr>
</tbody>
</table>

These starting densities are assumed to be densities after spring exploitation. On the first time step, breeder stock from these starting densities will be used to calculate recruits through the stock-recruitment function selected by the user. On all subsequent time steps, these starting densities will be ignored.

User can use the Rate Adjustment option to make percentage additions or subtractions to starting densities, the default value is one (no adjustment). Changes to the Rate Adjustment will not affect the starting densities shown under the Density tab. However, this adjustment will be applied prior to initiating the projection. By setting, e.g., the Rate Adjustment to 0.75 (as shown above), starting densities would be decreased by 25% before they were integrated into the projection. Set the Rate Adjustment to 1.5 and starting densities would be increased by 50% in the projection.

In order to convert from fish/ha to the other two density metrics (fish/rkm and fish/rmi), users must identify ha/rkm, \[ \text{ha/rkm} = 6.8 \]. When using the Change Starting Density option to set starting densities then this parameter (ha/rkm) will be updated automatically. It's critical that
users understand the relationship between hectares and fish densities and that they specify the correct ha/rkm for their projections. A quick study of the formulae under Other Options should be sufficient for clarifying these relationships and the importance of ha/rkm.

The Change Starting Density option (not available in the stand-alone version of the projection tool) should be a highly valuable aid for managers wishing to project smallmouth bass densities from reaches throughout the upper Colorado River basin.

Smallmouth bass density estimates from Yampa Canyon in 1993 (Haines and Modde 2007) can be applied using the option 1993 YC Densities. This option is provided for historical reasons, the influence of the Haines and Modde (2007) report in the earliest developments of this projection tool. More recently, the Reach-specific Densities option was implemented. This option opens the following form, only the top half of the form is shown below.

On this form the user selects a year and then a reach (or combination of reaches). Once they select a reach the projection tool automatically calculates age-specific starting densities and (if requested) exploitation rates based on a mark-recapture analysis performed by Breton et al. (2014) and field data (removals) provided by Recovery Program collaborators. There are a few limitations and exceptions which are clarified by pop-up messages
as the user navigates this pop-up form. Advanced users of this projection tool will want to familiarize themselves with the text at the bottom of the form (not shown above). Unless users feel comfortable that they understand all of the text, it is not advised that any of the button options provided here be executed.

An example of the **Change Starting Density** option may be helpful. Let's assume the user has selected densities from 2010. Next, they want to insert starting densities from Lily Park. To accomplish this they click on the *Lily Park* option below the *Yampa River Sub-basin* label.

As we've seen elsewhere, a small red and black form keeps the user informed as the request is carried-out. The first step is to allocate each individual bass estimated in the mark-recapture analysis (Breton *et al.* 2014) to an age (size) class.

The lower length for each size class is set by the user, see the column labeled *Lower Bound Length (mm)* under the **Density** tab. Lower length estimates from Little Yampa Canyon and (different dataset) Yampa Canyon can be loaded into this column by selecting the button labeled *LYC* or *YC*, respectively. The source of these lengths are provided after the user clicks on one of the options.

After allocating each bass to an age class,
the Change Density feature next calculates the pre-exploitation density of each age class. As these are calculated, they're transferred to the Starting Density fish/ha column under the Density tab.

Once this step has been completed, the user has the option to also calculate and apply age-specific exploitation rates from the reach and year selected.

Click no at this stage and the procedure is concluded. Otherwise exploitation rates are calculated and applied to the Exploit? column under the Density tab.

After applying exploitation rates, the user is given one more option.
Recall that *Starting Densities* under the **Density** tab are post-exploitation spring densities. If the user is not including spring exploitation in their population model then they'll want to click *no* when this option arises. Otherwise, densities based on the mark-recapture analysis from Breton *et al.* (2014) are pre-exploitation. To adjust them to post-exploitation click *yes* at this juncture. Note, the resulting density estimates will likely be inflated, by a few fish, due to rounding error.

Users can set the density of fish moving into (*Spring Immigrants*) and out-of (*Spring Emigrants*) the population at each time step in the spring prior to spring exploitation (see **Timeline** tab). As with *Starting Densities* described above, immigrant and emigrant densities can be entered as *fish/ha*, *fish/rkm*, or *fish/rmi*, preference is up to the user. Each time the user changes a text box in the column labeled, e.g., *fish/ha*, the other two columns will be automatically updated followed by the column *Totals*. *Rate Adjustments* function the same for immigrants and emigrants as it did for *Starting Densities*. The rate will be used to inflate or deflate the density of emigrants and immigrants at each time step. For example, if the user set the *Rate Adjustment* to 0.5 below *Spring Emigrants* then half of the emigrants indentified under the **Density** tab would be added to the population in the spring at each time-step. The *Rate Adjustment* feature is a convenience that precludes the need to modify each age-specific density to achieve, e.g., a 50% reduction or increase in emigrants. It is advisable to set *Starting*
Densities, Spring Immigrants, and Spring Emigrants to some baseline level and then use the Rate Adjustments to specify other population models. The Store Projections option is very useful in this context.

Lower Bound Length (mm) is described above along with the Change Starting Density option. Users can check/uncheck boxes in the Breeder Stock column to specify which age-specific components of the population contribute to the breeder stock. Another way to affect the breeder stock is by the 50/50 Length check box below Other Options.

This option is convenient if only a portion of an age class is considered breeder stock. For example, in the population model specified by Breton et al. (2015), the lower bound of their age-3 class was ≥171 mm and upper bound <246 mm. From this age class, they provided evidence that fish 200 mm and above were likely breeder stock. To accommodate this scenario in the projection tool, users would identify age-3 as breeder stock (check the box in this row) and set the 50/50 Length to 200 mm. The projection tool would allocate only those fish, in any age class, that were ≥200 mm to the breeder stock.

Any age class can be exploited, users identify which age class(es) they want to exploit by checking/unchecked boxes under the label Exploit?. These age classes will be exploited in both Project Population to Zero and Project Population to Management Goal simulations. When the Exploit? box is checked for an age class it will be exploited (this proportion removed from the population) on each time step at the rate provided by the user (u) in Project Population to Zero simulations; exploitation rates for Project to Management Goal simulations are set under
the Management tab. For example, in Project to Zero simulations, the second age class (age-2) shown below would be exploited at a rate of 0.375 or 37.5% on each time step.

<table>
<thead>
<tr>
<th>Age-2</th>
<th>Exploitation Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.30594</td>
<td>0.375</td>
</tr>
<tr>
<td>35.9438</td>
<td>0.5</td>
</tr>
<tr>
<td>57.8460</td>
<td>0.4</td>
</tr>
<tr>
<td>0.95</td>
<td>0</td>
</tr>
<tr>
<td>6.46</td>
<td>0</td>
</tr>
<tr>
<td>10.4</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td></td>
</tr>
<tr>
<td>141</td>
<td>0</td>
</tr>
<tr>
<td>0.375</td>
<td></td>
</tr>
</tbody>
</table>

Please note that in the projections exploitation of age-0 fish occurs in the fall; and for all others, exploitation occurs in the spring following emigration and immigration but before reproduction (see Events Timeline tab). As demonstrated elsewhere (above) for Starting Densities, Spring Immigrants, and Spring Emigrants, a convenient Rate Adjustment can be used to increase/decrease exploitation rates by a constant rate. Spring and Fall Rate Adjustments can be independently adjusted.

<table>
<thead>
<tr>
<th>Rate Adjustment (Spring)</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate Adjustment (Fall)</td>
<td>1</td>
</tr>
</tbody>
</table>

We suggest that users specify baseline exploitation rates in the Exploit? column and then use the Rate Adjustments to explore the effect of increasing or decreasing spring/fall exploitation. The Store Projections option is very useful in this context.

In order to convert stock to biomass for some of the stock-recruitment options (see Recruitment tab), fish length must be converted to weight. The formula and parameters for this procedure are shown below.

Length to Weight Conversion Formula and Parameters:

\[ W = a \times (L^b) \]

| Little Yampa Canyon | 0.000002959 | 3.284 |

As elsewhere, parameters have been estimated for many reaches, users need only select their preferred reach from the drop-down list. Above, estimates for Little Yampa Canyon are shown. Data source is provided in a pop-up message when a user selects a reach. Parameters \((a, b)\) in this model can also be modified by changing the numbers in the respective boxes. Also available
is a plotting option that allows users to visualize the relationship between weight (y-axis) and length based on the parameter values they provided.

The last option under the **Density** tab not previously described is labeled *Maximum Age 10 Yrs*.

Users can check the box provided to remove any fish age-11 years or more from the population, this feature was implemented to accommodate population models developed by Haines and Modde (2007). If this box is left unchecked then fish aged 11+ will survive at the adult over-summer (*Sa*) and over-winter rates (*Sa*) provided by the user under the **Survival** tab.

**Threshold Options.** Options under the **Thresholds** tab can be used to force environmental conditions to be poor over a proportion of time steps determined by a probability. This feature begins by setting the *Probability (P) of Poor Environmental Conditions: Spring & Summer, Winter* under the **Threshold** tab.

In this example, the user has set the probability of poor environmental conditions in spring, summer and winter to 0.8, under these settings the projection tool will force about 8 out of every 10 time steps to be poor for survival and growth. The user defines *poor* by providing poor condition thresholds for each environmental covariate listed under this tab.
In the example above, poor conditions in spring and summer are those where \textit{mean water temp C} and \textit{count of days $\geq 8000$ cfs} are $\leq 20^\circ$C and $\geq 25$ days, respectively; and poor conditions in winter are those where \textit{count of days $< 10^\circ$C} is $\geq 190$ days. None of the remaining covariates have been selected so their thresholds will be ignored.

The \textit{Info} button under the \textbf{Thresholds} tab describes how the probability of poor conditions and thresholds are combined and applied by the projection tool. A random value between 1 and 10 is drawn and then divided by 10 to arrive at a probability, this is done separately for Spring-Summer and Winter at each time step\textsuperscript{13}. These probabilities are compared to the \textit{Probability of Poor Environmental Conditions} in the Spring, Summer and Winter. When the former probability is less than the latter, then environmental covariates selected under the \textbf{Threshold} tab will be repeatedly drawn from their distributions until the draw is

\textsuperscript{13} As these text imply, in this version of the projection tool, poor conditions in winter and spring/summer are not correlated.
above/below the poor condition thresholds provided by the user. Assuming the user specified 0.8 for both poor condition probabilities,

then about 8 time steps out of 10 would experience poor environmental conditions in Spring, Summer and Winter.

Users should carefully read the notes below each Poor Environmental Condition Threshold section. These identify where each environmental effect is applied, such as a particular stock-recruitment function. Users are warned that if that feature, in each case, is not integrated into their population model then associated options selected under the Threshold tab will be ignored (have no effect on their projections).

Recall that at each time step a random value between 1 and 10 is drawn and then divided by 10 to arrive at a probability, and that this is done separately for Spring-Summer and Winter. The probability calculated for Spring & Summer can be used to adjust spring emigrants, immigrants, and the proportion of breeding stock that breeds at each time step.

The adjustment is performed by simply multiplying the probability by each spring immigrant/emigrant age-specific density and the proportion of breeder stock. When the probability is high, e.g., more fish come/go and a higher percentage of the potential breeding stock breeds.

Management Options. Two sets of options are set under the Management tab. A third was historically (earlier software versions) set under this tab but has been expanded and moved, for
convenience, to another location on the projection form. Recall that exploitation rates in the

**Project Population to Zero** simulations are age-specific and set by the user under the **Density**
tab. This fact is noted in the *Project Population to Zero* options.

See the section **Density Options** above for more details. The next suite of parameters on this
form affect **Project to Management Goal** simulations.

Users set the minimum \((u, \text{min})\) and maximum \((u, \text{max})\) exploitation rates and the amount to
increment between time steps. In this example, the projection would begin at an exploitation rate
of 0.45 and apply this rate to all age classes where the *Exploit?* box was checked under the
**Density** tab. It would then increment \((0.45 + 0.05)\) to 0.50 and repeat the simulation. The
simulation would terminate when the exploitation parameter reached 0.85.

**Simulation Options.** User set the **Number of Time Steps, Replicates, and Start Year** under the
**Simulation** tab. *Time Steps* are equivalent to years, see the **Events Timeline** tab for more details.
The projection will be repeated as many times as is identified by **Replicates.** By providing a *Start*
*Year*, sequential time-step numbers \((1, 2, 3 \ldots)\) will be replaced by four character years in
projection plots and export options \((\text{e.g., 2001, 2002, 2003 \ldots})\).

**Other Options.** Click on the **Convert** option on the projection form (bottom-left corner) to access
a convenient tool for converting between fish/ha, fish/rkm and fish/rmi.
Before deploying this tool, make sure you know the number of ha/rkm for the reach in question, e.g., Little Yampa Canyon has 6.8 ha/river kilometer (Breton et al. 2015). If you’re uncertain about a reach, try using the Change Density option under the Density tab — this option updates ha/rkm under the Density tab for all listed reaches. Assuming ha/rkm are known for the reach, any change to say, fish/ha, will automatically be recalculated in fish/rkm and fish/rmi.

The projection stages affecting age-0 fish were difficult to keep track of when developing the projection tool, new users may have the same experience when attempting to specify their population model. A schedule of events is available, as a reminder, by clicking on the Age-0 Projection Stages option.

Projection events for all stages can be recalled by clicking the options under the Run tab. Also helpful for developing population models are the diagrams under the Spring & Summer, Fall & Winter, and Events Timeline tabs.

When the projection form opens, the default parameter values are identical to the
population model used by Haines and Modde (2007) to produce their Figure 4. PMG and $P0$, convenient shortcuts, are equivalent to the Project to Management Goal and Project to Zero options under the Run tab.

The Save option allows users to store their population model, i.e., all of the check, text and combo box parameters under the tabs. Users can cancel the Save option if they accidentally request it.

![Save Option](image)

Otherwise, after clicking Yes they’re given the opportunity to name their saved projection parameters.

![Provide Name](image)

Provide a name and click OK or click Cancel to abort. After clicking OK the following form opens.
The *Name* provided by the user can be changed at this point, the *date-time* cannot be edited. Users should make use of the *Notes* option to recall details about their population model that otherwise might be lost. To close this form click the *Exit* option on the bottom right.

The real value of the *Save* feature is that stored sets of parameters can be, at any time down the road, re-applied to the projection form. To accomplish this click the *View* option and then use *Move To* to select the set of parameter values that you want to apply to the projection form. Once identified, click *Apply* on the top right. A small pop-up form will inform the user of progress, and close when the request has been completed. At this point, the set of stored parameters have been applied to the projection form and users can easily pick back up where they might have left off previously. Note, the *View* option also allows users to *Delete* sets of parameter values. Some sets have been archived and so cannot be deleted, a small pop-up message will inform the user of this fact if they attempt, e.g., to delete any of the Haines and Modde (2007) parameter sets. Please take care when deleting non-archived parameter sets, users should only delete sets that they saved.
Handling Error Messages. When an error occurs, send details to André Breton (andre.breton@colostate.edu) of what was being asked of the projection tool (such as, "I had just clicked Project Population to Zero") and all of the text provided in the error message. An equally useful alternative to writing out the text of the error message would be a screen capture that includes the error message itself. Never click an option to Debug if this is offered, always click End. If the Debug option is selected accidentally, please refrain from manipulating any of the Visual Basic code that is presented.

Conclusions. The population projection tool described in this report provides an opportunity to Recovery Program managers, and other stakeholders in the effort to recover non-native fish species in the upper Colorado River basin, to specify and compare scenarios (population models) through estimates of population densities projected through time. Given uncertainty in the values that are integrated into any population model, estimates from a single projection (or averages of identical projections) may be of limited value. For this reason, the strengths of the projection tool described here are its option to store projections and decrement a parameter. The former, e.g., allows managers to estimate and visualize the effect of a management action such as increasing exploitation over some baseline by 10%, 20% and 30%; or reducing fecundity, through nest disturbance or some other method, by a similar set of percentages. And by decrementing a parameter from a maximum to minimum value, such as over-winter adult survival from 0-1 (full range), managers can not only estimate the effect of a potential management action but they can also judge the sensitivity of density estimates from their population model to changes in the decremented parameter. This feature of the projection tool was utilized extensively by Breton et al. (2015) in their sensitivity analysis, as well as their assessment of management scenarios. Just like the seminal work provided by Haines and Modde (2007) contributed to and has been
overshadowed by recent advances and insights (Breton et al. 2015), this projection tool will hopefully inform another advance and so will likely not be the final contribution to the effort to manage smallmouth bass in the upper Colorado River basin. Nonetheless, the projection tool exceeds all the expectations outlined in the proposal to the Recovery Program authored by Winkelman et al. (2009) and so should be a much valued aid to managers for the coming years.

**Management Recommendations.** We recommend that Recovery Program managers become adept at running projections and that they integrate estimates, with caution, from these projections as evidence in future management decision making contexts. These users should be comfortable with the strengths of the projection tool, the options to store projections and decrement a parameter. From these exercises we expect that recommendations for projection tool updates will be forthcoming, eventually leading to a new advance in projection capabilities.
Literature Cited


Figure 7. A summary of annual events (events timeline) incorporated into the spring, summer, fall and winter life cycle components of our population model for smallmouth bass (*Micropterus dolomieu*). More details are provided in Figures 2-3.
Figure 8. The spring and summer life cycle components of our population model for smallmouth bass (*Micropterus dolomieu*). Adults and sub-adults immigrate to or emigrate from the population in the spring. Subsequently, these age classes can be subjected to exploitation (removal) through any method such as boat-based electrofishing ($\mu_{1,2,3,a}$). Following exploitation, adult stock produce age-0 recruits through a user-specified density-dependent stock-recruitment function. Remaining parameters, all assumed to be constant rates, are survival probabilities: egg ($S_e$); fry ($S_f$); age-0 ($S_0$); sub-adult ($S_{1,2,3}$) and adult ($S_a$). After reproduction, a proportion of the recruits can be removed by nest disturbance. Spring and summer growth of age-0 smallmouth bass can be a function of spring and summer river discharge and water temperature (rearing conditions).
Figure 9. The fall and winter life cycle components of our population model for smallmouth bass (*Micropterus dolomieu*). Prior to entering the winter, age-0 smallmouth bass can be exploited (removed) by electric seines ($\mu_0$) or any other method prior to over-winter mortality through equations that can accommodate body size and starvation days. Age-0 fish that survive are allocated to the age-1 component of the population at the next time-step (spring). Age-1 and age-2 sub-adult ($S_{1,2}$) survive by probabilities that can be drawn from distributions providing random variation in survival for these ages. All other sub-adult and adult rates are assumed to be constant (age-3+).